2018

An Examination of Beta Diversity Indices and Their Predictors in Two Large-scale Systems

Philip Schroeder

STARS Citation

Schroeder, Philip, "An Examination of Beta Diversity Indices and Their Predictors in Two Large-scale Systems" (2018). *Electronic Theses and Dissertations, 2004-2019*. 6160.
https://stars.library.ucf.edu/etd/6160

AN EXAMINATION OF BETA DIVERSITY INDICES AND THEIR PREDICTORS IN TWO LARGE-SCALE SYSTEMS

by
PHILIP JASON SCHROEDER
B.S. University of Iowa, 2011

A dissertation submitted in partial fulfillment of the requirements
for the degree of Doctor of Philosophy in Conservation Biology
in the Department of Biology
in the College of Sciences
at the University of Central Florida
Orlando, Florida

Fall Term
2018

Major Professor: David G. Jenkins

ABSTRACT

Biodiversity is what conservation biology was developed to conserve. It is the physical manifestation of life as a concept and, be it for practical or idealistic reasons, all conservationists seek to protect or, in some cases, enhance it. Because of its monolithic importance to the field, much effort has been expended trying to better measure and understand it. Recently, greater attention has been paid to the partition of diversity; the observation that the total diversity of a system (γ) can be broken down into within-site diversity (α) and between-site diversity (β). In particular, it has been noticed that the β component of diversity is not as well studied or understood as the α component. In this study I attempt to address this shortfall, by examining two questions: (1) how is β is best measured and (2) what drives β? To answer the first question, I look to find the measure of β that is most robust to sampling error. While many β indices have been proposed, few have considered how our methods of data gathering might affect those indices. Datasets collected from the real world will all likely have some sort of error within them as a result of the way they were sampled. Those errors will affect some indices more than others, and the indices that are least affected will be the most reliable for actual data. Once robust indices were identified, I used them to identify possible predictors of β in two large, national datasets. The first dataset was the National Lakes Assessment created by the USEPA, in which diatoms were sampled from over 1000 lakes across the country. The second was the eBird dataset from the Cornell Lab of Ornithology, which used citizen science to generate a continuous dataset spanning both the last decade and the boundaries of the conterminous United States. β calculated from these sources was regressed against relevant environmental variables to create a clearer understanding of the effects of the environment on the β of two very different ecological systems.

To all those who have supported me,
To my friends and my family,
And especially to my mother and father,
Thank you all, so very much

ACKNOWLEDGEMENTS

Thank you, Dr. Jenkins, for all you have done to support me academically, financially and emotionally through this long journey. Thank you Drs. Fedorka, Myers and King for all of your assistance in honing my research and communicating the results. Thank you D4 ecology lab for all of your support; for the laughter and comradery that has kept me going through the years. None of this would be possible without all of you.

TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

CHAPTER 1

This chapter is adapted an article that was previously published in *Ecosphere*. Ecosphere is a free and open source journal that claims no copyright on any of its publications. Rules for republication can be found at this address: https://esajournals.onlinelibrary.wiley.com/hub/journal/21508925/about/permissions-ecs2

History of Biodiversity measurement

Biodiversity is the axis on which all of conservation turns. For some it is a means to some greater end (Gowdy, 1997; Chavas, 2008; Berry et al., 2016; Hooper et al., 2005) and for others it is the end unto itself (Noss, 1990; Berry et al., 2016; Piccolo et al., 2018), but regardless of one's perspective it is impossible to separate biodiversity from conservation. Conservation biology is also a science, and to function correctly it must be able to measure all of its most critical components. Therefore, it is essential that conservationists be able to accurately measure and monitor biodiversity. This need is obvious, founded as it is on the basic principle of the scientific method, however meeting that need has proven complicated.

The earliest methods of assessing biodiversity were relatively simple. Species richness, the number of species present in an area of study, was the preferred method of some of the earliest biodiversity assays (Wallace, 1877; Klugh, 1912; Hashberger, 1915). Despite its simplicity, it has proven an attractive option for researchers even today, due to its ease of interpretation and collection (i.e. Blackburn et al., 2016; Gontijo et al., 2014; Algarte et al., 2017). However, while species richness can explain some aspects of biodiversity and is fairly robust to sampling error, it cannot fully explain the diversity of a region. Consider a landscape of 2 sites: Site A has 3 species of 4 individuals each and Site B has 3 species, one with 10 individuals and the others with 1 each. Assessing these two sites using species richness a researcher would be forced to conclude they are equally diverse; however, Site A is clearly more diverse than Site B at an intuitive level. To account for deficiency in the descriptiveness of species richness, scientists in the 1940s and 50s began incorporating evenness into their calculations (Preston, 1948; Good, 1953; Simpson, 1949). Evenness is simply how close in abundance each species within a region is to each other species. The lower the variance in population sizes, the greater the evenness and the greater the diversity. There are several possible formulations that incorporate both richness and evenness, including Shannon’s entropy and the Simpson’s index. These formulas are generally referred to as “diversity indices,” to denote the contrast with simple richness.

Partitioning of biodiversity

The development of true diversity indices greatly expanded biodiversity knowledge, however mathematical formulation was not the only issue with historical biodiversity measurements. Another large hurdle was in deficiencies in sampling. Because a thorough sampling of every inch of landscape was rarely, if ever, possible, ecological studies were usually done using a series of sites that were meant to be representative. However, ecological landscapes are typically heterogeneous, requiring a large number of samples to be taken to gain a full picture of its composition. To extrapolate a sample of sites to the landscape as a whole is to assume sites represent well the existing heterogeneity. This assumption was difficult to defend, so diversity was generally reported based on sites within the landscape. Thus, diversity came to be thought of as diversity per sampling unit. This approach was not optimal, however, as the typical diversity of a site within a system is not the same as the diversity of the whole system; trying to use the former to answer questions about the latter can lead to inaccuracies.

In 1960 a solution was proposed, almost inadvertently, by Dr. Robert Whittaker who was sampling the vegetation of the Siskiyou mountain range. Whittaker noted that as long as sites are approximately representative of the total landscape, the diversity of the system can be accounted for by considering both average diversity of sites and the differences between them (Whittaker, 1960). He proposed that the biodiversity of a region, which he termed γ, could be thought as consisting of two parts: α, the mean or median diversity of sites within a system, and β, the mean or median of pairwise compositional differences between sites. In his original formulation α and β were additive contributors to γ: $\alpha + \beta = \gamma$. Whittaker was actually, not the first researcher to identify β. Pierre Jaccard (1912), had described a "coefficient of community" nearly 50 years prior, in French. However, Whittaker's 1960 paper was the first to describe the relationship between β, α and γ, an association that would lead to a renewed interest in Jaccard's earlier work in modern days (Real and Vargas, 1996; Chase et al., 2011).

The measurement of β

The use of β as a measure of biodiversity has grown enormously in the years since its introduction (Tuomisto, 2010). However, with growing interest comes growing scrutiny. Though there is little argument over the validity of the concept some question the formula used to relate it to γ (Jost, 2007; Veech et al., 2002; de Bello et al, 2010; Chao et al., 2012) and others its exact measurement (Tuomisto, 2010a-b; Anderson et al., 2011). The engine driving the latter debate is accuracy, but researchers sometimes disagree about how to even define accuracy (Chao et al., 2004; Cardoso et al., 2009; Jost, 2006). Studies have been published in the past to try and summarize the various measures (Tuomisto, 2010a-b; Anderson et al., 2011) and some have even tried to unify the various sides through a single comprehensive theory (Hill, 1973; Veech, 2010). Today, most researchers advocate for a menu-like approach (Anderson et al., 2011; Koleff et al., 2003; Tuomisto and Ruokolainen, 2006), where the best measure of β is selected based on the question being asked. Another argument even suggests that thinking about β on its own is no more useful than thinking about γ in the years before Robert Whittaker's seminal paper. Advocates for this idea argue that β should be partitioned, just as γ was, into two components: nestedness and turnover (Baselga, 2009; Dobrovolski et al., 2011; Angeler, 2013). These arguments are all still very active and new evidence and arguments are being contributed every year (Soininen et al, 2018; Roden et al., 2018; Ricotta, 2018).

The drivers of biodiversity

The accurate measurement of biodiversity is, indeed, important, but is only one half of the equation. Beyond measuring β, conservationists must understand the forces that drive it. Naturally, uncovering these drivers is a primary goal of conservation and has been a major target of research for a long time (Gleason, 1922; Baas Becking and Nicolai, 1934). However, early research on this topic was hampered by matters of scale. Data was previously only available over limited scopes and field experiments informed by limited information could encounter issues with extrapolation. Over the last century transportation has become faster and cheaper making it easier to sample large areas, conservation spending has increased from government and private sources and communications between research institutions have improved, allowing for the compilation of data from multiple sources over larger scales. The most significant innovation for large-scale ecology research, however, has been the internet (Duda and Camp, 2008; Dickinson et al., 2012; Allen et al., 2018; Recknagel, 2011).

With the availability of data brought about during the information age, questions are being asked about large-scale ecological processes that would not have been possible to answer at any previous time (Dickinson et al., 2012). Naturally, many of these questions pertain to the drivers of biodiversity among different ecosystems and taxonomic groups. Most of these pertain to α or γ (i.e. Haberl et al., 2009; Rull 2011; Stendera et al., 2012), but some seek the drivers of β (i.e. Melo et al, 2009; Kraft et al., 2011; Al-Shami, 2013). Despite these considerable efforts, there are still significant gaps in our understanding of factors that drive β in different systems, at least relative to our knowledge of α drivers.

This project

This project seeks to help alleviate some of the problems discussed above. Specifically, I examine two main questions: what measure of β is least sensitivity to sampling error, and what are the drivers of β? For the second question, I used one dataset for lake diatoms and another for birds and compared their β to relevant environmental variables. These organisms were chosen for the ubiquity, their large preexisting body of literature (i.e. Veronique et al., 2000; Mann, 1999; Pienitz et al., 1995; Berthold, 1991; Brawn et al., 2001) and their use as ecological indicators in past studies (i.e. Fieldler, 2005; Schaumburg et al., 2006).

In Chapter 1 I use simulated data, created through R code (R Core Team, 2017) to create a baseline diversity pattern and then calculate β using 14 different β indices. I then apply one of three types of error to the simulated dataset and recalculate β with that error before noting the percent change between original and “errant” datasets. The three types of error reflect errors in real-world sampling: misidentifying the species of a sampled individual, sampling an insufficient number of individuals within a site (numerical undersampling) and sampling an insufficient number of sites within a landscape (geographic undersampling). I test error rates using both presence-absence and abundance data, enabling me to test the robustness of β measures based on either richness or diversity. Each type of error is also applied at five levels of severity to test whether top performers change depending on the magnitude of error. I compare error rates for each of the indices to determine the highest performers and make recommendations for future researchers.

Chapter 2 uses the National Lakes Assessment datasets (USEPA, 2016) for diatoms across the United States. I use a moving-frame technique that compiles a neighborhood around each site (lake) from neighboring sites within a predefined distance. This allows for neighborhoods to overlap and avoids the issue of two sites being very close together, but not counted as part of the same landscape due to arbitrary gridlines. I take Bray-Curtis dissimilarity values for each of these neighborhoods and compare them to the expected β of a random neighborhood with the same α. This procedure finds β deviations (i.e., deviations from a null expectation created from alpha diversity). Beta deviations allow me to better analyze β as its own aspect of diversity without conflating it with α. I also calculate means and standard deviations for a variety of environmental variables for each of those neighborhoods, representing chemistry, location, lake morphometry and land use. I pare these variables down to avoid correlations among them and use the remainder to construct a large number of mixed effect models, where the random effect is ecoregion to help account for the effect of spatial auto-correlation. I then use information theory and model averaging for a final model relating β deviations to environmental factors.

Chapter 3 has the same purpose as Chapter 2, but with a much different organismal group and different environmental variables. Chapter 3 utilizes the eBird dataset (Sullivan et al., 2009) for January and July from the years 2008 to 2014 in the conterminous United States. The eBird dataset is an example of citizen science; it was compiled by volunteers across the nation. Sampling procedures were codified to help prevent errors and all contributed data was screened during the creation of this dataset. This dataset is several orders of magnitude larger than the NLA dataset, so to help manage its size and be cautious about the data, I converted all data to presence-absence. I then organize data into a grid and aggregate sites into "cells." This process introduces arbitrary cutoffs to separate closely neighboring sites (i.e., those on either side of a grid edge), but analyses here examine overall patterns, so detrimental effects are minimal. Next, I examine 34 environmental variables as predictors of beta patterns, including elevation, temperature, precipitation, land use, net primary production (NPP) and ecoregions. I use the same process as in Chapter 2 to obtain predictive models.

The contrast between the two taxonomic groups used in this dissertation is not accidental. The purpose of this research is not merely to find β drivers in two select groups of organisms, but also to discover patterns in large-scale biogeography. Lake diatoms represent a group that is largely confined to a discrete environment. Moreover, diatoms are primary producers capable of only very simple behaviors. Birds, meanwhile, are active dispersers capable of traversing large territories. They are consumers and many of their species are among the most intelligent on earth, making them able to adapt their behaviors. By looking for patterns in both groups and comparing them, I was able to study whether these differences were truly significant at a biogeographic scale. If the patterns were the same between both groups that would suggest that species are largely interchangeable at large scales, while very different patterns would suggest that differences in traits are factors in biogeographic patterns.

My research provides a more thorough understanding of β and the factors that drive it across widely different organisms. Beta diversity is critical to achieving the long-term goals of conservation. My research addresses two fundamental questions currently surrounding β; which index to use, and what drivers predict it. Answers to both questions obtained here will help researchers obtain answers robust to real-world sampling errors and help better understand reasons for beta diversity. Chapter 5 examines the results of each of those studies, compares them and offers final analyses and suggestions based on their results.

References

Algarte, V. M., Siqueira, T., Landeiro, V. L., Rodrigues, L., Bonecker, C. C., Rodrigues, L. C., Santana, N.F., Thomaz, S.M. & Bini, L. M. (2017) Main predictors of periphyton species richness depend on adherence strategy and cell size. *Plos One,* 12.7,

Allan, B. M., Nimmo, D. G., Ierodiaconou, D., Vanderwal, J., Koh, L. P., & Ritchie, E. G. (2018) Futurecasting ecological research: The rise of technoecology. *Ecosphere,* 9.5.

Al-Shami, S. A., Heino, J., Salmah, M. R., Hassan, A. A., Suhaila, A. H., & Madrus, M. R. (2013) Drivers of beta diversity of macroinvertebrate communities in tropical forest streams. *Freshwater Biology,* 58.6, 1126-1137.

Anderson, D. R., & Burnham, K. P. (2002) Avoiding Pitfalls When Using Information-Theoretic Methods. *The Journal of Wildlife Management,* 66.3, 912-918

Anderson, M. J., Crist, T. O., Chase, J. M., Vellend, M., Inouye, B. D., Freestone, A. L., Sanders, N.J., Cornell, H.V., Comita, L.S., Davies, K.F., Harrison, S.P., Kraft, N.J.B., Stegen, J.C. & Swenson, N. G. (2010) Navigating the multiple meanings of β diversity: A roadmap for the practicing ecologist. *Ecology Letters,* 14.1, 19-28.

Angeler, D. G. (2013) Revealing a conservation challenge through partitioned long-term beta diversity: Increasing turnover and decreasing nestedness of boreal lake metacommunities. *Diversity and Distributions,* 19.7, 772-781.

Baas Becking, L., & Nicolai, E. (1934) On the ecology of a Sphagnum Bog. *Blumea - Biodiversity, Evolution and Biogeography of Plants,* 1.1, 10-45.

Baselga, A. (2009) Partitioning the turnover and nestedness components of beta diversity. *Global Ecology and Biogeography,* 19.1, 134-143.

Bello, F. D., Lavergne, S., Meynard, C. N., Lepš, J., & Thuiller, W. (2010) The partitioning of diversity: Showing Theseus a way out of the labyrinth. *Journal of Vegetation Science,* 21.5, 992-1000.

Berry, P. M., Fabók, V., Blicharska, M., Bredin, Y. K., Llorente, M. G., Kovács, E., Geamana, M., Stanciu, A., Termansen, R., Jääskeläinen, T., Haslett, J.R. & Harrison, P. A. (2016) Why conserve biodiversity? A multi-national exploration of stakeholders' views on the arguments for biodiversity conservation. *Biodiversity and Conservation,* 27.7, 1741-1762.

Berthold, P. (1991) Recent Advances In Studies Of Bird Migration. *Annual Review of Ecology and Systematics,* 22.1, 357-378.

Blackburn, T. M., Delean, S., Pyšek, P., & Cassey, P. (2015) On the island biogeography of aliens: A global analysis of the richness of plant and bird species on oceanic islands. *Global Ecology and Biogeography,* 25.7, 859-868.

Brawn, J. D., Robinson, S. K., & Iii, F. R. (2001) The Role of Disturbance in the Ecology and Conservation of Birds. *Annual Review of Ecology and Systematics,* 32.1, 251-276.

Cardoso, P., Borges, P. A., & Veech, J. A. (2009) Testing the performance of beta diversity measures based on incidence data: The robustness to undersampling. *Diversity and Distributions,* 15.6, 1081-1090.

Chao, A., Chazdon, R. L., Colwell, R. K., & Shen, T. (2004) A new statistical approach for assessing similarity of species composition with incidence and abundance data. *Ecology Letters,* 8.2, 148-159.

Chao, A., Chiu, C., & Hsieh, T. C. (2012) Proposing a resolution to debates on diversity partitioning. *Ecology,* 93.9, 2037-2051.

Chase, J. M., Kraft, N. J., Smith, K. G., Vellend, M., & Inouye, B. D. (2011) Using null models to disentangle variation in community dissimilarity from variation in α-diversity. *Ecosphere,* 2.2.

Chavas, J. (2008) On the Productive Value of Biodiversity. *Environmental and Resource Economics,* 42.1, 109-131.

Dickinson, J. L., Shirk, J., Bonter, D., Bonney, R., Crain, R. L., Martin, J., Philips, T. & Purcell, K. (2012) The current state of citizen science as a tool for ecological research and public engagement. *Frontiers in Ecology and the Environment,* 10.6, 291-297.

Dobrovolski, R., Melo, A. S., Cassemiro, F. A., & Diniz-Filho, J. A. (2011) Climatic history and dispersal ability explain the relative importance of turnover and nestedness components of beta diversity. *Global Ecology and Biogeography,* 21.2, 191-197.

Duda, J. J., & Camp, R. J. (2008) Ecology in the information age: Patterns of use and attrition rates of internet-based citations in ESA journals, 1997–2005. *Frontiers in Ecology and the Environment,* 6.3, 145-151.

Fiedler, W. (2009) Bird Ecology as an Indicator of Climate and Global Change. *Climate Change,* 181-195.

Gleason, H. A. (1922) On the Relation Between Species and Area. *Ecology,* 3.2, 158-162.

Gontijo, L., Vieira, M. C., Araújo, W. S., & Almeida-Neto, M. (2014) Proportion of exotics and relatedness of host species mediate the positive effect of plant richness on the species richness of fruit flies. *Ecological Entomology,* 39.6, 716-722.

Good, I. J. (1953) The Population Frequencies of Species and the Estimation of Population Parameters. *Biometrika,* 40.3/4, Gowdy, J. M. (1997) The Value of Biodiversity: Markets, Society, and Ecosystems. *Land Economics,* 73.1, 25-41.

Haberl, H., Gaube, V., Díaz-Delgado, R., Krauze, K., Neuner, A., Peterseil, J., . . . Vadineanu, A. (2009) Towards an integrated model of socioeconomic biodiversity drivers, pressures and impacts. A feasibility study based on three European long-term socio-ecological research platforms. *Ecological Economics,* 68.6, 1797-1812.

Hashberger, J. W. (1915) The Diversity of Ecologic Conditions and Its Influence on the Richness of Floras. *Proceedings of the Academey of Natural Sciences of Philadelphia,* 67.2, 419-425

Hill, M. O. (1973) Diversity and Evenness: A Unifying Notation and Its Consequences. *Ecology,* 54.2, 427-432.

Hooper, D. U., Chapin, F. S., Ewel, J. J., Hector, A., Inchausti, P., Lavorel, S., . . . Wardle, D. A. (2005) Effects Of Biodiversity On Ecosystem Functioning: A Consensus Of Current Knowledge. *Ecological Monographs,* 75.1, 3-35.

Jost, L. (2006) Entropy and diversity. *Oikos,* 113.2, 363-375.

Jost, L. (2007) Partitioning Diversity Into Independent Alpha And Beta Components. *Ecology,* 88.10, 2427-2439.

Klugh, A. B. (1912). The algae of a marshy pond. *Rhodora,* 14.162, 113-115.

Koleff, P., Gaston, K. J., & Lennon, J. J. (2003) Measuring beta diversity for presence-absence data. *Journal of Animal Ecology,* 72.3, 367-382.

Kraft, N. J., Comita, L. S., Chase, J. M., Sanders, N. J., Swenson, N. G., Crist, T. O., Stegen, J.C., Vellend, M., Boyle, B., Anderson, M.J., Cornell, H.V., Davies, K.F., Freestone, A.L., Inouye, B.D., Harrison, S.P. & Myers, J. A. (2011) Disentangling the Drivers of Diversity Along Latitudinal and Elevational Gradients. *Science,* 333.6050, 1755-1758.

Mann, D. G. (1999) The species concept in diatoms. *Phycologia,* 38.6, 437-495.

Martin-Jezequel, V., Hildebrand, M., & Brzezinski, M. A. (2000) Silicon Metabolism In Diatoms: Implications For Growth. *Journal of Phycology,* 36.5, 821-840.

Melo, A. S., Thiago Fernando L. V. B. Rangel, & Diniz-Filho, J. A. (2009) Environmental drivers of beta-diversity patterns in New-World birds and mammals. *Ecography,* 32.2, 226-236.

Noss, R. F. (1990) Indicators for Monitoring Biodiversity: A Hierarchical Approach. *Conservation Biology,* 4.4, 355-364.

Piccolo, J. J., Washington, H., Kopnina, H., & Taylor, B. (2018) Why conservation scientists should re-embrace their ecocentric roots. *Conservation Biology,* 32.4, 959-961.

Pienitz, R., Smol, J. P., & Birks, H. J. (1995) Assessment of freshwater diatoms as quantitative indicators of past climatic change in the Yukon and Northwest Territories, Canada. *Journal of Paleolimnology,* 13.1, 21-49.

Preston, F. W. (1948) The Commonness, And Rarity, of Species. *Ecology,* 29.3, 254-283.

R Core Team (2017) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.

Real, R., & Vargas, J. M. (1996) The Probabilistic Basis of Jaccards Index of Similarity. *Systematic Biology,* 45.3, 380-385.

Recknagel, F. (2011) Ecological informatics: A discipline in the making. *Ecological Informatics,* 6.1, 1-3.

Ricotta, C. (2018) A family of (dis)similarity measures based on evenness and its relationship with beta diversity. *Ecological Complexity,* 34, 69-73.

Roden, V. J., Kocsis, Á T., Zuschin, M., & Kiessling, W. (2018) Reliable estimates of beta diversity with incomplete sampling. *Ecology,* 99.5, 1051-1062.

Rull, V. (2011) Neotropical biodiversity: Timing and potential drivers. *Trends in Ecology & Evolution,* 26.10, 508-513.

Schaumburg, J., Schranz, C., Hofmann, G., Stelzer, D., Schneider, S., & Schmedtje, U. (2004) Macrophytes and phytobenthos as indicators of ecological status in German lakes — a contribution to the implementation of the water framework directive. *Limnologica - Ecology and Management of Inland Waters,* 34.4, 302-314.

Simpson, E. H. (1949) Measurement of diversity. *Nature,* 163, 688.

Soininen, J., Heino, J., & Wang, J. (2017) A meta-analysis of nestedness and turnover components of beta diversity across organisms and ecosystems. *Global Ecology and Biogeography,* 27.1, 96-109.

Stendera, S., Adrian, R., Bonada, N., Cañedo-Argüelles, M., Hugueny, B., Januschke, K., Pletterbauer, F. & Hering, D. (2012) Drivers and stressors of freshwater biodiversity patterns across different ecosystems and scales: A review. *Hydrobiologia,* 696.1, 1-28.

Sullivan, B.L., C.L. Wood, M.J. Iliff, R.E. Bonney, D. Fink, and S. Kelling. (2009) eBird: a citizen-based bird observation network in the biological sciences. Biological Conservation 142: 2282-2292.

Tuomisto, H., & Ruokolainen, K. (2006) Analyzing Or Explaining Beta Diversity? Understanding The Targets Of Different Methods Of Analysis. *Ecology,* 87.11, 2697-2708.

Tuomisto, H. (2010) A diversity of beta diversities: Straightening up a concept gone awry. Part 1. Defining beta diversity as a function of alpha and gamma diversity. *Ecography,* 33.1, 2-22.

Tuomisto, H. (2010) A diversity of beta diversities: Straightening up a concept gone awry. Part 2. Quantifying beta diversity and related phenomena. *Ecography,* 33.1. 23-45

USEPA. 2016. National Lakes Assessment 2012: A Collaborative Survey of Lakes in the United States. EPA 841-R-16-113. U.S. Environmental Protection Agency, Washington, DC. https://nationallakesassessment.epa.g

Veech, J. A., Summerville, K. S., Crist, T. O., & Gering, J. C. (2002) The additive partitioning of species diversity: Recent revival of an old idea. *Oikos,* 99.1, 3-9.

Veech, J. A., & Crist, T. O. (2010) Toward a unified view of diversity partitioning. *Ecology,* 91.7, 1988-1992.

Waldron, A., Miller, D. C., Redding, D., Mooers, A., Kuhn, T. S., Nibbelink, N., . . . Gittleman, J. L. (2017) Reductions in global biodiversity loss predicted from conservation spending. *Nature,* 551.7680, 364-367.

Wallace, A. R. (1877) The Comparative Richness of Faunas and Floras Tested Numerically. *Nature,* 17.423, 100-101.

Whittaker, R. H. (1960) Vegetation of the Siskiyou Mountains, Oregon and California. *Ecological Monographs,* 30.4, 279-338

CHAPTER 2: HOW ROBUST ARE POPULAR BETA DIVERSITY INDICES TO SAMPLING ERROR?

Chapter Summary

Beta diversity (β) is important to biogeography, ecology and conservation because it assesses heterogeneity of local communities. Ideally, researchers could consider sensitivity to error when choosing a β index, of which there are many. However, only numerical undersampling has been rigorously studied. This study compared multiple β indices to determine which are most robust to geographic undersampling, numerical undersampling, and taxonomic error. To this end, simulated landscapes were generated to create known patterns and then sampled with deliberately errant procedures at multiple error rates. Eight β indices were chosen to represent "families" of β and used to measure real and errant data. Six indices used both presence-absence (i.e., presence/absence) and abundance data, while two more used only abundance data. Versions of six abundance-based indices adjusted for individual undersampling and were also evaluated (total = 14 indices).

Presence-absence- and abundance-based indices were comparable in sensitivity to total method error. Numerical undersampling and taxonomic error generally caused more error in β than randomly-distributed geographic undersampling. Among presence-absence based indices, Jaccard's dissimilarity was most robust to error. Among abundance-based indices, Bray-Curtis and BD_{TOTAL} were most robust to error. But some commonly-used β indices (e.g. Sorensen, Simpson) are much less reliable given errors of taxonomy or numerical undersampling. Future studies of β should focus on using more robust indices (Jaccard, Bray-Curtis, BD_{TOTAL}, and past studies based on error-sensitive indices should be considered with caution. Studies of β should emphasize adequate numerical sampling and taxonomic accuracy to minimize causing errors in β.

Keywords: Metacommunity, Sorensen, Simpson, Jaccard, BD_{TOTAL}, Bray-Curtis, Cody, sampling error, taxonomic error

Introduction

Beta diversity (β) is important to ecology and biogeography because it indicates the changes in species composition that occur across a landscape. It was defined by Whittaker (1960) as the total regional diversity minus the mean diversity of the sites within the region (γ-α) but has been measured in many other ways since (Tuomosito 2010ac, Anderson et al. 2010). As one of the essential measures of biological diversity, it contributes greatly to our understanding of what drives diversity and to the conservation and preservation of ecosystems (Whittaker, 1960; Condit et al, 2002; Gabriel et al, 2006; McKnight et al, 2007; Passy and Blanchet, 2007; Devictor et al, 2010).

Much effort has been dedicated to effectively assessing β, resulting in more than 17 different β indices (reviewed by Tuomisto 2010a-b and Anderson et al. 2010). Recent work on β has also addressed the choice between multiplicative or additive indices (Jost, 2007) and partitioning between species turnover and nestedness components (Baselga, 2009). Beta diversity indices can be organized into four "families" (Table 1.1). The Whittaker family derives from Whittaker's initial formulation of β (Whittaker, 1960). The "min-max" family is also based on Whittaker's original formula, but adjusts for conceptual errors by using minimum and maximum values of unique species between sites. The Cody "family" follows a simplified approach by only using unique species. Finally, the "abundance" family includes indices for abundance data and thus differs from other families by its method rather than concepts.

The practical matter of how these indices respond to empirical error has received less attention. Here we address three kinds of error that are possible in empirical studies and that can affect beta diversity indices: numerical undersampling, taxonomic misidentification, and geographic undersampling. Numerical undersampling is the inclusion of insufficient individuals in a sample, which may result in the exclusion of rare species from a data set (Chao, 2005). Geographic undersampling is the use of an insufficient number of sampled sites, which may result in either reduced β (if a site with rare species is excluded) or increased β (if a site with common species is excluded). Taxonomic misidentification occurs while sampling (e.g., during counts in the field) or in subsequent sample processing (e.g., preserved samples). An investigator choosing among β indices should prefer an index that is less sensitive to these empirical errors.

Of the three kinds of error, only numerical undersampling has been considered for its effects on β. Numerical undersampling is possible in any study where actual abundance distributions are unknown, because rare species affect the value of most β indices (especially those based on presence-absence data), and so their exclusion can result in larger errors (Beck et al., 2013). Beck et al. (2013) observed that indices skewed towards abundant species tended to be more robust to numerical undersampling but did not recommend a specific index. Cardoso et al. (2009) found three β indices were robust to numerical undersampling in 2-site systems (β_{-2}, β_{-3} and β_{cc}), but both Cardoso et al. (2009) and Beck et al. (2013) restricted analyses to numerical undersampling and excluded some β families.

Of the other two error types, geographic undersampling is possible in any study where actual distributions are patchy and unknown in advance of sampling and is especially likely given fewer sample sites.

Taxonomic error increases β if a common species is mistaken for a rare species, or it can decrease β if a rare species is mistaken for a common species. Taxonomic error is most likely in studies that include cryptic species, where extensive taxonomic training is unavailable but needed, or in collaborative efforts involving multiple researchers, including biodiversity databases and citizen science studies. Training can mitigate taxonomic error, but cryptic species may be revealed only with molecular analyses (e.g., Bickford et al, 2007) and are difficult to fully resolve in practice.

All three error types are a risk in any study of natural biological diversity, and can affect β estimates in ways that remain largely unknown. This work examined the effectiveness of eight representative β indices under the three error types. Results should help researchers select the most robust index for their work and help focus β research on the most reliable indices for comparisons among study systems.

Materials and methods

Eight β indices were selected to represent four conceptually related "families" (Table 1.1). All but two indices were evaluated for both presence-absence data and abundance data, resulting in 14 total indices tested (Table 1.1). The six presence-absence-based indices (Beta$_{-2}$, Beta$_{-3}$, Cody's, Jaccard, Simpson and Sorensen) were assessed through component analysis (Koleff et al., 2003) and adapted to abundance data using the probabilistic method of Chao et al. (2005).

The Whittaker family was represented by Sorensen and Jaccard dissimilarities which descend from Whittaker's original work (Whittaker, 1960; Jost, 2007). The Cody family only contains Cody's β (Cody, 1975; Koleff et al, 2003) and was included for the simplicity of its design. The min-max family uses minimum and maximum values of presence values (or uniqueness probabilities in the case of abundance data) and includes Simpson β, β$_{-2}$ and β$_{-3}$. Finally, the abundance family indices included Bray-Curtis dissimilarity and Total Beta Diversity (BD$_{\text{TOTAL}}$; Legendre & DeCaceres, 2013). The Bray-Curtis index is widely used in abundance-based β (Li et al, 2016; Liu et al, 2016); for example, it is the default abundance-based β index in the vegan package of R. The BD$_{\text{TOTAL}}$ index is the most recent of indices evaluated here, and is based on variance partitioning, analogous to analysis of variance (Legendre & DeCaceres, 2013). The BD_{TOTAL} index is functionally identical to Cody's beta for presence-absence data but not for abundance data.

Unlike in Cardoso et al. (2009), we left β_{-3} in its original form because we were only concerned with error rates, not initial values. The abundance versions of all but the Bray-Curtis and BD_{TOTAL} indices were calculated with and without the numerical undersampling adjustments in Chao et al. (2005). These adjustments only change the types of components used and not the equations themselves; see Table 1.1 for the equations. Abundance data were chord-transformed prior to assessment by BD_{TOTAL} (Legendre & De Caceres, 2013).

The above β indices were tested in simulated metacommunities, where diversity was perfectly known and the effect of errors could be calculated by the difference. Artificial landscapes were generated as 3 x 3, 10 x 10, and 30 x 30 grids, with each cell representing a discreet habitat that could be occupied by multiple species. Each landscape was assigned a number of species; 9 for the 3 x 3 grid, 10 or 100 for the 10 x 10, and 10 species for the 30 x 30. This study design enabled us to evaluate potential scale effects (spatial extent, species density) on b without the unneeded complication of a factorial design and extensive computation for this subsidiary question. While we did not wish to make scale a focus of the study, we did want to ensure these results would still be applicable to greater or lesser species density.

Metacommunity assembly was kept deliberately simplistic because the process was not the subject of this study; rather the goal of assembly was to generate a pattern to analyze with β. Each species was assigned a recruitment value representing the likelihood of that species increasing its population by one in each timestep. The percent likelihood of recruitment ranged from 5% at the lowest to 50% at the highest. Extirpation values were assigned to each site (in the

3 x 3 grids) or column of sites (in the others) to represent general habitat suitability. Extirpation represents the likelihood of a species within a site decreasing by one and was applied equally to each species within a given site. Extirpation rates ranged from 40% to 85%. These simple processes represented the cumulative processes that affect the growth and decline of populations. Though these processes were simple, they were able to generate landscapes that were similar enough to represent true replicates, but different enough that our results could not be due to a single anomalous landscape (see Fig. 2.1 for visualization). The result of these processes was a reasonably complex landscape which averaged a Bray-Curtis dissimilarity of 0.675. Such a dissimilarity has been observed in nature (Ellingsen and Gray 2002, Nascimbene and Spitale 2017), suggesting the created landscapes are, at least, plausible.

Recruitment preceded extirpation in each time step and community assembly occurred for 1000 time steps. The most successful species could number up to *circa* 400 individuals in the most habitable sites while the least successful occurred in the single digits and only in the most habitable sites. Especially important was the fact that many species were absent from some sites but present in others which allowed for the testing of presence-absence-based β indices. In empirical studies it is possible the three types of error may interact (e.g., a study with significant numerical and geographic undersampling could under-represent diversity multiplicatively), but this matter of study design was unrelated to main interests here. Instead, error types were evaluated separately for clarity.

Numerical undersampling was measured as the total number of individuals sampled per site, ranging from 100-500 with intervals of 100. The same sampling effort was applied to each site within the landscape, analogous to processing a target number of individuals in field plots or preserved samples. A site sampled with 100 individuals but containing 1000 would be more undersampled than a similarly-sampled site containing 200 individuals. If the sampling effort exceeded the total number of individuals present at a site, then the site was considered “fully sampled” and was recorded with perfect accuracy.

Geographic undersampling was represented by randomly excluding sites from the calculation of β. The number of excluded sites varied with the size of the landscape in order to ensure the same error rate occurred across different landscapes. Percentage error ranged from 10-50% (in intervals of 10%), except for the 3x3 grid. In this grid 1-5 sites were excluded (intervals of one).

Taxonomic error was generated by reassigning the identity of a number of individuals within a site. Taxonomic error is semi-random in that it is partially dependent on training and skill (Clark and Hering, 2006). To represent this stochasticity, a random number was chosen from a Poisson distribution where the mean of the distribution represented the level of error. Five mean error levels (means = 1, 2, 3, 4, or 5 misidentified individuals per site) were used. The obtained random number of individuals per site were then randomly re-assigned to a different species. For a given mean level of error, misidentifications were applied independently to each site within the landscape. This approach may represent little error in sites with numerous populations or substantial error in sites with few individuals, precisely the way taxonomic identifications are conducted on individual organisms (i.e., independent of site conditions).

Both presence-absence- and abundance-based β indices (Table 2.1) were evaluated for every simulation. In all cases, β was calculated in a pair-wise fashion between sites with mean β (and ± 95% confidence intervals) taken for the entire landscape. The β for each “errant” metacommunity was compared to the β of its respective reference landscape (i.e., without error) and assessed for error and absolute percent error (i.e., positive or negative error).

Mean values of simple and absolute errors (both as percent) conveyed different messages. Simple errors are directional and reflect whether β is being over- or underestimated. However positive and negative errors can cancel within an individual treatment, underrepresenting the amount of variance introduced by the given type and amount of sampling error. Absolute error (i.e., 100 x |estimate – known|/known) corrects for this cancelling effect by showing the mean (with 95% confidence intervals) of total variances regardless of direction. Taken together, these error calculations show the direction and magnitude of each type of error for each index.

The simulation process was replicated 1000 times for each β index, each error type (numerical or site undersampling or taxonomic) and each scale (3 sites x 3 sites x 9 species, 10 x 10 x 10, 10 x 10 x 100 or 30 x 30 x 10 species). Differences from known β for both directional and absolute errors were reported (mean + 95% confidence intervals) for each error type and level.

Results

The results were not affected by species density or metacommunity scale. Instead, the same indices proved most effective regardless of the number of species or sites used. The rankings of weaker indices were shuffled at some of the largest scales or densities (Appendix A), but strongest indices remained so and the rankings of indices for the 9 sites x 9 species and 100 sites x 10 species simulations were not greatly different. Metacommunity scale was inversely proportional to the overall error rate across all indices, simply because one site represented 11% of a nine-site metacommunity but represented only 1% of a 100-site metacommunity. All of the following results were calculated for 10 site x 10 species metacommunities. In total 6000 simulations were computed with percent error calculated for each of them.

Results varied with error type (taxonomical, numerical or geographic) and data type (presence-absence or abundance). In general, geographic undersampling caused lower percent error (up to ~6%) than taxonomical and numerical undersampling errors in presence-absence data (up to ~50%; compare Figs. 2.2-4). This pattern held for abundance data (~22% for geographic error compared to values up to ~60% and 80%; Figs. 5-7). Substantial misrepresentation of β can occur given moderate sampling errors. Also, β indices varied substantially in error rates, however this was not necessarily related to calculation family.

Among presence-absence-based indices, the Jaccard index was most robust to taxonomic error (<10% error rates; Fig. 2.2) and numerical undersampling (<7% error rates; Fig. 2.3) The Jaccard index also had relatively low error rates for geographic undersampling (<4%; Fig. 2.2), very similar to several other indices (<3% error rate; Fig. 2.4). Other presence-absence-based indices traded places as having relatively high error rates, depending on the type of undersampling (Fig. 2.2 - 7). For example, the Cody index was most errant for taxonomic error and was the only index to consistently under-represent β given numerical undersampling (by up to ~20%), but performed about as well as the Jaccard index given geographic undersampling

Among β indices for abundance data, the Bray-Curtis index was most robust for taxonomic error (1 - 3% error; Fig. 2.5). The BD_{TOTAL} index was most consistently robust for numerical undersampling across all sampling levels (5 - 15% error; Fig. 2.6) and nearly as robust to taxonomic and geographic undersampling error as the Bray-Curtis index (Figs. 2.5,7). The Bray-Curtis index was also most robust to geographic undersampling (Fig. 2.7). Notably, Chao's adjustments for individual undersampling in abundance data did not create an all-around improvement but did reduce the rise in error rate with increasing undersampling; the net result was greater overall error rate after adjustment (Fig. 2.7). No index adapted from a presence-absence formula for abundance data (e.g. Jaccard, Sorensen) was as robust as the Bray-Curtis or BD_{TOTAL} indices.

The use of simple error rates (i.e., positive and negative) reveals a few potentially interesting patterns relative to absolute rates. Most indices stayed either negative (i.e., underrepresenting) or positive (i.e., overrepresenting) for a given error type. However, β_{-2} and the Jaccard indices crossed over from positive to negative errors for presence-absence data given taxonomic error (Fig. 2.2) and numerical undersampling, respectively (Fig. 2.3). Also, many indices showed a relatively muted response (either in the positive or negative direction) when compared to their absolute response, indicatting that positive and negative errors were counteracting to some degree between simulations. Wider 95% confidence intervals for some indices and error types supported that inference (e.g., Fig. 2.6). This was especially prominent for abundance data with geographic undersampling, where mean simple error rates ranged over ~3% but absolute rates ranged up to ~22% (Fig. 2.6).

Discussion

Error is a reality of any empirical study, especially if it is being performed at large spatial scales or by multiple investigative teams. Therefore, it makes sense to emphasize robust β indices in future analyses and experiments, especially when analyzing archived data sets and citizen science where errors are possible and unknown (Dickinson et al, 2010; Butt et al, 2013). Here we show that some β indices are more vulnerable to errors in empirical research than other indices. In general, the Bray-Curtis, BD_{TOTAL} and Jaccard indices are the least vulnerable to errors of taxonomy, enumeration or geography.

Fortunately, robust β indices are already in widespread use. The Bray-Curtis index is the default in the widely-used vegan package in R (Oksanen et al, 2016) and has been used in approximately >60 relevant studies since 2010 (based on a Web of Science search). The Jaccard index was one of the first β indices developed and is still featured prominently in modern research, with >80 articles using it since 2010. The BD_{TOTAL} index was developed more recently (Legendre and DeCáceres, 2013) and has not yet been widely adopted, but based on results here we think it should be.

Unfortunately, error-prone β indices are also commonly used. Sorensen dissimilarity performed poorly in simulations here but is quite popular (used in >60 publications since 2010). To be clear, Sorensen dissimilarity is *conceptually* useful for species turnover, but results here show it should be applied cautiously in empirical studies. The Simpson index is also frequently used (>60 recent publications since 2010), but was among the worst performers in simulations, much like other indices based on minimum and maximum values for species presence and absence. We recommend that researchers avoid indices based on minimum and maximum values (i.e. Simpson, β_{-2} and β_{-3}) unless those values can be independently supported. Consequently, prior studies of empirical systems that relied on Sorensen and Simpson indices should be interpreted with caution.

The results of this study differ from those of Cardoso et al. (2009) for multiple reasons. Our approach differed from Cardoso et al. (2009) in several ways. They calculated beta diversities among selected pairs of sites, whereas we calculated mean pairwise beta diversities across an entire simulated landscape. Moreover, Cardoso et al. (2009) pooled results for the Jaccard index with results for up to three other indices, whereas we analyzed it separately. Also, they focused on presence-absence-based indices only, whereas we also included abundance-based indices.

Finally, Cardoso et al. (2009) evaluated only numerical undersampling by cumulative curves given varying percent shared species, whereas we simulated numerical undersampling, taxonomic error and geographic undersampling of known landscapes and diversity, and considered β as a function of those errors.

Results here also differ in part from those of Beck et al. (2013), who evaluated only numerical undersampling to recommend that indices be selected based on the question asked, and warn that presence-absence-based indices were sensitive to rare species. Our results also showed that more undersampling affected all indices. However, presence-absence-based indices were at least comparable in error to abundance-based indices, and in some instances outperformed them (consider Figs. 1-3). In addition, the most robust presence-absence-based indices (Jaccard, Cody) were very similar in error rates to the most robust abundance-based indices (Bray-Curtis, BD_{TOTAL}) among all three error types. We evaluated some indices Beck et al. (2013) did not (e.g., Simpson, BD_{TOTAL}) and vice versa (e.g., Morisita-Horn). But both Beck et al. (2013; Fig. 3) and the current study (Fig. 5 & 6) permit comparisons of Jaccard and Bray-Curtis indices across numerical undersampling rates. The approximate comparability in error rate for those two indices in our study is similar to the results of Beck et al. (2013). Thus, we conclude that presence-absence- and abundance-based beta diversities are comparable in error rate, though rare species may certainly affect error risk among index choices.

We expect that presence-absence-based β indices (especially the Jaccard index) can be successful in situations where sampling errors do not omit many rare species, as may occur when only a small portion of all species dominate in abundance and distribution. We note that we used an average of pairwise β in our simulated landscapes; comparison of a site to the mean diversity of all other sites may attain different results and conclusions.

In summary, the most robust indices for pairwise β were Bray-Curtis, BD_{TOTAL} and Jaccard, and presence-absence-based and abundance-based β indices were comparable in error rates for numerical and geographic undersampling, as well as taxonomic errors. We recommend continued use of these three β indices to help ensure β remains a valuable tool for ecology and biogeography.

Figures and Tables

Table 2.1 Beta diversity indices compared here. Most indices used both presence-absence and abundance-based calculations. Jaccard, Sorensen, and Bray-Curtis indices are shown as dissimilarities. Bray-Curtis and BDTOTAL apply only to abundances, and all abundance-based indices used adjustments for individual undersampling (Chao et al. 2006).

Index	Presence-absence based[1]	Abundance based[2]	Family
Jaccard	1 - a/(a+b+c)	1 - ((UV)/(U+V-UV))	Whittaker
Sorensen	1 - (b+c)/(2a+b+c)	1 – ((2UV)/(U+V))	Whittaker
β_2	(min(b,c))/(max(b,c)+a)	min(U-UV,V-UV)/ (max(U-UV,V-UV) + UV)	Min-Max
β_3	(min(b,c))/(a+b+c)	min(U-UV,V-UV)/ (U + V + UV)	Min-Max
Simpson	min(b,c)/(min(b,c)+a)	min(U-UV,V-UV)/ (min(U-UV,V-UV) + UV)	Min-Max
Cody	(b+c)/2	(U+V-2UV)/2	Cody
Bray-Curtis		$1 – (2C_{ij})/(S_i + S_j)$	Abundance
BD_{TOTAL}		$SS_{total}/(n-1)$	Abundance

a =number of species shared between sites, b =number of species unique to site 1, and c = number of species unique to site 2.

U = total relative abundance of shared species in site 1, V = total relative abundance of shared species in site 2. For the Bray-Curtis index, C_{ij} = total number of specimens from species shared by both sites, S_i = total number of specimens in site 1, and S_j =total number of specimens in site 2. For BD_{TOTAL}, SS_{total} = total sum of squares for species abundances and n = total number of sites.

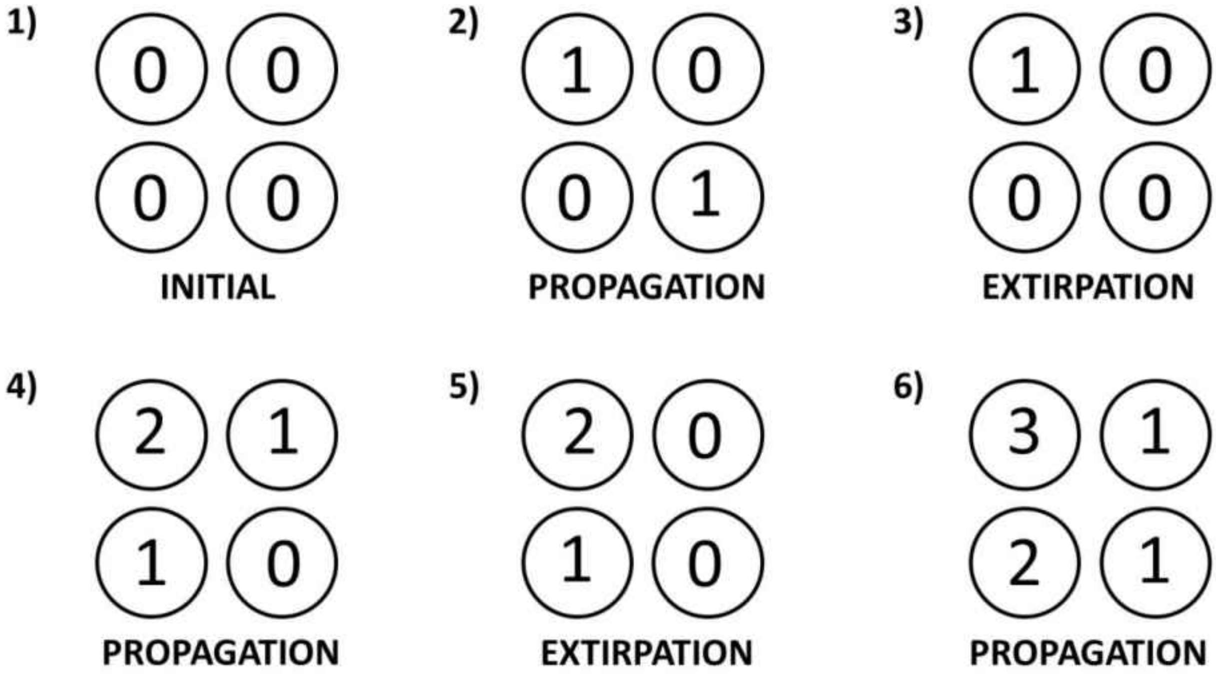

Figure 2.1 A simplified visualization of the method used to create each landscape. An initially blank landscape is populated by a few individuals, and then, a few individuals are removed and this process is repeated. In the actual simulation, the rate at which individuals were added or removed was set by the species and the site, respectively. The above figure only shows the landscape as it applies to a single species. In the actual simulation, this process would run on 10 species simultaneously.

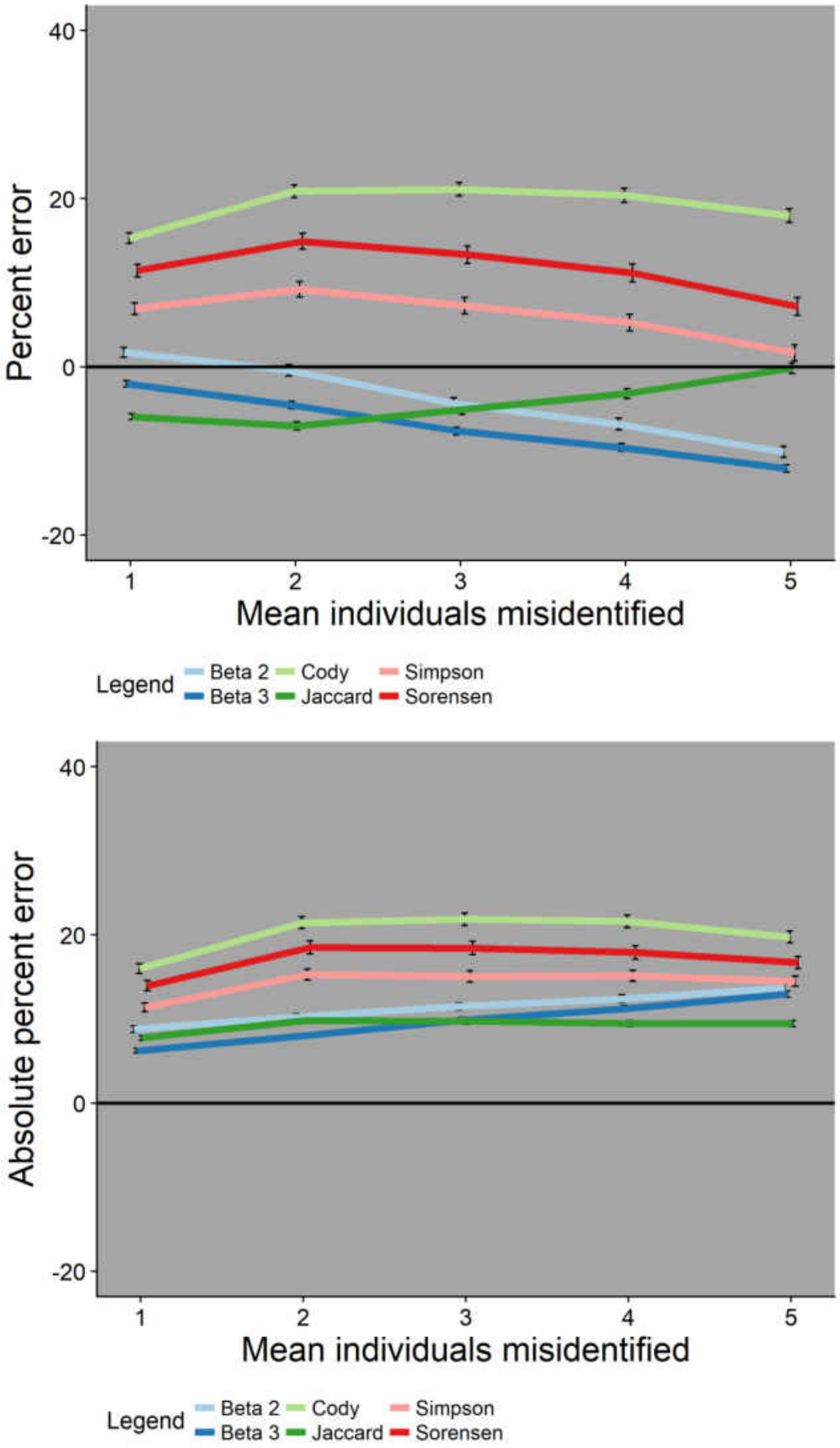

Figure 2.2 The directional and absolute percent errors, respectively, for taxonomic error based on presence-absence data. Directional errors are calculated as 100 x (estimate - known)/known, and absolute errors are calculated as 100 x |estimate - known|/known.

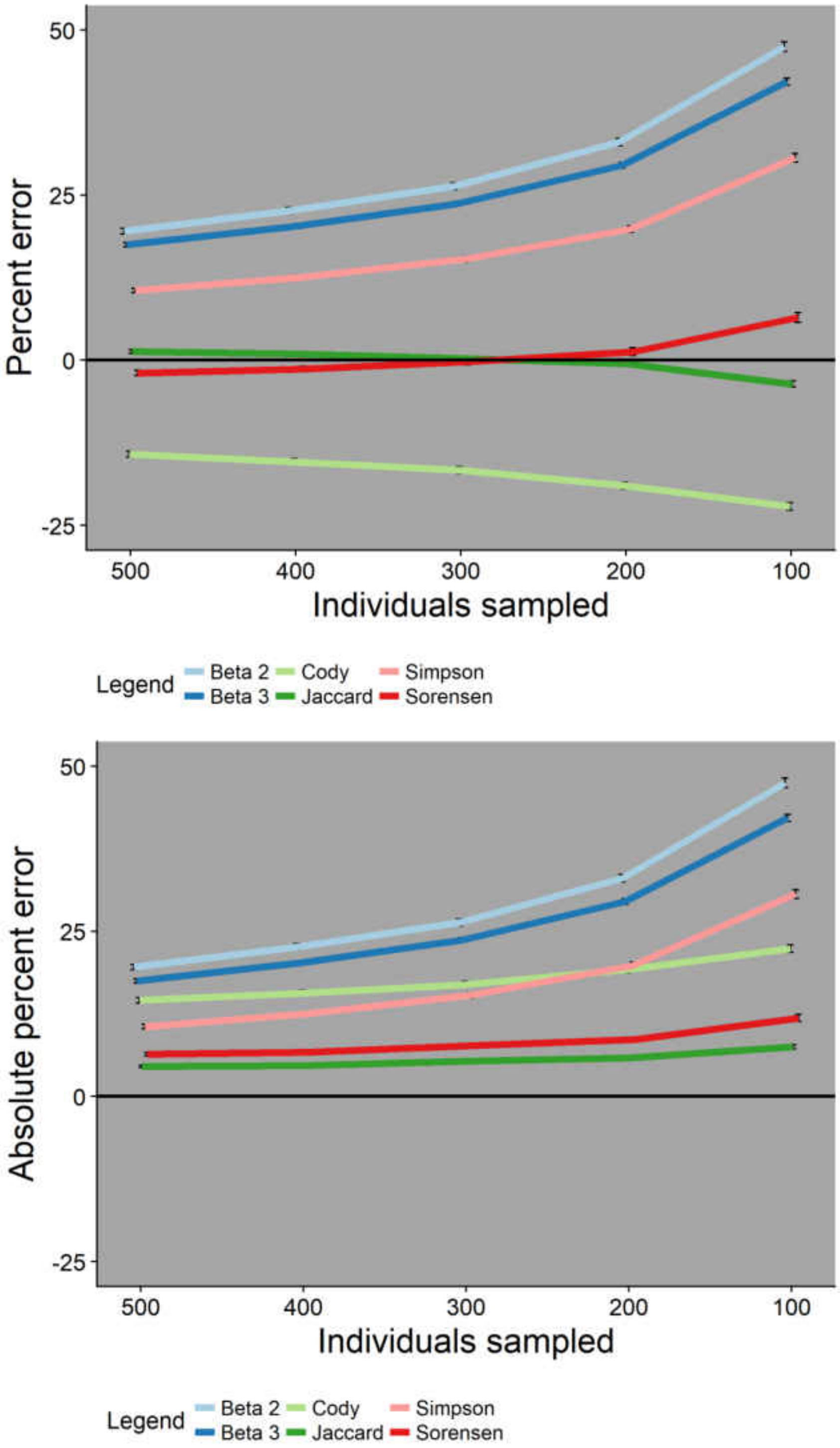

Figure 2.3 The directional and absolute percent errors, respectively, for numerical undersampling based on presence-absence data. Directional errors are calculated as 100 x (estimate - known)/known, and absolute errors are calculated as 100 x |estimate - known|/known.

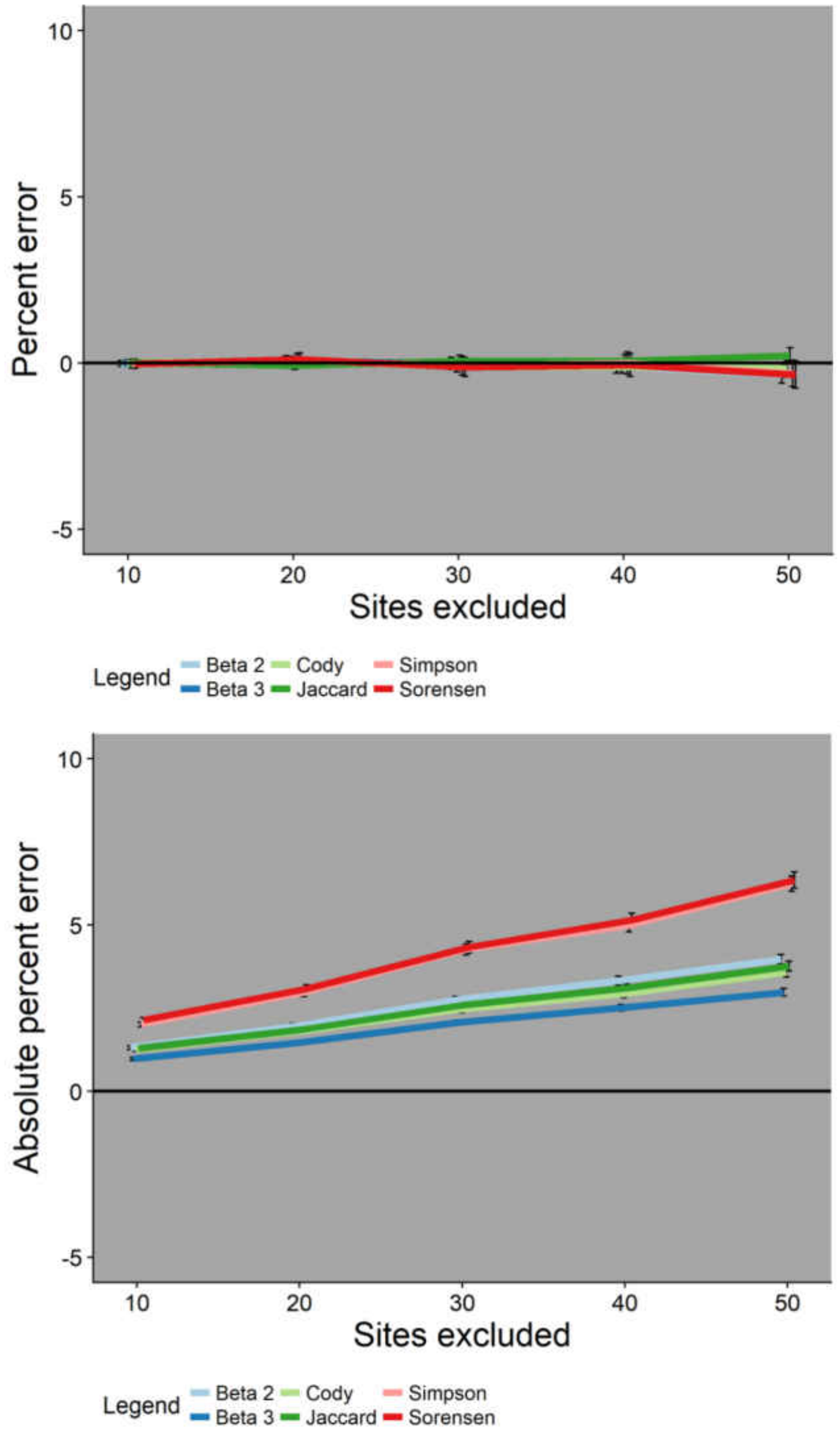

Figure 2.4 The directional and absolute percent errors, respectively, for geographic undersampling based on presence-absence data. Directional errors are calculated as 100 x (estimate - known)/known, and absolute errors are calculated as 100 x |estimate - known|/known.

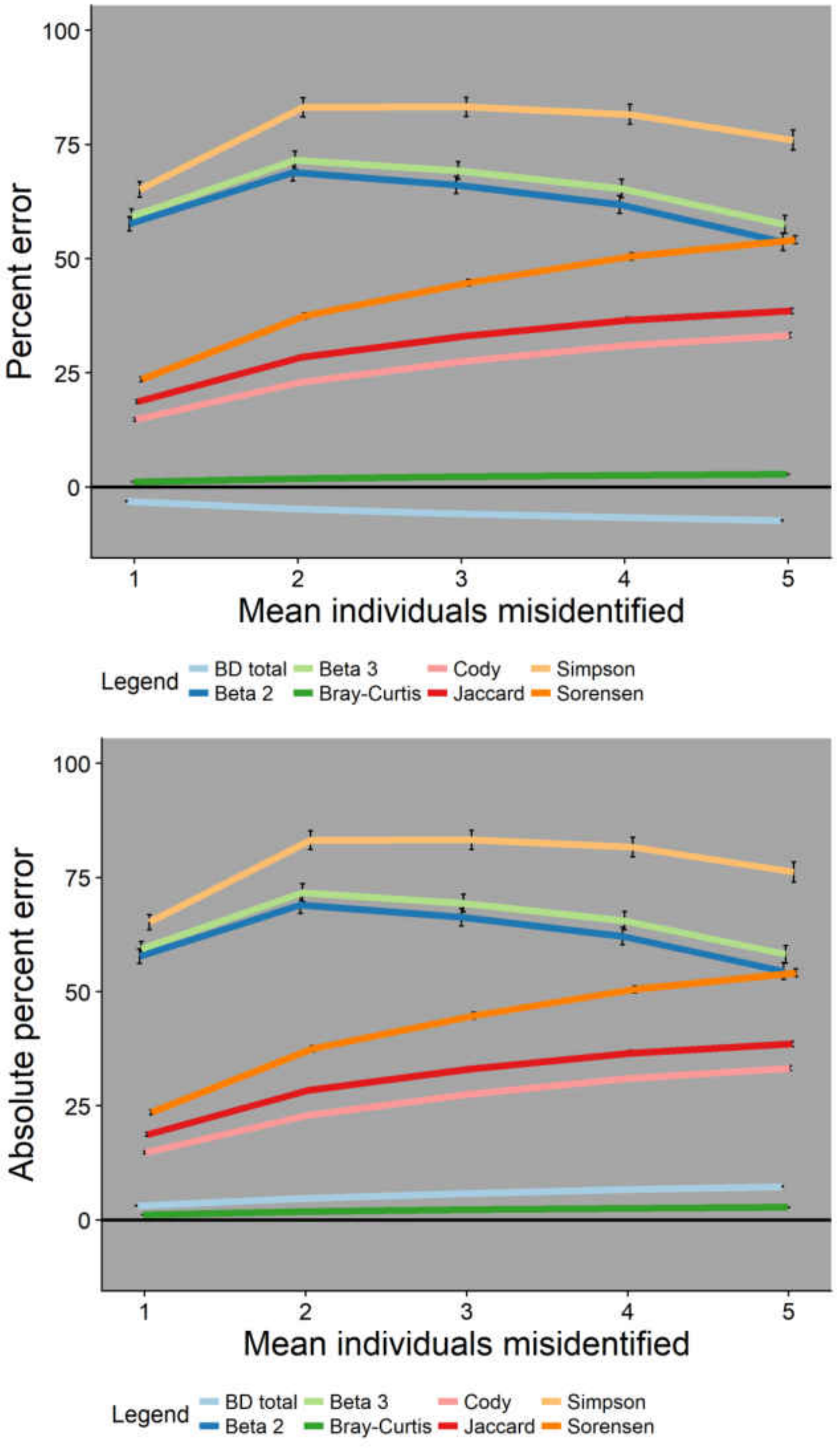

Figure 2.5 The directional and absolute percent errors, respectively, for taxonomic error based on abundance data. Directional errors are calculated as 100 x (estimate - known)/known, and absolute errors are calculated as 100 x |estimate - known|/known.

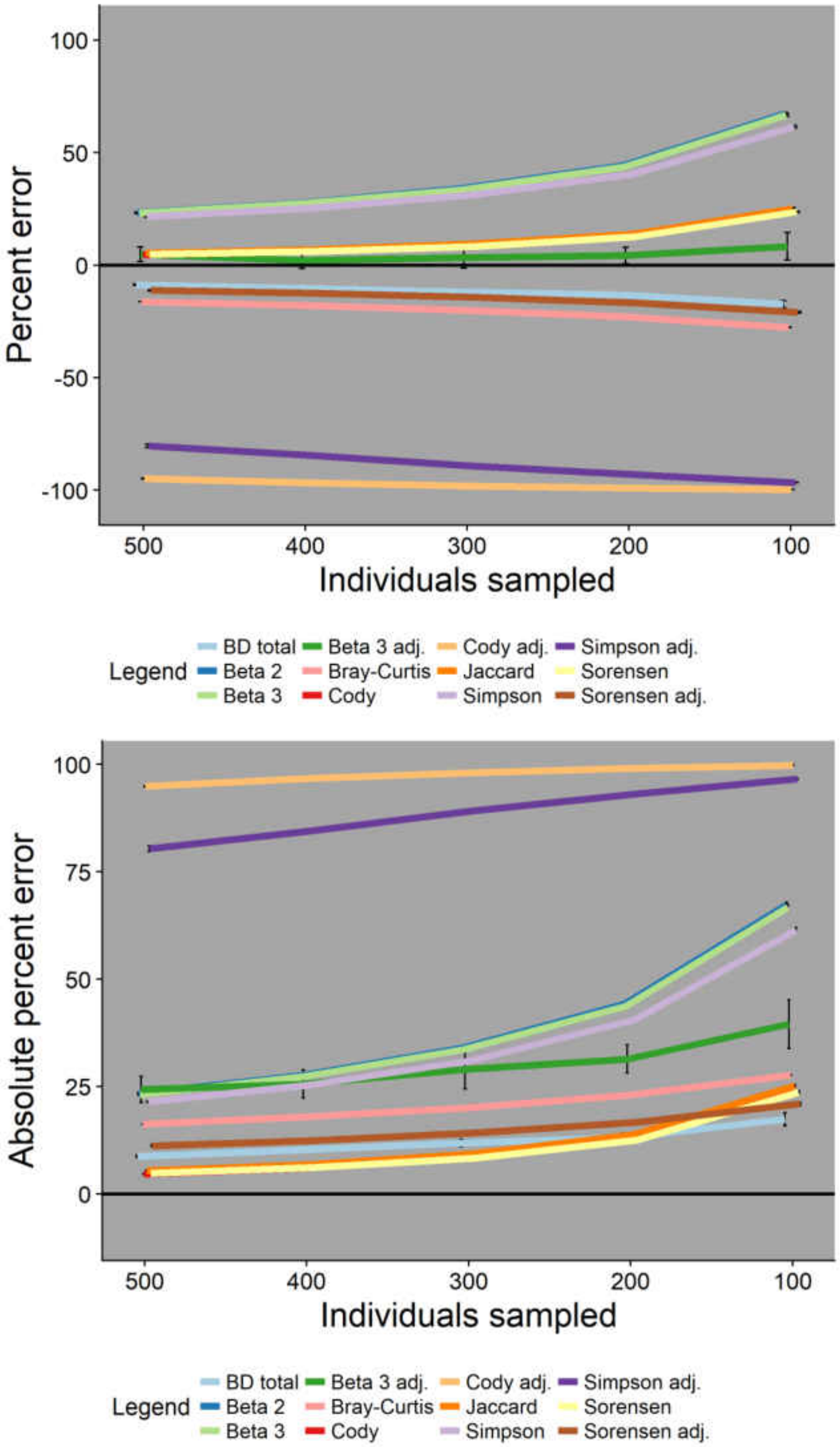

Figure 2.6 The directional and absolute percent errors, respectively, for numerical undersampling based on abundance data. Directional errors are calculated as 100 x (estimate - known)/known, and absolute errors are calculated as 100 x |estimate - known|/known.

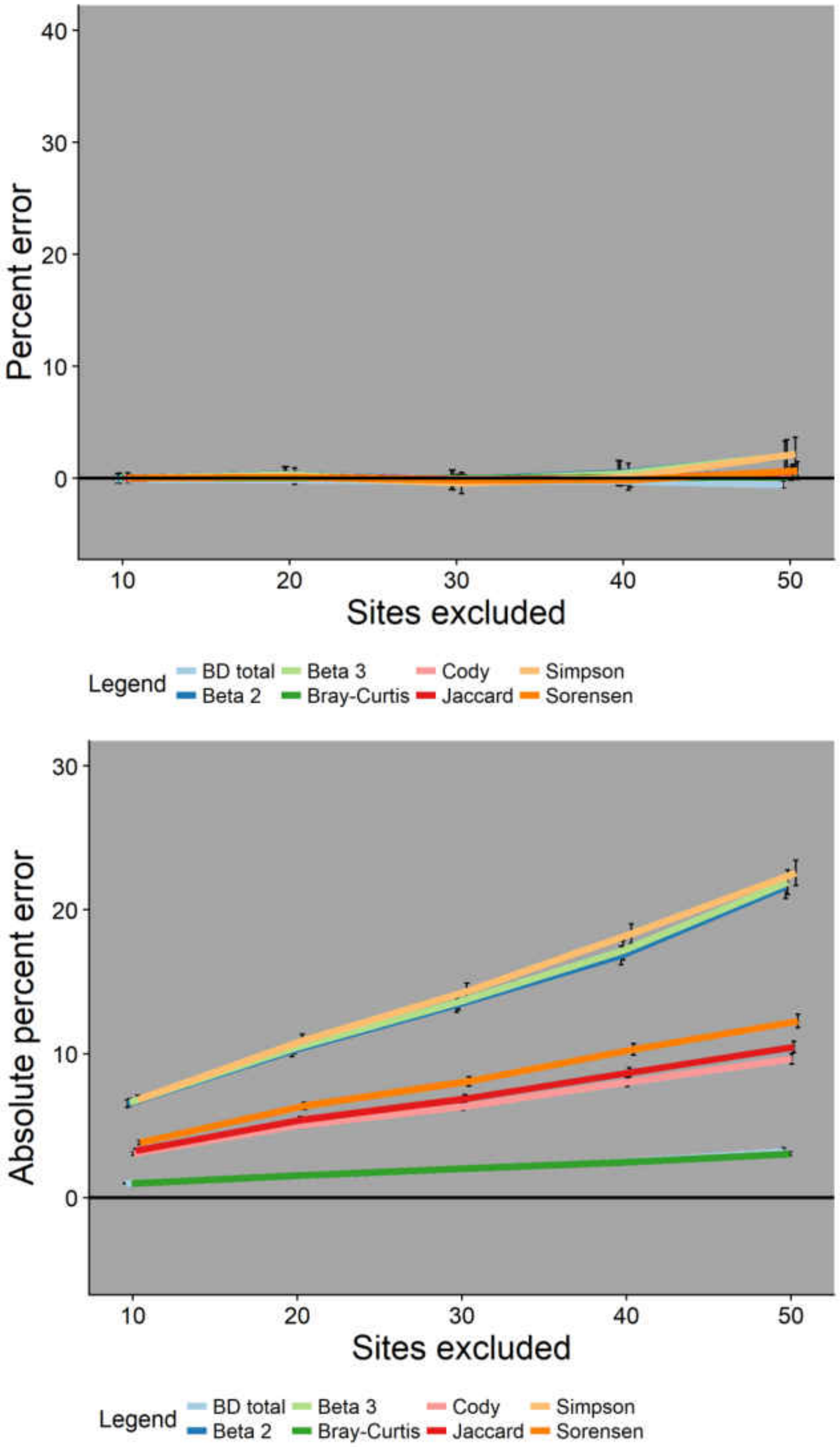

Figure 2.7 The directional and absolute percent errors, respectively, for geographic undersampling based on abundance data. Directional errors are calculated as 100 x (estimate - known)/known, and absolute errors are calculated as 100 x |estimate - known|/known.

References

Anderson, M.J., Crist, T.O., Chase J.M., Vellend, M., Inouye, B.D., Freestone, A.L., Sanders, N.J., Cornell, H.V., Comita, L.S., Davies, K.F., Harrison, S.P., Kraft, N.J.B., Stegen, J.C., & Swenson, N.G. (2010) Navigating the Multiple Meanings of β Diversity: A Roadmap for the Practicing Ecologist. *Ecology Letters*, 14.1, 19-28.

Baselga, A. (2009) Partitioning the Turnover and Nestedness Components of Beta Diversity. *Global Ecology and Biogeography*, 19.1, 134-43.

Beck, J., Holloway, J.D. & Schwanghart, W. (2013) "Undersampling and the Measurement of Beta Diversity." *Methods in Ecology and Evolution*, 4.4, 370-82.

Bickford, D., Lohman, D.J., Sodhi, N.S., Ng, P.K.L., Meier, R., Winker, K., Ingram, K.K., & Das, I. (2007) Cryptic Species as a Window on Diversity and Conservation. *Trends in Ecology & Evolution*, 22.3, 148-55.

Butt, N., Slade, E., Thompson, J., Malhi, Y. & Riutta, T. (2013) Quantifying the Sampling Error in Tree Census Measurements by Volunteers and Its Effect on Carbon Stock Estimates. *Ecological Applications*, 23.4, 936-43.

Cardoso, P., Borges, P.A. & Veech, J.A. (2009) Testing the performance of beta diversity measures based on incidence data: the robustness to undersampling. *Diversity and Distributions*, 15.1, 1081-1090.

Chao, A., Chazdon, R.L., Colwell, R.K. & Shen, T.J. (2006) Abundance-Based Similarity Indices and Their Estimation When There Are Unseen Species in Samples. *Biometrics*, 62.2, 361-71.

Clark, R.T., and Hering, D. (2006) Errors and Uncertainty in Bioassessment Methods – Major Results and Conclusions from the STAR Project and Their Application Using STARBUGS. *Hydrobiologia*, 566.1, 433-39.

Condit, R., Pitman, N., Leigh, Jr., E.G., Chave, J., Terborgh, J., Foster, R.B., Nunez, P., Aguilar, S., Valencia, R., Villa, G., Muller-Landau, H.C., Losos, E. & Hubbel, S.P. (2002) Beta-Diversity in Tropical Forest Trees. *Science*, 295.5555, 666-69.

Devictor, V., Mouillot, D., Meynard, C., Jiguet, F., Thuiller, W., & Mouquet, N. (2010) Spatial Mismatch and Congruence between Taxonomic, Phylogenetic and Functional Diversity: The Need for Integrative Conservation Strategies in a Changing World. *Ecology Letters,* 13.8, 1030-40

Dickinson, J.L., Zuckerberg, B., & Bonter, D.N. (2010) Citizen Science as an Ecological Research Tool: Challenges and Benefits. *Annual Review of Ecology, Evolution, and Systematics*, 41.1, 149-72.

Gabriel, D., Roschewitz, I., Tscharntke, T., & Thies, C. (2006) Beta Diversity At Different Spatial Scales: Plant Communities In Organic And Conventional Agriculture. *Ecological Applications*, 16.5, 2011-021.

Jost, L. (2007) Partitioning Diversity Into Independent Alpha And Beta Components. *Ecology*, 88.10, 2427-439.

Koleff, P., Gaston, K.J., & Lennon, J.J. (2003) Measuring Beta Diversity for Presence-absence Data. *Journal of Animal Ecology*, 72.3, 367-82.

Legendre, P. & De Cáceres, M. (2013) Beta Diversity as the Variance of Community Data: Dissimilarity Coefficients and Partitioning. *Ecology Letters*, 16.8, 951-63.

Li, H., Li, T., Beasley, D.E., Heděnec, P., Xiao, Z., Zhang, S., Li, J., Lin, Q., & Li, X. (2016) Diet Diversity Is Associated with Beta but Not Alpha Diversity of Pika Gut Microbiota. *Frontiers in Microbiology*, 7, 1169

Liu, J., Qian, H., Jin, Yi., Wu, C., Chen, J., Yu, S., Wei, X., Jin, X., Liu, J., & Yu, M. (2016) Disentangling the Drivers of Taxonomic and Phylogenetic Beta Diversities in Disturbed and Undisturbed Subtropical Forests. *Scientific Reports*, 6, 35926

McKnight, M.W., White, P.S., Mcdonald, R.I., Lamoreux, J.F., Sechrest, W., Ridgely, R.S., & Stuart, S.N. (2007) Putting Beta-Diversity on the Map: Broad-Scale Congruence and Coincidence in the Extremes. *PLoS Biology*, 5.10, 2424-32.

Oksanen, J., Blanchet, F.G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P.R., O'Hara, R. B., Simpson, G.L., Solymos, P., Stevens, M.H.H., Szoecs, E., Wagner, H., (2016) *Package 'vegan'*. R Foundation for Statistical Computing, Vienna. URL http://www.R-project.org [accessed 8 January 2017]

Passy, S.I., & Blanchet, F.G. (2007) Algal Communities in Human-impacted Stream Ecosystems Suffer Beta-diversity Decline. *Diversity and Distributions*, 13.6, 670-79.

Tuomisto, H. (2010) A Diversity of Beta Diversities: Straightening up a Concept Gone Awry. Part 1. Defining Beta Diversity as a Function of Alpha and Gamma Diversity. *Ecography*, 33.1, 2-22.

Tuomisto, H. (2010) "A Diversity of Beta Diversities: Straightening up a Concept Gone Awry. Part 2. Quantifying Beta Diversity and Related Phenomena." *Ecography*, 33.1, 23-45.

Whittaker, R. H. (1960) Vegetation of the Siskiyou Mountains, Oregon and California. *Ecological Monographs*, 30.3, 279-338.

CHAPTER 3: INCREASING BETA DIVERSITY IN LAKES IS A DOUBLE EDGED SWORD

Chapter Summary

The biodiversity of lake ecosystems is considered a priority for conservation. Lakes provide many resources to human civilization and to surrounding ecosystems. For this reason, much work has been done on the factors that determine lake biodiversity, however most of that work has focused on within-site (α) diversity; considerably less work has been done on between-site diversity (β), and what has been done has had issues of conflation between β and α. In this study we seek to better understand the β of lakes by determining its predictors in a national diatom dataset. Using the National Lakes Assessment (NLA) created by the United States Environmental Protection Agency (USEPA) we constructed null models for diatom β across the conterminous United States using Bray-Curtis dissimilarity, which was found to be robust to sampling error. We then compared these nulls to the observed β from the dataset to find a measure of β that was truly decoupled from α. Through the use of model averaging we were able to find environmental models that were highly predictive of diatom β deviations. Models were found to be most predictive at the largest scales, indicating that broad patterns are more reliable in diatoms than local ones. Within the models, we found that high mean nitrogen and phosphorous levels were positively correlated with high β deviations, as was the percent of land used for human development. These two variables correspond to two of the most significant threats to lake ecosystems: pollution and habitat destruction. Therefore, we conclude that β should not be thought of as a goal to pursue on its own, but as only one component of the truly desirable total system diversity (γ).

Keywords: beta diversity deviations, Bray-Curtis dissimilarity, conservation, diatoms, lakes, model averaging

Introduction

Lake ecosystems are among the most valuable to human civilization. They provide much of our fresh water, feed diversity in terrestrial ecosystems and provide direct economic benefits to human society through fishing and irrigation (Dudgeon et al., 2007; Holmlund and Hammer, 1999; Carpenter and Wilson, 1999; Reynaud and Lanzanova, 2017). Unfortunately, they are also among the most imperiled due to a combination of factors including fertilizer runoff, human development and disrupted hydrology (Dudgeon et al., 2007; Carpenter et al., 2011). It is, therefore, imperative to understand as much as possible about the diversity of these systems and the means by which it may be conserved. This goal can be achieved by examining the factors that drive diversity. While considerable work has already been done on this subject with regards to the diversity of individual lakes (Brucet et al., 2013; Moore, 1979; Larson and Belovsky, 2013), less has been done to study the factors that cause lakes to become differentiated from each other. In other words, the factors that drive β diversity in lakes have yet to be found.

To address the issues posed above, the United States Ecological Protection Agency (USEPA) launched the National Lakes Assessments (NLA) to take a full inventory of the algal diversity and physical characteristics of lakes throughout the conterminous United States. The NLA was launched in 2007, and repeated with some changes in 2012, using rigorous sampling methods and data management to ensure viable comparisons between lakes (USEPA, 2016). In total, nearly 1300 lakes were recorded in 2007 and their data was made publicly available. This large and reliable dataset has already been the subject of several research papers focusing on topics including, but not limited to, habitat structure (Kaufmann et al., 2014), stressor risk assessment (Sickle, 2013) and identifying water sources (Bowen et al., 2018), however there is still much it has left to tell us. Significantly, this dataset provides broad-scale geography with discrete sites (lakes) to address compositional differences (beta diversity) and predictors of those differences. It further allows us to examine the extent of aggregation amongst diatom species by examining the extent to which β varies across the conterminous United States.

Beta diversity (β) is the portion of diversity that stems from compositional differences between sites. It has previously been linked to ecosystem health (Passey and Blanchet, 2007; Santana et al., 2017) and is one of the two central components of diversity (Whittakker, 1960; Anderson et al., 2011; Jost, 2007). However, despite its ecological significance, its drivers are still not fully understood. The NLA offers a relatively rare opportunity for analysis of these drivers because its data were collected by standardized sampling protocols, conducted by trained professionals among many sites over a broad geographic extent (conterminous USA).

The purpose of this study was to develop predictive models of β in lake diatom systems. Diatoms (and algae in general) have been proposed as a measure of ecosystem health for decades (McCormick and Cairns, 1994, Omar, 2010; Stevenson, 1998), however most studies of diatoms look at α or γ diversity (Barnes et al., 2016; Ives and Carpenter, 2007). There have been a few serious examinations of lake diatom β, such as Winegardner et al. (2017) which looked at trends in diatom β over the last 150 years and Alahuta et al. (2017) which examined how β is partitioned between nestedness and turnover in a global macrophyte dataset. This study, however is unique in terms of its combination of methodology, scale and focus. Rather than looking at traditional measures of β, this study examines β as it deviates from its null expectation, using a methodology first established in Myers et al. (2013). This additional step compares the observed β to that of a hypothetical system with the same number of sites, species and total individuals, but different abundances. This process allows for a greater decoupling of α from β and, thus, an opportunity to look at how β responds to ecological variables on its own. It is hoped that by taking this approach, we can better understand the mechanisms that ultimately create γ and adapt conservation policy to accommodate those needs.

Methods

Ecological and community data were obtained from the USEPA's 2007 National Lakes Assessment (USEPA, 2016). Data analyzed here included diatoms in the shallow and deep sediment samples, and plankton. Other phytoplankton (called "soft algae"; USEPA, 2016) were also analyzed but varied without patterns here and are not discussed further, though results can be found in appendices S1 and S2. Planktonic diatoms were collected in the water column and should represent a more transient sample of diversity than sediment diatoms, which represent a cumulative record of recent (in shallow sediments) or long-term (in deep sediments) diatom diversity. Sediment diatoms were sampled from sediment cores that were 20cm - 25 cm long), where "shallow sediment" diatoms were extracted from the top 2cm of the core and "deep sediment" diatoms were extracted from the bottom 2cm of the core. In principle, shallower sediment diatoms should represent more recent conditions than those in deeper sediments, though elapsed time is not known for these many samples. Comparisons of shallow and deep sediment diatoms thus represent recent and former conditions. Sample processing and data quality steps conducted by USEPA are described in USEPA, 2016. The number of sites analyzed varied depending on the sample type and ranged from 535 (planktonic diatoms) to 1155 (shallow diatoms).

A distance matrix among sampled sites was made using haversine distances ($\sin^2(\frac{\emptyset}{2})$), based on longitude and latitude values of each site. These sites were then grouped into "neighborhoods" based on geographic distance, using custom R (R core team, 2017) code to set each site as a "node" and then collect that site and every sampled site within 100, 200, 300 or 400 km radii. Analyses based on those neighborhood sizes were used to evaluate the effect of spatial grain sizes within the same dataset. Neighborhoods were then evaluated for Bray-Curtis dissimilarities and then for β deviation (i.e., $\beta - \beta_{NULL}$) as defined by Myers et al. (2013). The Bray-Curtis dissimilarity index ($1 - 2C_{ij} / [S_i + S_j]$, where C_{ij} = the sum of the lesser values for species common to both sites, and S = the total number of specimens in sample i or j) is relatively robust to potential sampling errors (Schroeder and Jenkins, 2018), and uses abundance data. Bray-Curtis dissimilarities reported here are the means of all pairwise dissimilarities between sites in a neighborhood. We expected β deviations to decouple the effects of γ from β better than Bray Curtis β diversity alone. Deviations were calculated by creating a null expectation for β, based on γ diversity of the neighborhood, and comparing it to the observed β. Nulls were calculated by maintaining the relative abundance of each species within a community, as well as the total site occupancy, but assigning each individual organism to a random site within the neighborhood. Thus, deviations were created when *local* relative abundances differ from those expected by chance. The deviations from this expectation inform us of the amount of diversity in a neighborhood that is due to the actual distribution of individuals. Because null expectations are created through stochastic processes, we created 2000 nulls for every dataset and grain size and found their averages and standard deviations. In accordance with Myers et al. (2013), we then used the formula (Observed – Expected mean)/Expected SD to calculate our final β deviations.

Some sites lacked samples (especially for planktonic diatoms) or complete environmental data to use as predictors; these sites were excluded. Despite this reduction, minimum N among analyses was 433 for models of smaller neighborhoods (100 km radii) that tend to have fewer sites (Table 3.1).

To better understand factors contributing to β patterns, mean and standard deviation were calculated for 34 environmental variables (e.g., pH; Table 3.2) within each neighborhood. Those variables were then used in multiple regressions to predict β. Regressions based on mean predictors essentially predict that a trend in a variable drives β (e.g., neighborhoods with greater pH tend to have greater β). In contrast, using standard deviations as predictors essentially focuses on environmental variation within neighborhoods as the drivers of β (e.g., neighborhoods with greater variation in pH have greater β). Autocorrelation among environmental variables was evaluated with variable inflation factors (VIFs) after model computations, where redundant variables were removed, and models computed again. An exception was made for land use variables, where both agricultural land use and "developed" land use were included despite being heavily correlated. This was done to prevent the analysis of land use from becoming overly reductive. Morrisey and Graeme (2018) considered auto-correlation between independent variables to be less critical than formerly thought, as their results are predictable and interpretable. In particular, collinearity causes the misestimation of the effect sizes of individual variables within a model, however basic information about the effect can still be gleaned, and the overall fit of the model is unaffected. Based on the above process, the list of potential predictor variables was reduced from 34 to 13 (Table 3.2). Most of the discarded variables related to chemistry or land use and were heavily auto-correlated with variables without increasing the interpretability of the results.

Regression analyses here were exploratory, and so applied an inclusive model selection process and model averaging. Regressions were taken of mixed effect models, with a random intercept effect of ecoregion, and using lme4 in R (Bates et al., 2015). Every possible additive model from the available, scaled variables was computed with their AICc and ΔAICc scores, using the MuMIn package in R to calculate AICc values (Barton, 2018). Burnham and Anderson's (2004) rule of thumb for ΔAICs is that a 0-2 score reflects a highly likely model; a 3-7 score represents a less likely, but still possible, model, and models with an $\Delta AIC > 7$ have little to no support. With that rule in mind, models with $\Delta AICc > 7$ were discarded, but all other models were averaged. Model averaging represents the coefficient estimate (i.e., effect size) and significance of each independent variable across all likely models. After model averaging, the most important (relative importance > 85) and significant ($p < 0.05$) independent variables were collected into a single model and pseudo-R^2 scores were calculated also using the MuMIn package (Barton, 2018) (Tables 3.1 and 3.2). Psuedo-R^2 values were used because conventional R^2 values cannot be taken from mixed effect models. The R^2 values provided in this paper are, therefore, estimates. This final step generated a single model that could be used to advise future conservation efforts, using a modeling process consistent with (Simmons, 2010). The final variables were also organized into broad categories (Table 3.2) and the categories present in final models were reported (Tables 3.5 and 3.6) to summarize general patterns across all datasets. To test the relationship between β deviations and α diversity, the model averaging process was repeated for mean Shannon entropy values using the same moving node sampling system.

Results

Predictive models (pseudo-R^2 range = 0.16 – 0.88) were found for every diatom-based dataset, except planktonic diatoms at the 100 km grain size. Models became more predictive at higher grain sizes in an approximately linear fashion, so that models for 400 km grain size were always more predictive than those at lesser distances (Tables 3.3 and 3.4). The variables and their coefficients in final, averaged models varied within and across biological groups, though models were typically more predictive with the inclusion of a wider variety of variables. For example, the model for deep sediment diatoms and based on mean environmental variables at 100 km grain size used one variable model (total nitrogen concentration5) and has a pseudo-R^2 of 0.19 (Table 3.3). In contrast, the matching 400 km model used six variables (including total N) and has a pseudo-R^2 of 0.88. Important for inferences, predictors in final models changed differed if means or standard deviations were used to represent environmental predictors. However pseudo-R^2 values were comparable among models based on means or standard deviations.

Nitrogen and phosphorous levels were positively correlated with β when significant across both mean and standard deviation variables (Appendix B). Longitude and latitude were both usually correlated with positive β suggesting higher deviations in eastern and northern sites (the coordinate reference system used negative values for western longitudes). The percent of land developed within lake buffers and basins had positive effects on β, as was the percent of land in lake basins used for agriculture. In contrast, α diversity was usually negatively correlated with land-use predictors. The percent of land used for agriculture in the buffer (nearer to the lakes shore) was negatively correlated with β in most datasets. Shoreline development was negatively correlated with β deviations, indicating that neighborhoods with more reservoirs were more homogeneous than were neighborhoods with natural lakes. In contrast, pH was often negatively correlated with β. Depth, lake area and elevation all had variably positive or negative effects depending on the dataset and grain size. Variables that were insignificant within a model often broke from these patterns and commonly held values close to zero.

Amongst model coefficients there are a few noteworthy occurrences. At 300 and 400km grain sizes, mean agricultural land use in lake basins was found to have a strong, positive effect on shallow diatom β deviations (0.562 and 0.701 respectively). Mean basin agriculture was found to have an even stronger positive effect (1.07) in planktonic diatoms at the 400 km grain size. Conversely mean agriculture in the buffer region had a strongly negative effect (-0.739) on the same data. Standard deviation of longitude was found to have a sizeable positive effect on planktonic diatom β deviation at 200 and 300 km grain sizes (0.570 and 0.555, respectively). Finally, standard deviation of elevation was found to have a strong, negative effect on deep diatom β deviation at 200 and 300 km grain sizes (-0.501 and -0.534).

The most predictive model for each combination of biological group and variable type (mean or SD) was always found at the 400km grain size. Planktonic diatom β deviations were most plausibly predicted by β_{DEV} ~ Basin agriculture + Buffer agriculture + Developed basin + Elevation + SLD + Lake area + Total N + Total P + (1 | Ecoregion) for mean variables. SD variables produced a model of β_{DEV} ~ Agriculture buffer + Elevation + Lake area + Longitude + pH + Depth + Latitude + (1 | Ecoregion). Their pseudo-adjusted R^2 values were 0.64 and 0.60 respectively. Mean and SD values for shallow diatoms were β_{DEV} ~ Agriculture basin + Depth + Developed basin + Elevation + Lake area + Latitude + (1 | Ecoregion) and β_{DEV} ~ Agriculture basin + Agriculture buffer + Developed buffer + Latitude +Longitude + pH + SLD + Total P + (1 | Ecoregion). Pseudo-adjusted R^2 values were 0.80 and 0.76. Finally, the most plausible models for deep diatoms were β_{DEV} ~ Agriculture basin + Developed basin + SLD + Developed buffer + Total N + Latitude + (1 | Ecoregion) with a pseudo-adjusted R^2 of 0.88 for mean values and β_{DEV} ~ Agriculture basin + Depth + Developed basin + Elevation + Lake area + Latitude + pH + SLD + Total N + (1 | Ecoregion) with an pseudo-adjusted R^2 of 0.87. Results for other grain sizes can be found in Tables 3.3 and 3.4.

Differences between conventional Bray-Curtis measures and β deviations are illustrated in maps for the conterminous US (Figs 3.1 – 3.3). Deviations are noticeably greatest throughout the Southwest, the Great Lakes and northernmost region of Montana, with smaller deviations near the Florida panhandle. This differs significantly from a visual assessment of the same data based the Bray-Curtis index, which places greater emphasis on eastern regions or, in the case of shallow diatoms (Fig. 3.2a), is largely random. Deviations also showed cleaner aggregations, as both Figures 3.2 and 3.3 show greater differences between neighboring regions and more randomness in conventional Bray-Curtis measures than in their corresponding deviations. It is also noteworthy that Figure 3.1a (planktonic diatoms) appears to be the inverse of Figure 3.1b. This may be due to the greater potential for deviance in very low Bray-Curtis values, however it is curious that the other two figures do not appear to replicate this trend.

Discussion

A regional perspective helps natural resources management sustain biodiversity by recognizing site heterogeneity, and that no one site is optimal for all species (Gustafson and Gardner, 1996). A regional species pool among multiple sites may be managed for maximal regional diversity. To do so requires better recognition (and management of) natural habitat heterogeneity among sites (Tews et al., 2003). Beta diversity is, or should be, an essential analytical tool for regional natural resources management. More specifically, deviation from a null expectation for beta diversity (β deviation) is essential, because it accounts for the impact that regional alpha diversity has on beta diversity measures (Myers et al., 2013). In order maximize γ, it is necessary to reach the optimal combination of α and β. Conventional β measures can be confounded by α leading to strategies that are more heavily biased toward α than is optimal.

Our research found multiple positive predictors of β deviation, but some predictors are double edged swords. While it is true that greater N or P are positively correlated with high β deviations, results here do not translate to a recommendation that eutrophication benefits biodiversity. Deleterious effects caused by algal blooms are well documented (e.g. Anderson et al., 2002; Smith, 2003; Gilbert, 2017) and reducing fertilizer run-off is a priority in conservation (Carpenter et al., 2008). The mechanism for the increase in β deviations may also be undesirable. Phosphorous and nitrogen are positively correlated through both their means and standard deviations. The correlations between standard deviations of N and P with β deviations were expected based on previous research which found chemical heterogeneity can be a driver of β (Chen et al., 2011; Lowell et al, 2009). The correlations with mean N and P were less expected, as previous research has indicated there would be no response (Gudmundsdottir et al., 2013). The NLA used a lake selection design that randomly sampled from a pool of all accessible lakes of a certain size and natural history. This pool explicitly included lakes that had been identified as eutrophic in the past, so it does not appear to be an issue of sampling bias. It is possible that the differences in β response may be due to those studies using conventional measures of β, rather than deviations, but further assessment would be necessary to confirm this.

Agricultural and urban land use also correlated with raised β deviations. In some cases, such as planktonic diatoms at 300 and 400km grainsizes, the effects of these variables could be quite large. This pattern bears similar problems to the above correlation between nitrogen and phosphorus and β, because mitigating land use effects on biodiversity is one of the cornerstones of conservation biology (Carpenter et al., 1998; Sharpley et al., 2000) and encroaching human developments and agriculture is one of the most commonly implicated drivers of our current mass extinction (Brooks et al., 2002). Once again, the probable mechanism behind this correlation is problematic. We think the effect of land use reflects the impact of habitat fragmentation, which causes communities to become more physically isolated from one another, and thus more distinct over time. To test this possibility, we used the same experimental framework that we used to find β deviation drivers, but substituted α. We found that α was usually negatively correlated with mean development and agriculture (Appendix B), an expected result if geographic isolation is the driving mechanism. The negative correlation between β deviations and agriculture within the buffer zone may be explained by the buffer zone's smaller size and closer proximity to the lake shore relative to the basin zone. Agriculture that close to a body of water may result in herbicide pollution which would cause homogenization as only certain species would be able to survive.

Negative correlations were found between β deviations and pH, as well as SLD. A more isolated negative correlation was also found between deep diatom β deviations and standard deviations of elevation. The correlation with pH is likely explained by traditional habitat filtering; diatoms most prefer circumneutral lakes (Pither and Aarsen, 2005), so higher pHs would result in greater specialization in community assemblages and thus lower β as the same specialists will survive most places. Relatively few acidic lakes were sampled in this study (mean pH = 8, standard deviation = 0.77), a skew which may explain the apparent tolerance of diatoms to more acidic lakes. “Acidic” lakes in this case were circumneutral or close to it. High SLDs are associated with reservoirs, which tend to have more elongation, while low SLDs are associated with natural lakes. Thus, the negative correlation suggests that β deviations will be highest in systems dominated by natural lakes. Given the probable role of evolution and natural history in driving β deviations, this outcome is not surprising. However, it should be noted that the only group in which this trend is found is deep sediment diatoms. Shallow sediment and planktonic diatoms do not reflect this trend or any other; SLD does not appear in any of their models. This trend (or the lack thereof) is further reinforced by in the maps. Natural lakes tend to be more prevalent in the North and the area around Florida, while reservoirs are more common in much of the rest of the country. Indeed, we see that deep diatom β deviations are highest in the North and in Florida, but shallow and planktonic diatom β deviations are highest in the Southwest and Montana, with planktonic deviations also being high in Florida. Deep sediment diatoms represent more of a historical record than the other categories, which could indicate that SLD was a bigger factor in the past than it is today. It is harder to explain why heterogeneity in elevation would cause homogenization in deep sediment diatoms. Elevational heterogeneity could correspond to more water flowing into lake and river basins, simultaneously causing up-elevation diatom communities to become connected to down-elevation communities. If so, the lack of a homogenizing effect found in shallow sediment and planktonic diatoms may match current hydrological literature that suggests modern hydrological regimes have changed drastically from their historical conditions (Tharm, 2003; Gordon et al., 2008). It is also possible that the differences between the shallow and deep sediment diatoms are being driven by biotic factors. Recent centuries have given rise to a number of invasive species in America’s freshwater systems especially along the Mississippi river and the Great Lakes (Johnson et al., 2006; Riciardi and MacIsaac, 2000), which is also where we see high β deviations in deep sediment (historic) diatoms and low β deviations in shallow sediment (current) diatoms. Further studies linking diatom diversity and invasive species (or the commerce tendencies that drive freshwater species invasions (MacIsaac et al, 2002; Rixon et al., 2005)) may further elucidate this possible relationship.

No one model proved overwhelmingly descriptive for all grain sizes or biological groups, and the general consensus across models was that most variables matter to at least some extent. Data taken at larger scales (300 – 400 km) produced models that were especially inclusive. This result is not wholly unexpected, as all of these variables have been previously demonstrated or suggested as having some kind of effect of diversity in general. Perhaps the best advice that can be construed from the models is to adopt a holistic approach to conservation and attempt support diversity in as many ways as possible. This is consistent with many modern approaches (e.g. Stokes et al., 2010; Gruber et al., 2017; Ganeshaiah and Shaanker, 1998) and supports a general strategy of trying to preserve as much land as possible as thoroughly as possible.

The results of our analyses support previous research that β deviations reveal patterns that normal calculations of β do not (e.g. Myers et al., 2013; Xu et al., 2015). By incorporating null models into the calculation of β we can see which areas are exceeding or falling short of expectations and better account for the effects of factors like α and sample area. Deviations are still consistent with several expectations about β in general; for example, neighborhoods that incorporate physical dividers like mountain ranges should have high β while more homogeneous ones should have low β. However, we also see that areas which appear to be doing well in β owe their high value to a high overall species richness, which are better considered as factors of α and γ especially along the southern half of California.

This research serves to illustrate to potential pitfalls of pursuing just one type of diversity. When taken at face value, our results indicate that dumping fertilizer into lakes and building as much as possible would be great benefit to the environment. In reality, it hardly bears mentioning how harmful such policies would be for ecosystem health. Factors that drive β deviations are potentially harmful to α diversity and the reverse may also be true. However, β itself is never the end goal of conservation. Rather, β is pursued with the intention of maximizing γ. β deviations allow researchers to better isolate β from α, which is valuable when building theory. However, it should not cause conservationists to lose sight of the fact that they are ultimately working towards high γ. Therefore, we recommend that policy makers take care to not lose sight one form of diversity for another and give due consideration to how each management decision will affect all forms of diversity before proceeding.

Tables and Figures

Table 3.1The number of sites in the original NLA datasets and the number that were used in this study. Sites were excluded if they had incomplete data or if they were too isolated to form part of a neighborhood.

Biological group	**Grain size (km radius)**	**NLA sites**	**Sites/neighborhoods used (N)**
Planktonic diatoms	100	1155	433
	200		481
	300		484
	400		484
Shallow sediment diatoms	100	1071	947
	200		980
	300		981
	400		981
Deep sediment diatoms	100	535	454
	200		473
	300		475
	400		479

Table 3.2 The variables initially considered for analysis and the general categories they fall into. Asterisks denote variables that were selected for use in final analysis.

Predictor	**Group**
pH*	Chemistry
Conductivity	
Turbidity	
N*	
P*	
Dissolved organic carbon	
Cl	
SO_4	
Mg	
Cation-anion balance	
Mean Secchi transparency	
Water buffer/basin	Land use
Developed buffer/basin*	
Agriculture buffer/basin *	
Wetland buffer/basin	
Shrubland buffer/basin	
Barren buffer/basin	
Grass buffer/basin	
Forest buffer/basin	
Shoreline development (SLD) *	Morphometry
Lake area*	
Lake perimeter	
Sampling depth*	
Longitude*	Locality
Latitude*	
Elevation*	

Table 3.3 Models constructed from mean environmental data using the most relevant and significant variables identified through model averaging. Adjusted R^2 values are pseudo-R^2 values taken from the MuMin package of R.

Bio group	Grain Size	Model (Averaged Coefficient)	Adj R^2
Planktonic Diatoms	100	Depth (0.262) + Longitude (0.340) + SLD (0.194) + pH (-0.234) + (1 | Ecoregion)	0.1636
	200	Developed basin (0.277) + (1 | Ecoregion)	0.2458
	300	Lake area (-0.124) + (1 | Ecoregion)	0.4287
	400	Agriculture basin (1.07) + Agriculture buffer (-0.739) + Developed basin (0.506) + Lake area (-0.337) + Total N (0.411) + Elevation (0.232) + Total P (-0.240) + SLD (0.199) + (1 | Ecoregion)	**0.6356**
Shallow sediment diatoms	100	Developed buffer (0.160) + SLD (-0.171) + Total N (0.181) + Longitude (0.329) + Elevation (-0.154) + Depth (0.118) + (1 | Ecoregion)	0.4215
	200	Agriculture basin (0.277) + Developed buffer (0.300) + Latitude (0.288) + Total N (0.180) + SLD (-0.096) + (1 | Ecoregion)	0.5249
	300	Agriculture basin (0.562) + Developed buffer (0.249) + Elevation (0.188) + Latitude (0.400) + Total N (0.106) + (1 | Ecoregion)	0.7053
	400	Agriculture basin (0.701) + Depth (-0.160) + Developed basin (0.207) + Elevation (0.301) + Lake area (-0.110) + Latitude (0.364) + (1 | Ecoregion)	**0.7964**
Deep sediment diatoms	100	Total N (0.338) + (1 | Ecoregion)	0.1982
	200	Depth (0.226) + Elevation (0.290) + SLD (-0.328) + Developed basin (-0.289) + Total N (0.304) + (1 | Ecoregion)	0.5706
	300	Agriculture basin (0.322) + Lake area (0.204) + Latitude (0.543) + SLD (-0.181) + Total P (0.188) + Developed buffer (0.343) + (1 | Ecoregion)	0.7936
	400	Agriculture basin (0.467) + Developed basin (0.584) + SLD (-0.445) + Developed buffer (-0.568) + Total N (0.224) + Latitude (0.255) + (1 | Ecoregion)	**0.8752**

Table 3.4 Models constructed from standard deviations of environmental data using the most relevant and significant variables identified through model averaging. Adjusted R^2 values are pseudo-R^2 values taken from the MuMin package of R.

Bio group	**Grain Size**	**Model (Averaged Coefficient)**	**Adj R^2**
Planktonic Diatoms	100	none	-
	200	Agriculture buffer (-0.253) + Developed basin (0.290) + pH (-0.164) + (1 | Ecoregion)	0.2894
	300	Agriculture buffer (-0.239) + Elevation (0.465) + Longitude (0.570) + pH (-0.391) + Developed buffer (0.131) + (1 | Ecoregion)	0.5551
	400	Agriculture buffer (-0.311) + Elevation (0.473) + Lake area (-0.140) + Longitude (0.555) + pH (-0.524) + Depth (-0.226) + Latitude (0.214) + (1 | Ecoregion)	**0.6018**
Shallow sediment diatoms	100	Agriculture basin (0.163) + Depth (0.161) + Developed basin (0.155) + Longitude (0.399) + Total N (0.184) + Elevation (-0.141) + (1 | Ecoregion)	0.3333
	200	Agriculture basin (0.166) + Developed basin (0.277) + Latitude (0.215) + Longitude (0.407) + pH (-0.121) + Total N (0.143) + Total P (0.116) + (1 | Ecoregion)	0.4931
	300	Developed buffer (0.264) + Lake area (0.109) + Latitude (0.326) + Longitude (0.420) + pH (-0.300) + Total P (0.141) + (1 | Ecoregion)	0.6784
	400	Agriculture basin (0.175) + Agriculture buffer (0.162) + Developed buffer (0.140) + Latitude (0.291) + Longitude (0.281) + pH (-0.320) + SLD (-0.151) + Total P (0.087) + (1 | Ecoregion)	**0.7551**
Deep sediment diatoms	100	Elevation (-0.269) + Latitude (-0.473) + SLD (0.172) + Total N (0.226) + (1 | Ecoregion)	0.3168
	200	Depth (0.223) + Developed basin (0.351) + Elevation (-0.501) + Total N (0.331) + (1 | Ecoregion)	0.5354
	300	Developed buffer (0.331) + Elevation (-0.534) + Lake area (0.206) + SLD (-0.117) + Total N (0.334) + Depth (0.174) + (1 | Ecoregion)	0.7961
	400	Agriculture basin (0.365) + Depth (0.218) + Developed basin (0.174) + Elevation (-0.314) + Lake area (0.213) + Latitude (0.270) + pH (-0.161) + SLD (-0.345) + Total N (0.279) + (1 | Ecoregion)	**0.8721**

Table 3.5 The theoretical categories represented in the models taken from mean environmental values.

Bio group	Grain Size	Model
Planktonic Diatoms	100	Morphometry + Chemistry + Locality
	200	Land use
	300	Morphometry
	400	Morphometry + Chemistry + Locality + Land use
Shallow sediment diatoms	100	Morphometry + Chemistry + Locality + Land use
	200	Morphometry + Chemistry + Locality + Land use
	300	Chemistry + Locality + Land use
	400	Morphometry + Locality + Land use
Deep sediment diatoms	100	Chemistry
	200	Morphometry + Chemistry + Locality + Land use
	300	Morphometry + Chemistry + Locality + Land use
	400	Morphometry + Chemistry + Locality + Land use

Table 3.6 The theoretical categories represented in the models taken from the standard deviations of environmental values.

Bio group	Grain Size	Model
Planktonic Diatoms	100	Morphometry
	200	Chemistry + Land use
	300	Chemistry + Locality + Land use
	400	Morphometry + Chemistry + Locality + Land use
Shallow sediment diatoms	100	Morphometry + Chemistry + Locality + Land use
	200	Chemistry + Locality + Land use
	300	Morphometry + Chemistry + Locality + Land use
	400	Morphometry + Chemistry + Locality + Land use
Deep sediment diatoms	100	Morphometry + Chemistry + Locality
	200	Morphometry + Chemistry + Locality + Land use
	300	Morphometry + Chemistry + Locality + Land use
	400	Morphometry + Chemistry + Locality + Land use

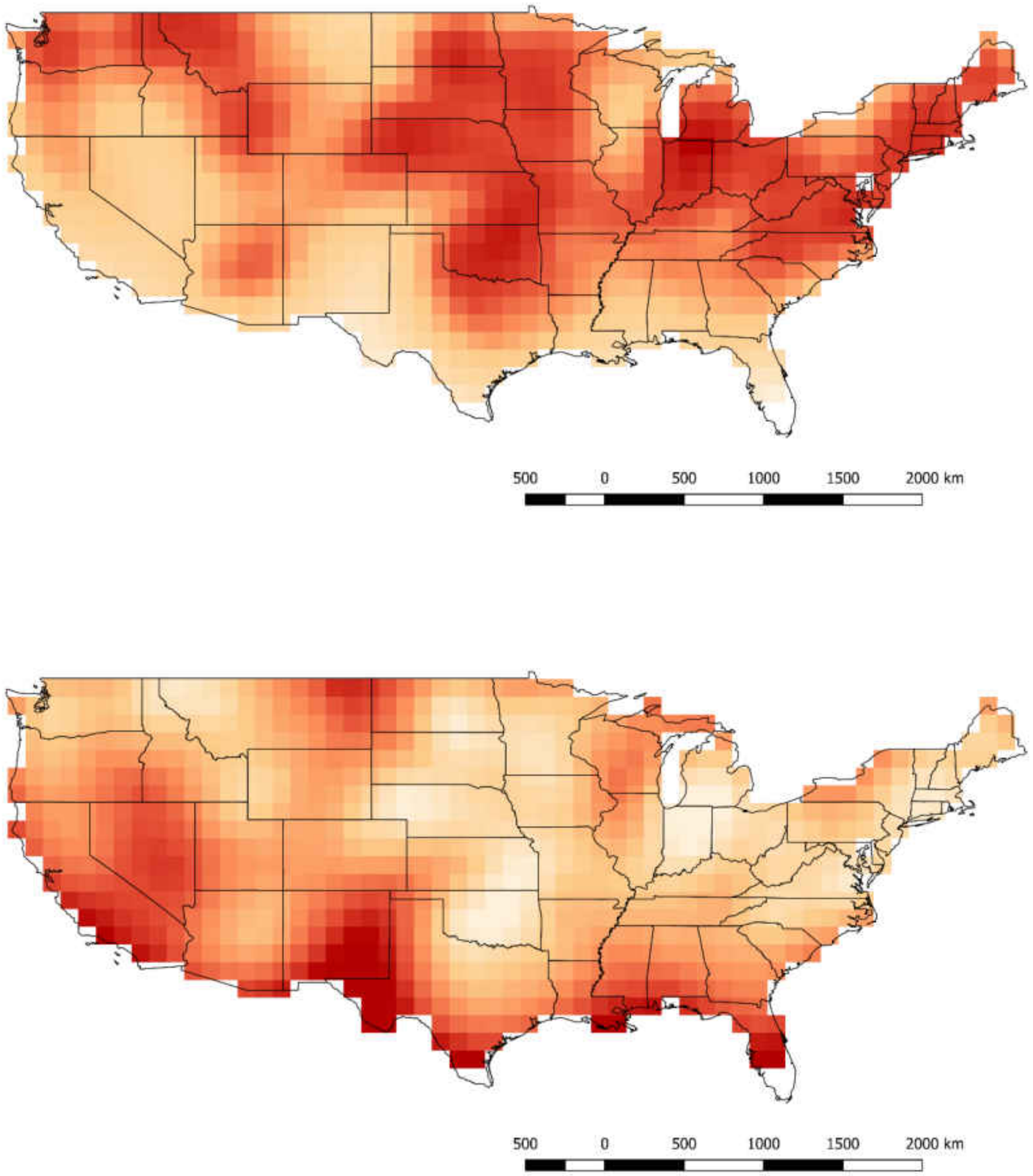

Figure 3.1 β and β deviation distributions for planktonic diatoms. Conventional Bray-Curtis analysis suggests that diversity is highest along the Mississippi River and in the Pacific Northwest, the Great Lakes region and the Northeast. Deviations suggest that diversity is actually highest in the Southwest, the Gulf Coast and the Montana/Wyoming regions. Values depicted are kriging estimates and do not pertain to specific values of β or β deviation. Darker red colors indicate higher relative values while lighter orange ones indicate lower relative values.

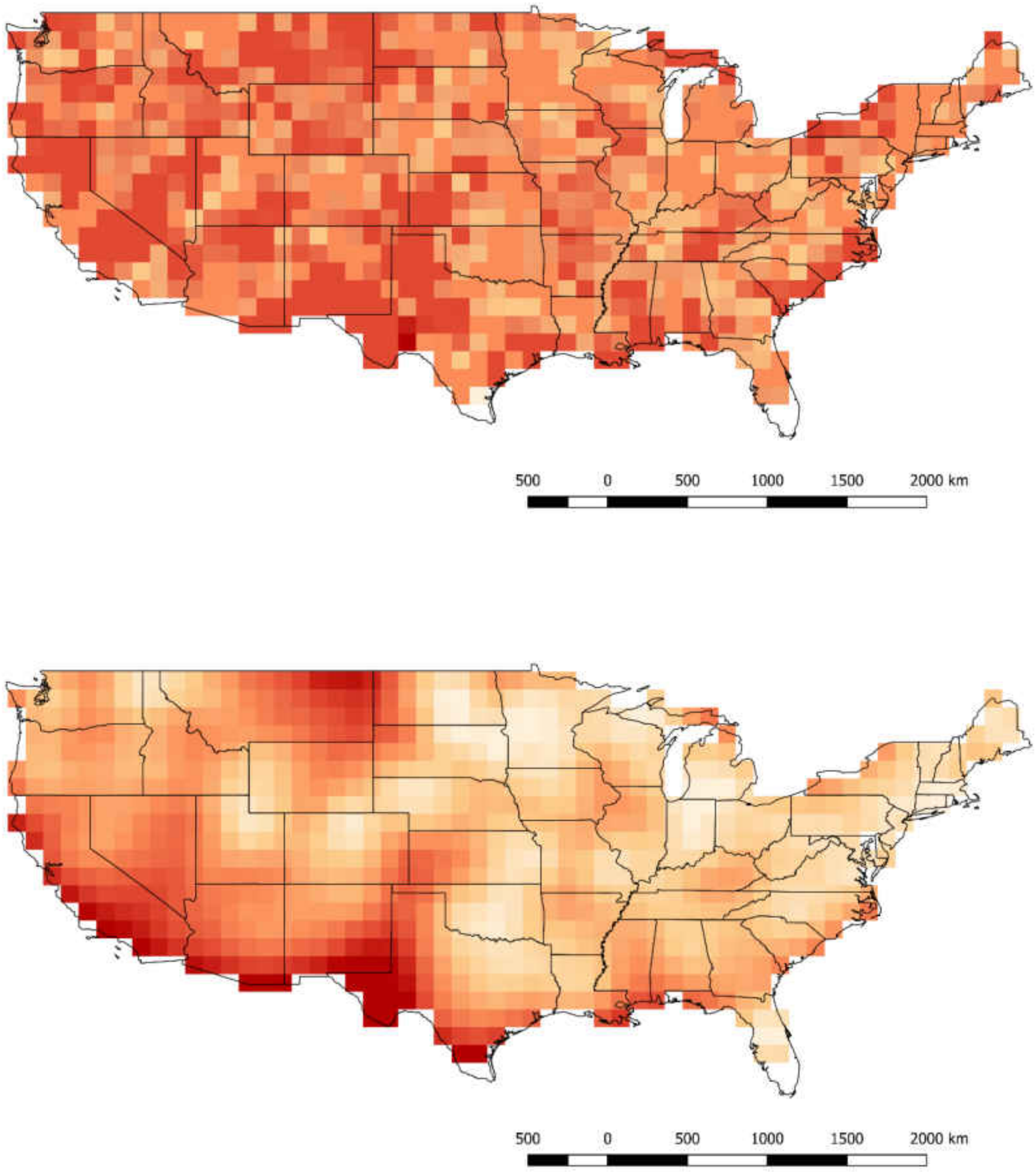

Figure 3.2 β and β deviation distributions for shallow diatoms. Deviations suggest that diversity is greatest in Montana and throughout the Southwest, while conventional Bray-Curtis assessments suggest that it is randomly distributed. Values depicted are kriging estimates and do not pertain to specific values of β or β deviation. Darker red colors indicate higher relative values while lighter orange ones indicate lower relative values.

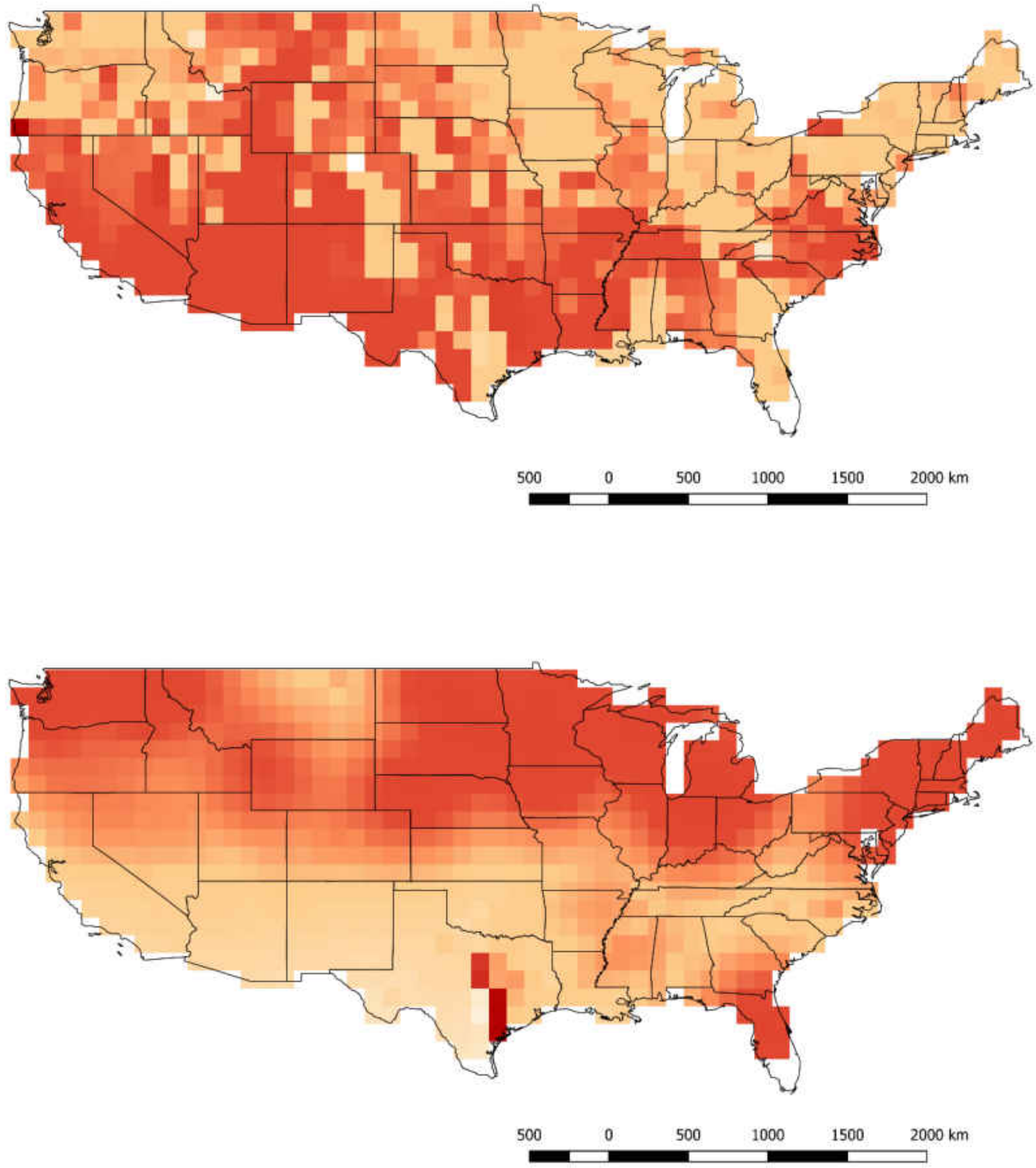

Figure 3.3 β and β deviation distributions for deep diatoms. Deviations suggest that diversity is greatest in the Great Lakes region and the glacial north, while conventional Bray-Curtis assessments suggest that it is highest Southwest. Values depicted are kriging estimates and do not pertain to specific values of β or β deviation. Darker red colors indicate higher relative values while lighter orange ones indicate lower relative values.

References

Alahuhta, J., Kosten, S., Akasaka, M., Auderset, D., Azzella, M. M., Bolpagni, R., Bove, C. P., Chambers, P. A., Chappuis, E., Clayton, J., de Winton, M., Ecke, F., Gacia, E., Gecheva, G., Grillas, P., Hauxwell, J., Hellsten, S., Hjort, J., Hoyer, M.V., Ilg, C., Kolada, A., Kuopalla, M., Lauridsen, T., Hua Li, E., Luckács, B., Mjelde, M., Mikulyuk, A., Mormul, R. P., Nishiro, J., Oertli, B., Rhazi, M., Sass, L., Schranz, C., Søndergaard, M., Yamanouchi, T., Yu, Q., Wang, H., Willby, H., Zhang, X. K. & Heino, J. (2017). Global variation in the beta diversity of lake macrophytes is driven by environmental heterogeneity rather than latitude. *Journal of Biogeography,* 44.8, 1758-1769.

Anderson, D. M., Glibert, P. M., & Burkholder, J. M. (2002). Harmful algal blooms and eutrophication: Nutrient sources, composition, and consequences. *Estuaries,* 25.4, 704-726

Anderson, M. J., Crist, T. O., Chase, J. M., Vellend, M., Inouye, B. D., Freestone, A. L., . . . Swenson, N. G. (2010). Navigating the multiple meanings of β diversity: A roadmap for the practicing ecologist. *Ecology Letters,* 14.1, 19-28.

Barnes, M. D., Craigie, I. D., Dudley, N., & Hockings, M. (2016). Understanding local-scale drivers of biodiversity outcomes in terrestrial protected areas. *Annals of the New York Academy of Sciences,* 1399.1, 42-60.

Barton, K. (2018). MuMIn: Multi-Model Inference. R package version 1.40.4. https://CRAN.R-project.org/package=MuMIn

Bates, D., Maechler, M., Bolker, B. & Walker S. (2015). Fitting Linear Mixed-Effects Models Using lme4. Journal of Statistical Software, 67.1, 1-48.

Bowen, G. J., Putman, A., Brooks, J. R., Bowling, D. R., Oerter, E. J., & Good, S. P. (2018). Inferring the source of evaporated waters using stable H and O isotopes. *Oecologia,* 187.4, 1025-1039.

Brooks, T. M., Mittermeier, R. A., Mittermeier, C. G., Fonseca, G. A., Rylands, A. B., Konstant, W. R., Flick, P., Pilgrim, J. & Hilton-Taylor, C. (2002). Habitat Loss and Extinction in the Hotspots of Biodiversity. *Conservation Biology,* 16.4, 909-923.

Brucet, S., Pédron, S., Mehner, T., Lauridsen, T. L., Argillier, C., Winfield, I. J., Volta, P., Emmrich, M., Hesthagen, T., Holmgren, K., Benejam, L., Kelly, F., Krause, T., Palm, A., Rask, M. & Jeppesen, E. (2013). Fish diversity in European lakes: Geographical factors dominate over anthropogenic pressures. *Freshwater Biology,* 58.9, 1779-1793.

Carpenter, S. R., Caraco, N. F., Correll, D. L., Howarth, R. W., Sharpley, A. N., & Smith, V. H. (1998). Nonpoint Pollution of Surface Waters with Phosphorus and Nitrogen. *Ecological Applications,* 8.3, 559.

Carpenter, S. R., Stanley, E. H., & Vander Zanden, M. (2011). State of the World's Freshwater Ecosystems: Physical, Chemical, and Biological Changes. *Annual Review of Environment and Resources,* 36, 75-99.

Chen, G., Saulnier-Talbot, E., Selbie, D. T., Brown, E., Schindler, D. E., Bunting, L., Leavitt, P.R., Finney, B.P. & Gregory-Eaves, I. (2010). Salmon-derived nutrients drive diatom beta-diversity patterns. *Freshwater Biology,* 56(2), 292-301.

Dudgeon, D., Arthington, A. H., Gessner, M. O., Kawabata, Z., Knowler, D. J., Lévêque, C., . . . Sullivan, C. A. (2007). Freshwater biodiversity: Importance, threats, status and conservation challenges. *Biological Reviews,* 81.02, 163-182.

Ganeshaiah, K. I., & Shaanker, R. (1998). Contours of conservation – A national agenda for mapping biodiversity. *Current Science,* 75.3, 292-298.

Gilbert, P. M. (2017). Eutrophication, harmful algae and biodiversity — Challenging paradigms in a world of complex nutrient changes. *Marine Pollution Bulletin,* 124.2, 591-606.

Gordon, L. J., Peterson, G. D., & Bennett, E. M. (2008). Agricultural modifications of hydrological flows create ecological surprises. *Trends in Ecology & Evolution,* 23.4, 211-219.

Gruber, J., Mbatu, R., Johns, R., & Dixon, B. (2017). Measuring conservation success beyond the traditional biological criteria: The case of conservation projects in Costa Rica, Mekong Valley, and Cameroon. *Natural Resources Forum,* 42.1, 19-31.

Gudmundsdottir, R., Palsson, S., Hannesdottir, E. R., Olafsson, J. S., Gislason, G. M., & Moss, B. (2013). Diatoms as indicators: The influences of experimental nitrogen enrichment on diatom assemblages in sub-Arctic streams. *Ecological Indicators,* 32, 74-81.

Gustafson, E. J., & Gardner, R. H. (1996). The Effect of Landscape Heterogeneity on the Probability of Patch Colonization. *Ecology,* 77.1, 94-107.

Hill, N. M., Keddy, P. A., & Wisheu, I. C. (1998). A Hydrological Model for Predicting the Effects of Dams on the Shoreline Vegetation of Lakes and Reservoirs. *Environmental Management,* 22.5, 723-736.

Holmlund, C. M., & Hammer, M. (1999). Ecosystem services generated by fish populations. *Ecological Economics,* 29.2, 253-268.

Ives, A. R., & Carpenter, S. R. (2007). Stability and Diversity of Ecosystems. *Science,* 317.5834, 58-62.

Johnson, L. E., Bossenbroek, J. M., & Kraft, C. E. (2006). Patterns and Pathways in the Post-Establishment Spread of Non-Indigenous Aquatic Species: The Slowing Invasion of North American Inland Lakes by the Zebra Mussel. *Biological Invasions,* 8.3, 475-489.

Jost, L. (2007). Partitioning Diversity Into Independent Alpha And Beta Components. *Ecology,* 88.10, 2427-2439.

Kaufmann, P. R., Peck, D. V., Paulsen, S. G., Seeliger, C. W., Hughes, R. M., Whittier, T. R., & Kamman, N. C. (2014). Lakeshore and littoral physical habitat structure in a national lakes assessment. *Lake and Reservoir Management,* 30.2, 192-215.

Larson, C. A., & Belovsky, G. E. (2013). Salinity and nutrients influence species richness and evenness of phytoplankton communities in microcosm experiments from Great Salt Lake, Utah, USA. *Journal of Plankton Research,* 35.5, 1154-1166.

Lowell, J. L., Gordon, N., Engstrom, D., Stanford, J. A., Holben, W. E., & Gannon, J. E. (2009). Habitat Heterogeneity and Associated Microbial Community Structure in a Small-Scale Floodplain Hyporheic Flow Path. *Microbial Ecology,* 58.3, 611-620.

Maas, B., Clough, Y., & Tscharntke, T. (2013). Bats and birds increase crop yield in tropical agroforestry landscapes. *Ecology Letters,* 16.12, 1480-1487.

MacIsaac, H. J., Robbins, T. C., & Lewis, M. A. (2002). Modeling ships ballast water as invasion threats to the Great Lakes. *Canadian Journal of Fisheries and Aquatic Sciences,* 59.7, 1245-1256.

Moore, J. W. (1979). Factors Influencing the Diversity, Species Composition and Abundance of Phytoplankton in Twenty One Arctic and Subarctic Lakes. *Internationale Revue Der Gesamten Hydrobiologie Und Hydrographie,* 64.4, 485-499.

Myers, J. A., Chase, J. M., Jiménez, I., Jørgensen, P. M., Araujo-Murakami, A., Paniagua-Zambrana, N., & Seidel, R. (2013). Beta-diversity in temperate and tropical forests reflects dissimilar mechanisms of community assembly. *Ecology Letters,* 16.2, 151-157.

Omar, W. (2010). Perspectives on the Use of Algae as Biological Indicators for Monitoring and Protecting Aquatic Environments, with Special Reference to Malaysian Freshwater Ecosystems. *Tropical Life Sciences Research,* 21.2, 51-67.

Palacín, C., Gili, J., & Martín, D. (1992). Evidence for coincidence of meiofauna spatial heterogeneity with eutrophication processes in a shallow-water Mediterranean bay. *Estuarine, Coastal and Shelf Science,* 35.1, 1-16.

Passy, S. I., & Blanchet, F. G. (2007). Algal communities in human-impacted stream ecosystems suffer beta-diversity decline. *Diversity and Distributions,* 13.6, 670-679.

Pither, J., & Aarssen, L. W. (2005). The evolutionary species pool hypothesis and patterns of freshwater diatom diversity along a pH gradient. *Journal of Biogeography,* 32.3, 503-513.

R Core Team (2017). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.

Ricciardi, A., & MacIsaac, H. J. (2000). Recent mass invasion of the North American Great Lakes by Ponto–Caspian species. *Trends in Ecology & Evolution,* 15.2, 62-65.

Rixon, C. A., Duggan, I. C., Bergeron, N. M., Ricciardi, A., & Macisaac, H. J. (2005). Invasion risks posed by the aquarium trade and live fish markets on the Laurentian Great Lakes. *Biodiversity and Conservation,* 14.6, 1365-1381.

Santana, J., Porto, M., Reino, L., Moreira, F., Ribeiro, P. F., Santos, J. L., Rotenberry, J. & Beja, P. (2017). Using beta diversity to inform agricultural policies and conservation actions on Mediterranean farmland. *Journal of Applied Ecology,* 54.6, 1825-1835.

Sharpley, A., Foy, B., & Withers, P. (2000). Practical and Innovative Measures for the Control of Agricultural Phosphorus Losses to Water: An Overview. *Journal of Environment Quality,* 29.1, 1-9

Sickle, J. V. (2013). Estimating the risks of multiple, covarying stressors in the National Lakes Assessment. *Freshwater Science,* 32.1, 204-216.

Smith, V. H. (2003). Eutrophication of freshwater and coastal marine ecosystems a global problem. *Environmental Science and Pollution Research,* 10.2, 126-139.

Stevenson, R. J. (1998). Diatom Indicators of Stream and Wetland Stressors in a Risk Management Framework. *Monitoring Ecological Condition at Regional Scales,* 51.1-2, 107-118.

Stokes, E. J., Strindberg, S., Bakabana, P. C., Elkan, P. W., Iyenguet, F. C., Madzoké, B., Malanda G. A. F., Mowawa, B. S., Moukoumbou, C., Ouakabadio, F. K. & Rainey, H. J. (2010). Monitoring Great Ape and Elephant Abundance at Large Spatial Scales: Measuring Effectiveness of a Conservation Landscape. *PLoS ONE,* 5.4.

Tatters, A. O., Schnetzer, A., Xu, K., Walworth, N. G., Fu, F., Spackeen, J. L., Sipler R. E., Bertrand E. M., McQuaid, J. B., Allen, A. E., Bronk, D. A., Gao, K., Sun. J., Hutchins, D. A. (2018). Interactive effects of temperature, CO2 and nitrogen source on a coastal California diatom assemblage. *Journal of Plankton Research,* 40.2, 151-164.

Tews, J., Brose, U., Grimm, V., Tielbörger, K., Wichmann, M. C., Schwager, M., & Jeltsch, F. (2003). Animal species diversity driven by habitat heterogeneity/diversity: The importance of keystone structures. *Journal of Biogeography,* 31.1, 79-92.

Tharme, R. E. (2003). A global perspective on environmental flow assessment: Emerging trends in the development and application of environmental flow methodologies for rivers. *River Research and Applications,* 19.5-6, 397-441.

Whittaker, R. H. (1960). Vegetation of the Siskiyou Mountains, Oregon and California. *Ecological Monographs,* 30.4, 407-407.

Wilson, M. A., & Carpenter, S. R. (1999). Economic Valuation Of Freshwater Ecosystem Services In The United States: 1971–1997. *Ecological Applications,* 9.3, 772-783.

Winegardner, A. K., Legendre, P., Beisner, B. E., & Gregory-Eaves, I. (2017). Diatom diversity patterns over the past c. 150 years across the conterminous United States of America: Identifying mechanisms behind beta diversity. *Global Ecology and Biogeography,* 26.11, 1303-1315.

USEPA. 2016. National Lakes Assessment 2012: A Collaborative Survey of Lakes in the United States. EPA 841-R-16-113. U.S. Environmental Protection Agency, Washington, DC. https://nationallakesassessment.epa.g

Xu, W., Chen, G., Liu, C., & Ma, K. (2015). Latitudinal differences in species abundance distributions, rather than spatial aggregation, explain beta-diversity along latitudinal gradients. *Global Ecology and Biogeography,* 24.10, 1170-1180.

CHAPTER 4: BETA DIVERSITY IN BIRDS ONLY WEAKLY PREDICTED IN CLIMATIC VARIABLES

Chapter summary

Beta (between site) diversity is an understudied aspect of diversity. In particular, little is presently known about what factors can be used to predict it. While recent work has attempted to fill in that gap in our knowledge of diversity, most of those studies have focused on a single ecosystem or have used measures of β that are conflated with within-site (α) diversity. There is presently a dearth of large-scale biogeographic studies of the drivers of true β. This study seeks to ameliorate some of that shortfall by examining a large-scale bird dataset (eBird) over a seven year period from 2008 - 2014. To counteract possible conflation with α diversity, we constructed null models for β in bird neighborhoods across the conterminous United States using a measure of β that was found to be robust to error (Jaccard's dissimilarity). These nulls represented the amount of β that should have been present in a system simply due to differences in α. By comparing the null βs to the observed, we created β deviations which represent only real β without conflation from α. These β deviations were compared to a suite of environmental variables including mean annual temperature, precipitation and land use percentages amongst others. We regressed those variables against β deviations using an exhaustive collection of mixed effects models and model averaging. Our results indicate that climatic and land use variables can only weakly predict bird β deviations and those predictions change year to year. We found stronger, but still weak, regressions when using a conventional measure of β, indicating that our results were not an artifact of methodology. Our findings are consistent with previous research which found that bird diversity in general is heavily influenced by non-environmental factors such as evolutionary history and dispersal limitations. New studies are recommended using more dynamic environmental variables, to better match the mobility of the bird population and to confirm whether climatic and land use variables are ineffective predictors of bird β.

Keywords: Beta diversity, birds, Jaccard's dissimilarity, model averaging

Introduction

Biodiversity and its preservation are fundamental goals of conservation. However, to achieve those goals we must study the probable causes of biodiversity and we must know them for many systems. Birds represent one useful system for such study. Birds are among the most diverse organisms in the world and serve many vital functions. From their place in various food webs (Steinmetz et al., 2003; Woolhead 1994; Mooney and Linhart, 2006) to their role as seed dispersers (Ning et al., 2018; Nogales et al., 2012) they are thoroughly intertwined with the ecosystems they inhabit (Sekercioglu, 2006; Philpott et al., 2009). Their value is further enhanced through their simple charisma; few other organisms have inspired so much public interest and organizations supporting their wellbeing and documentation are plentiful (Bock 1997). As such the health and general ecology of bird populations throughout the world have long been a matter of some interest to ecologists (e.g. Chace and Walsh, 2006; Wiens, 1995; MacArthur and MacArthur, 1961; Chapin, 1923). Yet despite all the effort that has already been expended on bird ecology research, there is still much to learn. Fortunately, the advent of the digital age and citizen science has made those questions far more approachable by giving researchers access to observational data on a scale that would have been impossible a short time ago. Access to such data allows us to examine broader scale questions that have not previously been answerable. Many researchers have taken advantage of these new opportunities to both map out the diversity of birds and seek the origin of that diversity. For example, McCain (2009) found strong evidence for the effect of elevation and current climate on bird species richness and Aronson et al. (2014) found that urban environments decrease biodiversity in general but could still support endemic species. These carefully described patterns offer valuable insights into the structure and drivers of biodiversity in general. Keen interest from researchers such as these has yielded considerable insights into the biodiversity patterns of birds.

Presently, there are 9,993 species of birds across the globe (Jetz et al., 2014). Their geographic ubiquity and robust evolutionary history (Jetz et al., 2012) make them excellent subjects for broad-scale studies of diversity. Jetz et al. (2012) attempted to summarize what was known about bird diversity today and in the past. Interestingly, they found evidence of a strong latitudinal gradient to species richness, however that gradient varied in its descriptiveness based on the region it was observed in. This variation would seem to suggest a significant effect of evolutionary history on bird diversity. This observation was further supported by the high diversification rates that were predicted more by hemisphere (East – West) than by latitude, which implies that the Earth’s physical history is a major factor in modern species distributions. It is important to note, however, that this research was based around species richness, which is only one piece of the larger biodiversity puzzle.

Biodiversity is generally identified as a positive in ecology (Grime, 1998; Balmford et al. 2002). Though the arguments for its value vary from focuses on ecosystem services (Hooper et al., 2005) to intrinsic value (Angermeier, 2000), it is hard to name a reason why a conservationist or ecologist would ever want less of it. Thus, the measurement of diversity has been a focus of conservation efforts since the very advent of conservation as a science (Sheldon, 1969; Preston, 1948; Jaccard, 1912). Today biodiversity is often broken into more fundamental components, often using the framework first proposed by Robert Whittaker (1960). This framework takes the overall diversity of an ecosystem or neighborhood (γ) and divides it into two components: the average diversity of each site with the system (α) and the differences in community assemblage between sites (β). It is the addition or multiplication (Jost, 2007) of α and β that results in γ, thus to fully appreciate an ecosystems diversity you must account for both of its components. These components must also be kept separate, to avoid conflation. To this end Myers et al. (2013) proposed the calculation of β deviations which compare observed β to the expected β of a random community with the same α as the observed community. This method has been shown to detect patterns that were missed or contradicted in terrestrial vertebrates (Qian and Xiao, 2012) and similar hidden patterns may exist in birds as well.

This study seeks to contribute to the scientific understanding of bird diversity by examining the β for birds across the contiguous United States and attempting to discern the environmental factors that may drive it. To this end we use the unique eBird dataset compiled by the Cornell Lab of Ornithology. This dataset uses observational data collected from volunteers across the world. Detailed instructions are given on appropriate ways to sample and report findings, however the researchers for this dataset were not technicians or necessarily scientists. Rather they were simply people from any number of backgrounds united by their appreciation of birds and their desire to aid in their conservation. Using volunteers to compile vast datasets in this way has increasingly come to be known as “citizen science” (Silvertown, 2009). Because this approach is relatively new, exact information on its efficacy is not available, however the sheer scale of data provides a substantial buffer against sampling error. The distribution of data is concentrated mostly in North America, and especially in the United States and data has been collected since 2002. With such a large dataset, the danger posed by sampling error should be negligible as long as proper statistical methods are employed. To ensure that such methods are employed, eBird uses an automated filter followed by analysis by regional experts to vet all incoming data. These data are compared against known historical records and the ecology of each datum's geographic location to ensure that reports are feasible before they are uploaded to the main dataset.

The eBird dataset was created at a critical time for ecology in general and birds in particular. Recent trends in climate change appear to present an immediate threat to bird diversity (Jarzyna et al., 2016; Kissling et al., 2010). Additionally, many bird populations are imperiled by habitat destruction and pollution (Mortelliti et al., 2010; Zimmerling et al., 2013; Belskii, 2013; Eeva et al., 2012). With rapid climate change likely to continue for the foreseeable future (Easterling et al., 2000; Bakkenes et al., 2002) and industrialization continuing forward in many parts of the world (Alshuwaikhat, 2005) it is more important than ever to understand the diversity of organisms and how that diversity comes about. This study will seek to elucidate one aspect of diversity in birds in the hopes that it will be of use in predicting future bird diversity and, if necessary, adopting strategies to conserve as much of the current diversity as possible. Furthermore, since birds have been shown to act as indicators of overall biodiversity trends (Gregory et al., 2008; Gregory and Strein, 2010; Scholefield et al., 2011), the results of this study may extrapolate to β in general. The size of this dataset therefore offers unique opportunities to expand scientific knowledge of β and its drivers.

Methods

Our study used data for the conterminous United States from the eBird dataset compiled by the Cornell Lab of Ornithology using citizen science (eBird, 2007). This dataset collects observation data from volunteers using standardized methodology (Sullivan et al., 2009) to construct the largest database of bird occurrences in the world. Our data were pulled from January and July of each year from 2008 to 2014. We chose those months to capture the possible effect of migration on β diversity. The range was chosen to see if observed relationships were maintained between years in modern times. Each month and year were analyzed separately, so both annual and seasonal differences were evaluated.

Data for temperature and precipitation were obtained from the WorldClim raster database (Hijmans et al., 2005), net primary production (NPP) data was taken from Terra/MODIS (ORNL DAAC, 2018), elevation data were obtained from the National Elevation Dataset (NED)(National Elevation Dataset, 2002), land use data were taken from the GAP landcover dataset (US Geological Survey, 2011) and ecoregion data were taken from the World Wildlife Federation (WWF)(Olson et al., 2001). These variables were selected for the breadth of their coverage in datasets and for their established link to biodiversity, although mostly to α and γ diversity (Costanza et al., 2007; Sergio and Pedrini, 2007; Mayhew et al., 2012; Konar et al., 2010). For a full list of the variables pulled from these sources, see Table 4.1.

Birds data extracted from the eBirds dataset averaged over 200,000 sites; more than could be realistically analyzed in a full landscape-pairwise framework. Moreover, a fully pairwise approach, as is done in some smaller-scale studies, would have ascribed undue meaning to high β diversity between sites on opposite ends of the United States. To address both issues, the data were organized into a grid of 5472 cells of 0.5 x 0.5 degrees each and all datapoints within a cell were collapsed. Cell size was chosen based on preliminary work which suggested 0.5 x 0.5 degrees were the optimal dimension for capturing β. The majority of these grid cells were empty; many were from sparsely populated areas that had received no data, and still more were located over major bodies of water. The number of populated grid cells varied depending on the dataset ranged from 1199 to 1976. From there, a moving frame system was established that measured β between each grid cell and each of its neighbors, which could range from 1 to 8 depending on occupancy.

Mean pairwise β diversity was calculated using Jaccard's dissimilarity index within each neighborhood, which is relatively robust to sampling errors (Schroeder and Jenkins, 2018). Jaccard's dissimilarity is built around comparing two sites, necessitating this pairwise approach. Given the citizen science nature of these data, some sampling error was expected, however the methodologies were thorough enough that this was not believed to be a danger to the study, provided a robust measure was used. Additionally, because Jaccard's dissimilarity is based on presence-absence data the effect of errors in abundance counts was eliminated. Pairwise Jaccard's β was averaged for each of the neighborhoods defined by the moving frame, and its deviations were calculated. β deviations ((Observed – Mean Expected β)/Standard Deviations of β) were employed to properly decouple the γ and β. Essentially, β deviations compare the β measured in a system to the β expected of a random system with the same γ. They does this by holding constant the relative abundance of each species as well as the total occupancy of each site, but randomly redistributing the individuals within the system. Thus, the only thing left to vary is the relative abundance local to each site, which in turn is the source of any deviations in β. This process produces a number that reflects the extent of community heterogeneity that is not a result of γ and, thus, better reflects the actual β within a system (Myers et al., 2013). β deviations, once calculated, were mapped for visual assessment.

Our analysis excluded some grid cells due to their isolation preventing a nearest neighbor from being available for comparison. Other sites were excluded due to incomplete data in one or more variable set. After exclusions, the data analyzed for this study ranged from 724 to 1832 grid cells (Table 4.2). The high variance between datasets is mainly due to differences in the amount of data collected between years, and with a trend towards more data being available in more recent years (Table 4.2).

We processed the environmental variables through the same moving frame system as the bird occurrence data, this time with the means and standard deviations of each neighborhood being calculated for all continuous variables. Means provide a general overview of a neighborhood's environmental conditions, while standard deviations compare local effects; including both allows for consideration of conditions at multiple scales within a community. Furthermore, standard deviations provide valuable insights into environmental heterogeneity. We scaled the data to ensure that the apparent impact of one variable was not arbitrarily higher than another. We then assigned longitude, latitude and ecoregion values to each neighborhood based on the location of the central grid cell. Once compiled, we tested the variables for collinearity using variance inflation factors (VIFs). These VIFs revealed that all temperature related variables, including solar radiation, were heavily collinear. We chose mean annual temperature, mean diurnal range and temperature seasonality to represent the group. Precipitation variables encountered the same problem and were reduced to mean annual precipitation and precipitation seasonality, which reduced VIFs to no more than 5. We chose these five variables partially because they reduced the VIFs to more acceptable levels, and partially to ensure that some element of temporal environmental volatility (mean diurnal range, temperature seasonality and precipitation seasonality, in this case) was included in the analysis. The remaining variables were found to be within accepted tolerances of collinearity.

Because we were performing exploratory analyses, and not testing specific hypotheses, we used a broad and inclusive approach. All possible additive mixed effect models were constructed, with ecoregions included as random effects to help account for the possibility of spatial autocorrelation. These models were tested against each other to determine their relative likelihood using corrected Aikaike information criterion (AICc). The lowest AICc was then subtracted from every other AICc to create ΔAICc's. According to Burnham and Anderson (2004) $\Delta AICc < 3$ indicates a highly probable model, and those between 4 and 7 indicate a model that is at least somewhat likely. Models with a ΔAICc above 7 have little to no chance of being explanatory. With that rule of thumb in mind, models with a ΔAICc score above 7 were excluded and the remainder were averaged. Model averaging creates average coefficient estimates for all the variables that appear in likely models and tests them for significance. From the results of our average models, we took the significant variables ($p \leq 0.05$) with the highest relative importance (≥ 0.85) and used them to construct final models. Those models were then evaluated for their adjusted pseudo-R^2 values, as measured by the MuMIn in package of R (Barton, 2018). Adjusted pseudo-R^2 values were used instead of R^2 values because these final models used mixed effects. Thus, the correlation values reported in the results are estimates. This process was repeated using conventional Jaccard dissimilarity in place of β deviations for comparison purposes.

Results

Significant models were found for most months regardless of whether means or standard deviations were used for environmental variables. None of the models (Tables 4.3 & 4) were found to be highly predictive, however most demonstrated some level of contribution to β deviation. Adjusted R^2 values ranged from 0.01 to 0.16 with most falling between 0.10 and 0.14. Selected models varied in their composition based on both month and type of environmental variable. No significant models were found for January 2013, January 2014 or July 2009 with standard deviations of environmental variables. Additionally, no model was found for January 2013 with means of environmental variables. Models constructed through conventional Jaccard dissimilarity tended to have higher pseudo-adjusted R^2 values (between 0.09 and 0.29) and only failed to produce a significant model once (January 2009) (Tables 4.5 & 6).

Visual assessment of β deviation distributions suggests that there were periods of rapid change in bird distributions. In January, the years 2012 to 2014 (Fig. 3.1) have β deviations nearly two orders of magnitude higher than any value seen in the remaining years. In July, the same phenomenon is observed in 2009, 2011 and 2014 (Fig. 3.2). It is, perhaps, worth noting that these years were also the years for which the worst performing models were found, and three of them produced no model at all. In the years where β deviations were relatively low, patterns appear to stable with higher deviations to the North in July and along the coasts in January. January and July within the same year did not appear to be closely related, especially relative to the same months between years. This result is expected, due to the large migratory population within the dataset.

Temperature (mean and seasonality) and mean precipitation dominated most models and negatively affected beta deviations (Table 4.3). Precipitation seasonality, though only occurring in a few models, also had a negative impact. Mean temperature seasonality had the largest averaged coefficients of any variable regardless of month or year. Its coefficients were highest in all but one model it appeared it and was greater than 0.45 five times. The magnitudes of its coefficients were especially remarkable given that the remaining variables never exceeded 0.41 in absolute value. Also of note, every significant mean environmental variable correlated negatively with β deviations, although many of those same variable correlated positively with conventional Jaccard's dissimilarity (Appendix C).

Data based on standard deviations of environmental variables were less consistent in the models they produced than mean environmental variables. The most common variable of interest was NPP, which occurred in 8 of the 11 significant models. Its effect was found to be positive in every instance where it was significant or nearly significant. The next most common variables were precipitation and precipitation seasonality, with 4 and 5 occurrences respectively. Interestingly, while their mean values were negatively correlated with β diversity, their standard deviations were positively correlated. The percent of land used for agriculture and the percent used for urban development each occurred four times and were negatively correlated with β each time. Full details about these models and their coefficients can be found in Appendix D.

Variables also differed in importance based on the month of observation. One especially noteworthy trend is that precipitation or precipitation seasonality occur in all but one of the standard deviation models in July but are nearly absent in January. This pattern suggests that precipitation is more important to beta deviations of birds in the summer months than in winter. Additionally, mean annual temperature was more often relevant in July than in January for mean environmental variables, occurring in only 2 years for January, but 7 for July. Finally, standard deviations of mean diurnal range was present in the January of three years. Its relationship with β deviations was positive each of those times.

Discussion

The findings of this study indicated no strong relationships between environmental variables and β deviations, in contrast to previous research done on terrestrial vertebrates (Qian and Xiao, 2012). We found slightly stronger models when examining traditional Jaccard's dissimilarity and different variables were emphasized depending on which measurement of β was used. Deviation-based analysis tended to favor more climatic variables like temperature seasonality and mean precipitation, while standard Jaccard's dissimilarity was most correlated with elevation, consistent with some previous findings (McCain, 2009; Jankowski et al., 2013). Furthermore, the directionality (sign) of the relationships between environmental variables and β often flipped depending on whether conventional or deviation-based analyses were used. The latter observation indicates that positive relationships found between bird β and environmental factors in other studies, may actually be artifacts of α.

A visual analysis of maps indicates that β deviations were highest to the North in July and along the coasts in January, however there were some years where deviations were uniformly high. The latter years corresponds with the weakest models found during this study. It is not immediately clear why some years have such higher deviations than others. Mathematically, the explanation appears to be a lower than usual standard deviation within the null models resulting in very small denominators, however it is not clear what would cause this to happen. One possible explanation relates back to the citizen science nature of data acquisition. Because there is no broad scale coordination of where data gets sampled, harsh weather conditions may have caused a greater spatial aggregation around relatively "pleasant" areas. January and July are important months when considering a partially migratory dataset, but conditions of extreme cold and heat may have affected volunteer sampling behavior during those times. Total sampling was not lower in these years and visually there does not appear to be greater aggregation than normal, however only one sampling incident and one occupied neighbor were necessary for a cell to appear occupied in our analysis. A further analysis of these years over all twelve months may be necessary to fully understand the patterns being witnessed in this study.

This study found that neither the β deviations nor the conventional βs of birds are easily predicted by climate, vegetation, land cover, or ecoregions. Nevertheless, there are a few noteworthy trends present in the data. First, it is apparent that β deviation is generated through different processes in the summer than in the winter. This observation is evidenced by the different variable that were present in January versus July models. It is, perhaps, noteworthy that there was greater difference between January and July when using standard deviations than when using means. For instance, in January the heterogeneity of mean diurnal temperature ranges is sometimes important, while this is never so in July. Meanwhile, mean values for such features as temperature and precipitation maintain the same approximate level of relevance in winter and summer. Mean environmental variables define neighborhoods in a broad sense, while standard deviations arise from among the details of the grid cells within a neighborhood. Thus, if standard deviation-based models are changing based on the month, fine-scale drivers of β fluctuate more over time than large-scale drivers. This finding is consistent with previous work done by Gambi et al. (2013) and Bernhart-Römermann et al. (2015), which found significant changes in predictive variables depending on the scale of analysis.

Another interesting finding was the generally negative relationship between mean temperature and precipitation values and β deviations. Previous work has suggested that this relationship should be positive (Qian and Xiao, 2012). Previous work in this field relied on baseline values of β, rather than β deviations, and a reanalysis of our data using unmodified Jaccard's dissimilarity index indeed showed many positive correlations between β and temperature and precipitation variables. However, these correlations changed dramatically on a year-to-year basis, even flipping signs in some cases. Because the coefficients were not high for any of these variables, it may simply be the relationship between temperature, precipitation and β is generally weak and susceptible to volatility.

The remaining difference between this work and previous studies is the focus organisms. It is possible that bird communities, being relatively mobile, are more susceptible to homogenization under favorable temperature conditions than less mobile organisms. It is also interesting that seasonality values produced negative correlations. Seasonality naturally pertains to heterogeneity, so the logical expectation is that would drive β higher. This apparent contradiction may be explained by different types of heterogeneity. Our study used the more conventional spatial β as our response variable, while seasonality represents temporal heterogeneity. It may be worth performing another analysis focusing on temporal β deviations to see if this relationship is reversed.

A likely reason that no highly correlated models were found is seen in the maps of β deviation (Figures 4.1 and 4.2). For both January and July there were found to be many instances of massive increases in β deviations through the years. The high deviation years for January and July did not usually correspond, suggesting these that these rapid increases in β deviation are happening within a span of six months or fewer. Outside of this study, other researchers have found bird communities change dramatically, and frequently, over time (Boulinier et al., 2001; Kampichler et al., 2014), especially in areas that have been affected by human encroachment and habitat fragmentation, which are both expanding in the US (McGuire et al., 2016). As such, it is not wholly surprising that accurate predictors are hard to identify among static environmental variables. Indeed, birds may simply be more adaptable and less tethered to environmental conditions than other organisms for which strong β deviation predictors have been found (e.g. Qiao et al., 2015; Murphy et al., 2015; Ch. 2). Of course, predictors for bird α diversity have been discovered in the past (McCain, 2009; Pastur et al., 2015; Aronson et al., 2014; Rompré et al., 2007), so bird diversity in a broad sense may still be predictable, but the rate at which birds are able to shuffle populations and assemble new communities may make β hard or even impossible to anticipate. Future research may benefit from focusing on more dynamic variables like the normalized difference vegetation index, which could be used to try and relate changes in bird communities with changes in vegetation cover.

Our results also differed from the results of Melo et al. (2009), which found that bird β is largely driven by differences in elevation. Our own study rarely found any significance to elevation differences as a factor. This difference likely stems from differences in method. A reexamination of our own data focusing only on Jaccard ~ standard deviation of elevation + (1|ecoregion) found a significant, positive correlation for all months and years (Appendix E). This secondary analysis still differs in some ways from the analysis in Melo et al. (2009) (e.g. no regression trees, different approach to spatial autocorrelation), but these results suggest the main difference between our findings is a product of use of deviations over conventional Jaccard dissimilarity. Though our results cannot be used to draw conclusions on the data used in Melo et al. (2009), within our own data it suggests that the apparent effect of elevational differences on β is actually the result of differences in α between sites at different elevations. This finding helps to illustrate the very different results that can emerge when using deviations to represent β.

Another matter of note in our results is a particular commonality between all of the most relevant variables: they were all based on climate or NPP (which is strongly affected by climate). Though variables such as elevation, longitude and latitude were included, they were almost never significant contributors to our models. Elevation was present in most models that used conventional Jaccard's dissimilarity, but its absence in most deviation-based models suggests it is actually the lower α of high elevation sites that is driving this trend. Locality variables are important to modern conservation because they are static and will remain so even in the face future climate change. Were they found to be significant contributors to β it would have offered some hope that they might have a stabilizing effect on bird diversity in general, with the caveat that latitude is also correlated with climatic variables. However, climate related variables were only weakly correlated with β deviations to begin with, so the effects of climate change may not be very acute. Indeed, our findings offer some hope that at least one aspect of bird diversity will be relatively insensitive to climate change, although we would caution that the likely effects on α are still negative (Kissling et al., 2010; Jaryzna et al., 2016). Conversely, it may be fortunate that the correlation between β deviations and temperature and precipitation variables was not very high, as that suggests there may be other factors not included in this study that will supply that buffering effect and will be more useful in predicting β.

The possibility that bird β may be robust to climate change is not the only meaningful insight given by the low pseudo-R^2 values of our models. The variables we chose represented a fairly wide spectrum of factors that have been shown to affect beta diversity in other organisms and systems (e.g. Hillebrand et al., 2010; Zhang et al., 2014; McCain, 2009; Fugère et al., 2009), although that research did not use deviations. Temperature and precipitation, in particular, are thought of as biodiversity predictors for a wide variety of organisms (Kreft and Jetz, 2007; Olff et al., 2002; Rohde, 1992), and the effects of land-use are very well documented in the literature (Fugère et al., 2016; Newbold et al., 2016; Edge et al., 2016). Yet none of these variables could strongly predict β deviations in birds. One possible implication of this finding is that bird β deviations simply aren't driven by the environment. As found in Jetz et al. (2012), bird diversity appears to be very strongly associated with evolution. Obviously, that's true to some extent in every group, but in the case of birds it's strong enough to create an East – West gradient that has no obvious basis in climate, nutrients or weather patterns. The findings of this paper seem to suggest that birds, with their relatively low generation time and unparalleled mobility among vertebrates can simply find new habitats or adapt to old ones as the need emerges. In fact, there is an existing body of work that suggests β in highly mobile, actively dispersing organisms like fish (Griffiths, 2017) or, indeed, birds (Cáceres et al., 2014) is more affected by dispersal limitations than climate or the variation thereof. Truthfully, the survivability of birds should come as no great surprise; they survived the last mass extinction through a process of dramatic adaptation (Xu et al., 2014), so it would not be unprecedented for them to do so again. However even if the *Aves* class survives as a whole, individual species of bird (especially flightless ones) may be susceptible to climate change and efforts should still be made to preserve individual species on principle, if nothing else.

There are other possible interpretations to our findings. The absence of one trend, after all, does not prove the presence of another. While our lack of strongly correlated models may be explained by an independence of bird β from environmental factors, it is also possible that the data we used were simply too flawed to be used for this kind of research. While all of the data used were vetted by experts, they were still collected by volunteers. Indeed, the variability in β deviations over time (as represented in our maps) may be an indicator of quality issues in the data. Alternatively, if the data is not at fault, then perhaps the patterns we observed in β deviations were being driven by biotic interactions, rather than the environment or dispersal. Biotic interactions are hard to quantify and therefore hard to incorporate into models, however further research using food webs may elucidate any possible relationship.

With current trends in ecology and human development conserving biodiversity is more important than ever. To be successful in this endeavor we must understand the factors that contribute to that diversity. To that end our study sought to identify the critical predictors of an understudied aspect of diversity in bird communities: β diversity. Though none of the models were able to predict β strongly, they were able to identify several key trends in modern bird diversity. Understanding these trends and building on them to better predict β will be critical in the near future for those wishing to protect bird communities. Our data suggests a national bird population that is largely robust to changes in climate and land-use, however that should not be taken as an excuse to deprioritize bird conservation. Though it seems β deviations are likely to remain unaffected by future conditions, that only accounts for half of bird diversity. Previously established links between bird α and habitat degradation and climate change are very serious concerns and the conservation of bird diversity should remain a top priority for conservation.

Tables and Figures

Table 4.1 All variables used before elimination through VIFs analysis. Asterisks mark the variables that were retained after VIFs analysis.

Variable	**Source**
Average annual wind speed*	Worldclim
Solar radiation (kJ m^{-2} day^{-1}) *	
Water vapor pressure (kPa)*	
Mean temperature*	Worldclim::Bioclim
Mean diurnal range of temperature*	
Isothermality (Mean temp./Annual temp range)	
Temperature seasonality (SD of temp/time)*	
Maximum temperature	
Minimum temperature	
Temperature of wettest month	
Temperature of driest month	
Temperature of warmest month	
Temperature of coldest month	
Precipitation*	
Precipitation of wettest month	
Precipitation of driest month	
Precipitation seasonality (SD of precip./time)*	
Precipitation of wettest quarter	
Precipitation of driest quarter	
Precipitation of warmest month	
Precipitation of coldest month	
Net Primary Production*	Terra/MODIS
Elevation*	National elevation dataset
Percent of urban development*	GAP landcover dataset
Percent of agriculture*	
Percent of water	
Percent of disturbed habitat	
Percent of land with introduced species	
Ecoregion*	World Wildlife Fund

Table 4.2 The number of grid cells used for each dataset in the final analysis

Dataset	Grid cells used
January 2008	1077
January 2009	802
January 2010	789
January 2011	781
January 2012	1087
January 2013	1122
January 2014	1154
July 2008	724
July 2009	1097
July 2010	834
July 2011	880
July 2012	1085
July 2013	1832
July 2014	1114

Table 4.3 Top three variables and their coefficients for models based on β deviations and mean environmental variables. Fields with fewer than three top variables listed had fewer than three variables for the entire model. In the event of a tie, both are listed. Pseudo-adjusted R^2 (P-adj. R^2) scores are completed models (Appendix D).

Year	**January**	**P-adj. R^2**	**July**	**P-adj. R^2**
2008	(-0.661) Temp. seasonality (-0.367) Elevation (-0.294) Precip. (-0.294) Mean temp.	**0.208**	(-0.269) Temp. seasonality	**0.101**
2009	(-0.457) Temp. seasonality (-0.326) Precip. (-0.298) Elevation	**0.173**	(-0.283) Mean temp. (-0.240) Elevation (-0.223) Temp. seasonality	**0.049**
2010	(-0.516) Temp. seasonality (-0.288) Elevation (-0.284) Precip. (-0.284) Precip. seasonality	**0.118**	(-0.536) Temp. seasonality (-0.407) Mean temp. (-0.135) Precip.	**0.164**
2011	(-0.279) Temp. seasonality (-0.180) Precip.	**0.081**	(-0.377) Temp. seasonality (-0.233) Mean temp.	**0.105**
2012	(-0.220) Temp. seasonality	**0.042**	(-0.378) Temp. seasonality (-0.292) Mean diurnal range (-0.247) Mean temp.	**0.146**
2013	N/A	**N/A**	(-0.450) Temp. seasonality (-0.342) Mean temp. (-0.184) Mean diurnal range	**0.165**
2014	(-0.167) Temp. seasonality (-0.127) NPP (-0.107) Elevation	**0.068**	(-0.283) Mean temp. (-0.250) Temp. seasonality	**0.080**

Table 4.4 Top three variables and their coefficients for models based on β deviations and standard deviations of environmental variables. Fields with fewer than three top variables listed had fewer than three variables for the entire model. In the event of a tie, both are listed. Pseudo-adjusted R^2 (P-adj. R^2) scores are completed models (Appendix D).

Year	**January**	**P-adj. R^2**	**July**	**P-adj. R^2**
2008	(0.196) Mean diurnal range (-0.139) Percent agriculture (0.119) Wind avg.	**0.135**	(-0.183) Percent agriculture (0.140) NPP	**0.102**
2009	(0.169) Wind avg. (0.159) NPP (-0.156) Percent urban	**0.154**	N/A	**N/A**
2010	(-0.129) Percent urban (0.126) NPP (-0.114) Precip. Seasonality	**0.080**	(0.195) Precip. seasonality (0.184) NPP (0.152) Precip.	**0.163**
2011	(0.230) Mean diurnal range (-0.150) Elevation (-0.133) Percent agriculture	**0.147**	(0.157) Wind avg. (0.135) Precip. seasonality (-0.099) Percent agriculture	**0.110**
2012	(0.137) Mean diurnal range	**0.014**	(0.163) NPP (0.150) Precip. (-0.135) Percent urban	**0.128**
2013	N/A	**N/A**	(0.219) Precip. (0.170) NPP (0.112) Precip. seasonality	**0.162**
2014	N/A	**N/A**	(0.194) Precip. (0.102) Precip. seasonality	**0.089**

Table 4.5 Top three variables and their coefficients for models based on Jaccard's dissimilarity and mean environmental variables. Fields with fewer than three top variables listed had fewer than three variables for the entire model. In the event of a tie, both are listed. Pseudo-adjusted R^2 (P-adj. R^2) scores are completed models (Appendix D).

Year	**January**	**P-adj. R^2**	**July**	**P-adj. R^2**
2008	(0.284) Elevation (0.272) Precip. seasonality (0.253) Temp. seasonality	**0.207**	(0.309) Temp. seasonality (0.250) Elevation (0.149) Precip. seasonality	**0.129**
2009	(-0.385) Mean temp. (0.260) Mean diurnal range (0.223) Precip. seasonality	**0.266**	(0.298) Elevation (0.258) Precip. seasonality	**0.219**
2010	(-0.236) Mean temp. (0.210) Mean diurnal range	**0.094**	(0.318) Elevation (0.198) Temp. seasonality (0.172) Precip. seasonality	**0.182**
2011	(0.331) Elevation	**0.113**	(0.358) Precip. seasonality (0.223) Temp. seasonality (0.201) Elevation	**0.221**
2012	(0.399) Elevation (0.224) Precip. seasonality (0.202) Precip.	**0.168**	(0.302) Elevation (0.210) Precip. seasonality	**0.238**
2013	(-0.291) Mean temp. (-0.237) NPP (0.197) Elevation	**0.270**	(0.249) Elevation (0.199) Precip. seasonality (-0.144) NPP	**0.289**
2014	(0.337) Elevation (0.217) Temp. seasonality (0.211) Precip. seasonality	**0.213**	(0.232) Elevation (0.202) NPP (-0.132) Precip. seasonality	**0.243**

Table 4.6 Top three variables and their coefficients for models based on Jaccard's dissimilarity and standard deviations of environmental variables. Fields with fewer than three top variables listed had fewer than three variables for the entire model. In the event of a tie, both are listed. Pseudo-adjusted R^2 (P-adj. R^2) scores are completed models (Appendix D).

Year	**January**	**P-adj. R^2**	**July**	**P-adj. R^2**
2008	(-0.184) NPP (0.142) Elevation (0.137) Percent urban	**0.142**	(0.171) Elevation (-0.155) Average wind (0.153) Percent urban (-0.153) NPP	**0.161**
2009	(0.188) Elevation (-0.167) Average wind (0.142) Percent urban	**0.169**	(0.157) Elevation (0.144) Percent urban (0.122) Precip. seasonality	**0.146**
2010	(-0.179) NPP (0.179) Percent urban (0.156) Precip. seasonality	**0.102**	(0.142) Percent agriculture (0.115) Percent urban	**0.092**
2011	(0.220) Precip. seasonality (-0.162) NPP (0.135) Percent urban	**0.109**	(0.137) Percent urban (-0.117) Average wind (0.112) Percent disturbed	**0.114**
2012	(0.168) Precip. seasonality (-0.134) NPP (0.103) Percent urban	**0.084**	(0.166) Percent urban (-0.153) Average wind (0.122) Precip. seasonality	**0.143**
2013	(0.237) Precip. seasonality (0.182) Elevation (-0.176) NPP	**0.162**	(0.262) Percent urban (0.262) Precip. seasonality (0.215) Elevation	**0.262**
2014	(0.276) Precip. seasonality (0.197) Percent urban (0.148) Percent water	**0.205**	(0.284) Elevation (0.189) Precip. seasonality (0.133) Percentage urban	**0.176**

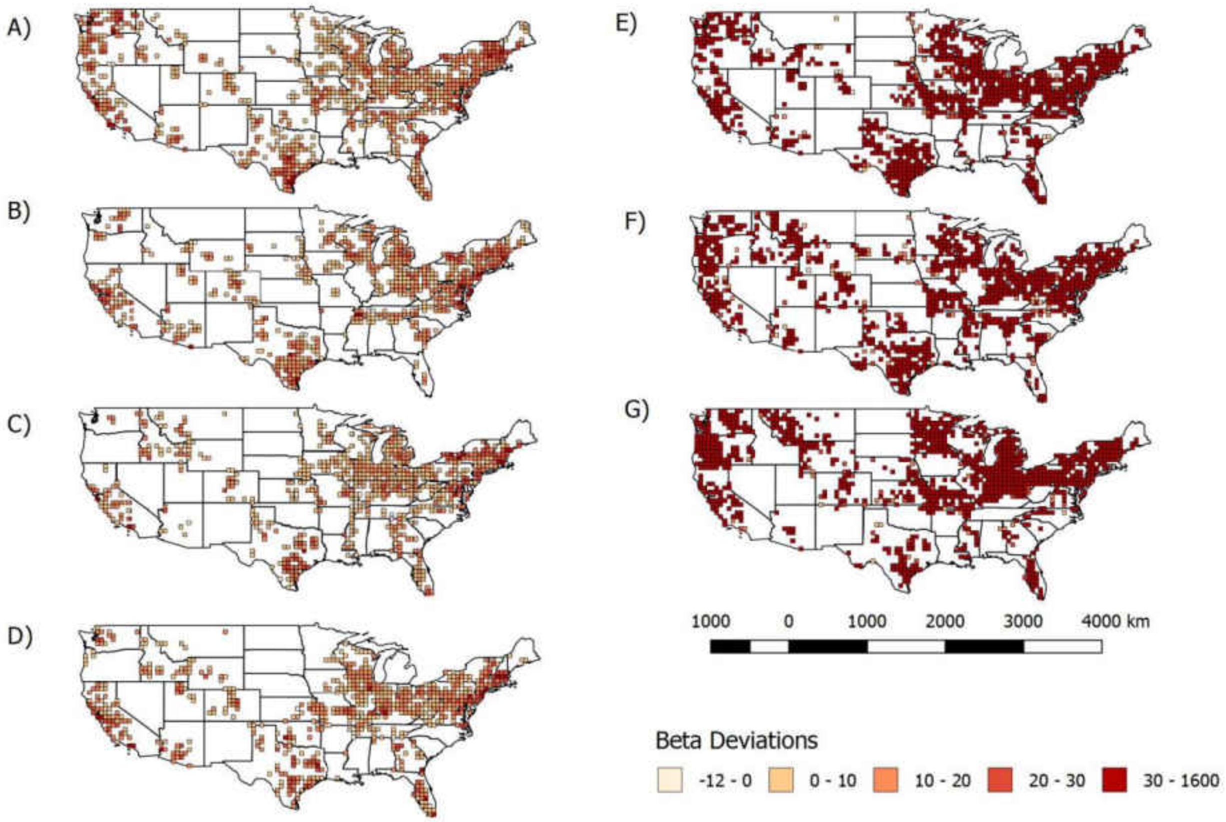

Figure 4.1 Beta deviations for all years (2008-2014) in January. For years 2008 – 2011 (A – D) β deviations are highest along the west coast, in the Northeast and in the south of Texas. For years 2012-2014 (E – G) β deviations are much higher and evenly distributed across the US.

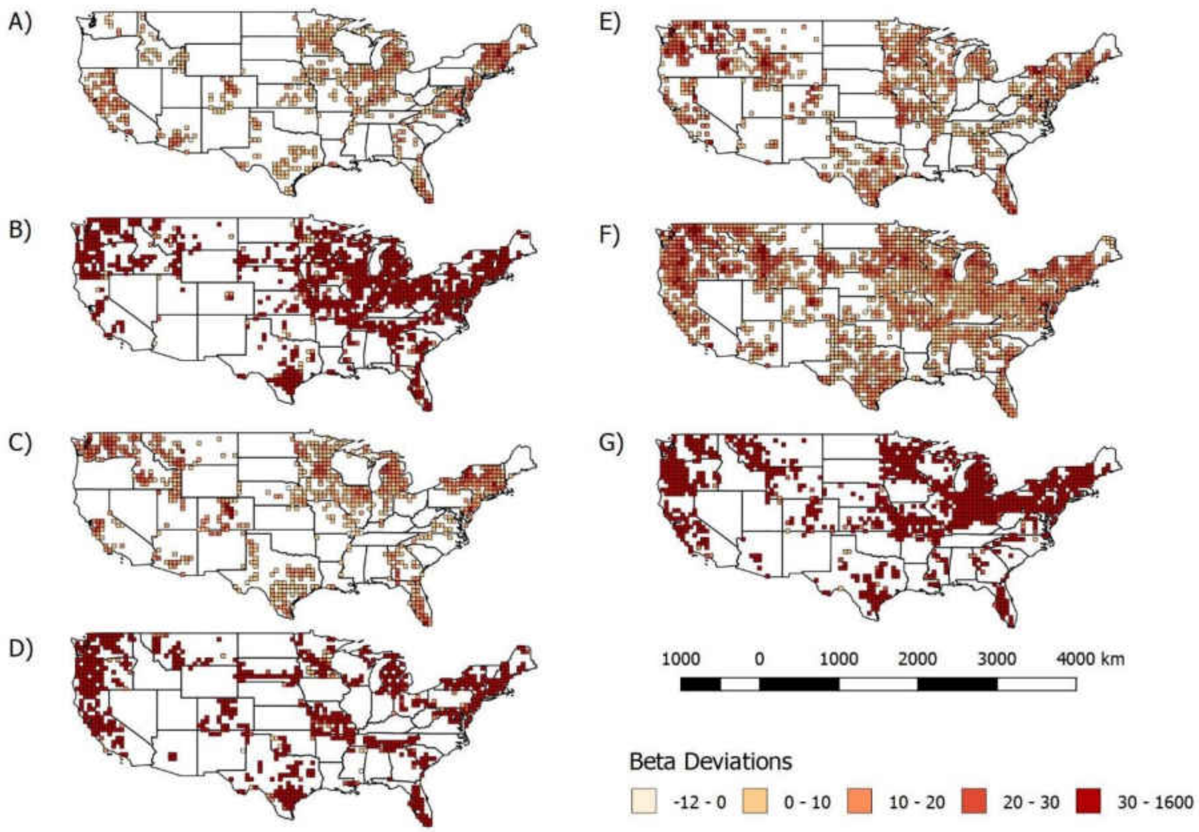

Figure 4.2 Beta deviations in July from 2008 - 2014. For years 2008, 2010, 2012 and 2013 (A, C, E and F), β deviations tend to be highest in the North. The years 2009, 2011 and 2014 (B, D and G) show uniformly high deviations across the US.

References

Alshuwaikhat, H. M. (2005). Strategic environmental assessment can help solve environmental impact assessment failures in developing countries. *Environmental Impact Assessment Review,* 25.4, 307-317.

Angermeier, P. L. (2000). The Natural Imperative for Biological Conservation. *Conservation Biology,* 14.2, 373-381.

Aronson, M. F., Sorte, F. A., Nilon, C. H., Katti, M., Goddard, M. A., Lepczyk, C. A., . . . Winter, M. (2014). A global analysis of the impacts of urbanization on bird and plant diversity reveals key anthropogenic drivers. *Proceedings of the Royal Society B: Biological Sciences,* 281.1780.

Bakkenes, M., Alkemade, J. R., Ihle, F., Leemans, R., & Latour, J. B. (2002). Assessing effects of forecasted climate change on the diversity and distribution of European higher plants for 2050. *Global Change Biology,* 8.4, 390-407.

Balmford, A. (2002). Ecology - Economic Reasons for Conserving Wild Nature. *Science,* 297.5583, 950-953.

Barton, K. (2018). MuMIn: Multi-Model Inference. R package version 1.40.4. https://CRAN.R-project.org/package=MuMIn

Belskii, E. A., & Belskaya, E. A. (2013). Bird population in birch forests of the Southern Urals affected by industrial pollution: Report 1. Reactions of species and the community. *Contemporary Problems of Ecology,* 6.3, 315-322.

Bernhardt-Römermann, M., Baeten, L., Craven, D., Frenne, P. D., Hédl, R., Lenoir, J., Bert, D., Brunet, J., Chudomelová, M., Decocq, G., Dierschke, H., Dirnböck, T., Dörfler, I., Heinken, T., Hermy, M., Hommel, P., Jaroszewicz, B., Keczynski, A., Kelly, D., Kirby, K., Kopecky, M., Macek, M., Malis, F., Mirtl, M., Mitchell, F., Naaf, T., Newman, M., Peterken, G., Petrik, P., Schmidt, W., Standovár, T., Tóth, Z., Van Calster, H., Verstraeten, G., Vladovic, J., Vild, O., Wulf, M. & Verheyen, K. (2015). Drivers of temporal changes in temperate forest plant diversity vary across spatial scales. *Global Change Biology,* 21.10, 3726-3737.

Bock, C. E. (1997). The Role of Ornithology in Conservation of the American West. *The Condor,* 99.1, 1-6.

Boulinier, T., Nichols, J. D., Hines, J. E., Sauer, J. R., Flather, C. H., & Pollock, K. H. (2001). Forest Fragmentation and Bird Community Dynamics: Inference at Regional Scales. *Ecology,* 82.4, 1159-1169

Cáceres, N. C., Dambros, C. S., Melo, G. L., Sponchiado, J., Della-Flora, F., & Moura, M. O. (2014). Local randomness, vegetation type and dispersal drive bird and mammals diversity in a tropical South American region. *Ecosphere,* 5.9.

Chace, J. F., & Walsh, J. J. (2006). Urban effects on native avifauna: A review. *Landscape and Urban Planning,* 74.1, 46-69.

Chapin, J. P. (1923). Ecological Aspects of Bird Distribution in Tropical Africa. *The American Naturalist,* 57.649, 106-125.

Costanza, R., Fisher, B., Mulder, K., Liu, S., & Christopher, T. (2007). Biodiversity and ecosystem services: A multi-scale empirical study of the relationship between species richness and net primary production. *Ecological Economics,* 61.2-3, 478-491.

Easterling, D. R., Meehl, G. A., Parmesan, C., Changnon, S. A., Karl, T. R., & Mearns, L. O. (2000). Climate Extremes: Observations, Modeling, and Impacts. *Science,* 289.5487, 2068-2074.

eBird. 2012. eBird: An online database of bird distribution and abundance [web application]. eBird, Ithaca, New York. Available: http://www.ebird.org. (Accessed: Date [e.g., February 2, 2012]).

Edge, C. B., Fortin, M., Jackson, D. A., Lawrie, D., Stanfield, L., & Shrestha, N. (2016). Habitat alteration and habitat fragmentation differentially affect beta diversity of stream fish communities. *Landscape Ecology,* 32.3, 647-662.

Eeva, T., Belskii, E., Gilyazov, A. S., & Kozlov, M. V. (2012). Pollution impacts on bird population density and species diversity at four non-ferrous smelter sites. *Biological Conservation,* 150.1, 33-41.

Fugère, V., Kasangaki, A., & Chapman, L. J. (2016). Land use changes in an afrotropical biodiversity hotspot affect stream alpha and beta diversity. *Ecosphere,* 7.6.

Gambi, C., Pusceddu, A., Benedetti-Cecchi, L., & Danovaro, R. (2013). Species richness, species turnover and functional diversity in nematodes of the deep Mediterranean Sea: Searching for drivers at different spatial scales. *Global Ecology and Biogeography,* 23.1, 24-39.

Gregory, R. D., Vořišek, P., Noble, D. G., Strien, A. V., Klvaňová, A., Eaton, M., . . . Burfield, I. J. (2008). The generation and use of bird population indicators in Europe. *Bird Conservation International,* 18.S1. S223-S244

Gregory, R. D., & Strien, A. V. (2010). Wild Bird Indicators: Using Composite Population Trends of Birds as Measures of Environmental Health. *Ornithological Science,* 9.1, 3-22.

Griffiths, D. (2017). Connectivity and vagility determine beta diversity and nestedness in North American and European freshwater fish. *Journal of Biogeography,* 44.8, 1723-1733.

Grime, J. P. (1998). Benefits of plant diversity to ecosystems: Immediate, filter and founder effects. *Journal of Ecology,* 86.6, 902-910.

Hijmans, R.J., S.E. Cameron, J.L. Parra, P.G. Jones & Jarvis, A. (2005) Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology* 25, 1965-1978

Hillebrand, H., Soininen, J., & Snoeijs, P. (2010). Warming leads to higher species turnover in a coastal ecosystem. *Global Change Biology,* 16.4, 1181-1193.

Hooper, D. U., Chapin, F. S., Ewel, J. J., Hector, A., Inchausti, P., Lavorel, S., Lawton, J. H., Lodge, D. M., Loreau, M., Naeem, S., Schmid, B., Setälä, H., Symstad, A. J., Vandermeer, J. & Wardle, D. A. (2005). Effects Of Biodiversity On Ecosystem Functioning: A Consensus Of Current Knowledge. *Ecological Monographs,* 75.1, 3-35.

Jaccard, P. (1912). The Distribution Of The Flora In The Alpine Zone.1. *New Phytologist,* 11.2, 37-50.

Jankowski, J. E., Merkord, C. L., Rios, W. F., Cabrera, K. G., Revilla, N. S., & Silman, M. R. (2012). The relationship of tropical bird communities to tree species composition and vegetation structure along an Andean elevational gradient. *Journal of Biogeography,* 40.5, 950-962.

Jarzyna, M. A., Zuckerberg, B., Finley, A. O., & Porter, W. F. (2016). Synergistic effects of climate and land cover: Grassland birds are more vulnerable to climate change. *Landscape Ecology,* 31.10, 2275-2290.

Jetz, W., Thomas, G. H., Joy, J. B., Hartmann, K., & Mooers, A. O. (2012). The global diversity of birds in space and time. *Nature,* 491.7424, 444-448.

Jetz, W., Thomas, G., Joy, J., Redding, D., Hartmann, K., & Mooers, A. (2014). Global Distribution and Conservation of Evolutionary Distinctness in Birds. *Current Biology,* 24.9, 919-930.

Jost, L. (2007). Partitioning Diversity Into Independent Alpha And Beta Components. *Ecology,* 88.10, 2427-2439.

Kampichler, C., Angeler, D. G., Holmes, R. T., Leito, A., Svensson, S., Jeugd, H. P., & Wesołowski, T. (2014). Temporal dynamics of bird community composition: An analysis of baseline conditions from long-term data. *Oecologia,* 175.4, 1301-1313.

Kissling, W. D., Field, R., Korntheuer, H., Heyder, U., & Bohning-Gaese, K. (2010). Woody plants and the prediction of climate-change impacts on bird diversity. *Philosophical Transactions of the Royal Society B: Biological Sciences,* 365.1549, 2035-2045.

Konar, M., Muneepeerakul, R., Azaele, S., Bertuzzo, E., Rinaldo, A., & Rodriguez-Iturbe, I. (2010). Potential impacts of precipitation change on large-scale patterns of tree diversity. *Water Resources Research,* 46.11.

Kreft, H., & Jetz, W. (2007). Global patterns and determinants of vascular plant diversity. *Proceedings of the National Academy of Sciences,* 104.14, 5925-5930.

Li, N., Wang, Z., Li, X., & Li, Z. (2018). Bird functional traits affect seed dispersal patterns of China's endangered trees across different disturbed habitats. *Avian Research,* 9.1.

MacArthur, R. H., & MacArthur, J. W. (1961). On Bird Species Diversity. *Ecology,* 42.3, 594-598.

Mayhew, P. J., Bell, M. A., Benton, T. G., & Mcgowan, A. J. (2012). Biodiversity tracks temperature over time. *Proceedings of the National Academy of Sciences,* 109.38, 15141-15145.

McCain, C. M. (2009). Global analysis of bird elevational diversity. *Global Ecology and Biogeography,* 18.3, 346-360.

McGuire, J. L., Lawler, J. J., Mcrae, B. H., Nuñez, T. A., & Theobald, D. M. (2016). Achieving climate connectivity in a fragmented landscape. *Proceedings of the National Academy of Sciences,* 113.26, 7195-7200.

Melo, A. S., Thiago Fernando L. V. B. Rangel, & Diniz-Filho, J. A. (2009). Environmental drivers of beta-diversity patterns in New-World birds and mammals. *Ecography,* 32.2, 226-236.

Mooney, K. A., & Linhart, Y. B. (2006). Contrasting cascades: Insectivorous birds increase pine but not parasitic mistletoe growth. *Journal of Animal Ecology,* 75.2, 350-357.

Mortelliti, A., Fagiani, S., Battisti, C., Capizzi, D., & Boitani, L. (2010). Independent effects of habitat loss, habitat fragmentation and structural connectivity on forest-dependent birds. *Diversity and Distributions,* 16.6, 941-951.

Murphy, S. J., Audino, L. D., Whitacre, J., Eck, J. L., Wenzel, J. W., Queenborough, S. A., & Comita, L. S. (2015). Species associations structured by environment and land-use history promote beta-diversity in a temperate forest. *Ecology,* 96.3, 705-715.

National Elevation Dataset; 2002; Web site; U.S Geological Survey

Newbold, T., Hudson, L.N., Hill, S.L., Contu, S., Gray, C.L., Scharlemann, J.P., Börger, L., Phillips, H.R., Sheil, D., Lysenko, I. & Purvis, A. (2016). Global patterns of terrestrial assemblage turnover within and among land uses. *Ecography,* 39.12, 1151-1163.

Nogales, M., Heleno, R., Traveset, A., & Vargas, P. (2012). Evidence for overlooked mechanisms of long-distance seed dispersal to and between oceanic islands. *New Phytologist,* 194.2, 313-317.

Olff, H., Ritchie, M. E., & Prins, H. H. (2002). Global environmental controls of diversity in large herbivores. *Nature,* 415.6874, 901-904.

Olson, D. M., Dinerstein, E., Wikramanayake, E. D., Burgess, N. D., Powell, G. V. N., Underwood, E. C., D'Amico, J. A., Itoua, I., Strand, H. E., Morrison, J. C., Loucks, C. J., Allnutt, T. F., Ricketts, T. H., Kura, Y., Lamoreux, J. F., Wettengel, W. W., Hedao, P., Kassem, K. R. (2001) Terrestrial ecoregions of the world: a new map of life on Earth. *Bioscience,* 51.11, 933-938

ORNL DAAC 2018. MODIS and VIIRS Land Products Global Subsetting and Visualization Tool. ORNL DAAC, Oak Ridge, Tennessee, USA. Accessed Aug. 1, 2018. Subset obtained for MOD17A2 from 2008 - 2014.

Pastur, G. M., Lencinas, M. V., Gallo, E., Cruz, M. D., Borla, M. L., Esteban, R. S., & Anderson, C. B. (2015). Habitat-specific vegetation and seasonal drivers of bird community structure and function in southern Patagonian forests. *Community Ecology,* 16.1, 55-65.

Philpott, S. M., Soong, O., Lowenstein, J. H., Pulido, A. L., Lopez, D. T., Flynn, D. F., & Declerck, F. (2009). Functional richness and ecosystem services: Bird predation on arthropods in tropical agroecosystems. *Ecological Applications,* 19.7, 1858-1867.

Preston, F. W. (1948). The Commonness, And Rarity, of Species. *Ecology,* 29.3, 254-283.

Qian, H., & Xiao, M. (2012). Global patterns of the beta diversity–energy relationship in terrestrial vertebrates. *Acta Oecologica,* 39, 67-71.

Qiao, X., Jabot, F., Tang, Z., Jiang, M., & Fang, J. (2015). A latitudinal gradient in tree community assembly processes evidenced in Chinese forests. *Global Ecology and Biogeography,* 24.3, 314-323.

Rohde, K. (1992). Latitudinal Gradients in Species Diversity: The Search for the Primary Cause. *Oikos,* 65.3, 514.

Rompré, G., Robinson, W. D., Desrochers, A., & Angehr, G. (2007). Environmental correlates of avian diversity in lowland Panama rain forests. *Journal of Biogeography,* 34.5, 802-815.

Scholefield, P., Firbank, L., Butler, S., Norris, K., Jones, L. M., & Petit, S. (2011). Modelling the European Farmland Bird Indicator in response to forecast land-use change in Europe. *Ecological Indicators,* 11.1, 46-51.

Sekercioglu, C. (2006). Increasing awareness of avian ecological function. *Trends in Ecology & Evolution,* 21.8, 464-471.

Sergio, F., & Pedrini, P. (2007). Biodiversity gradients in the Alps: The overriding importance of elevation. *Biodiversity and Conservation in Europe Topics in Biodiversity and Conservation,* 16.12, 1-12.

Sheldon, A. L. (1969). Equitability Indices: Dependence on the Species Count. *Ecology,* 50.3, 466-467.

Silvertown, J. (2009). A new dawn for citizen science. *Trends in Ecology & Evolution,* 24.9, 467-471.

Steinmetz, J., Kohler, S. L., & Soluk, D. A. (2003). Birds Are Overlooked Top Predators In Aquatic Food Webs. *Ecology,* 84.5, 1324-1328.

Sullivan, B.L., C.L. Wood, M.J. Iliff, R.E. Bonney, D. Fink, and S. Kelling. 2009. eBird: a citizen-based bird observation network in the biological sciences. Biological Conservation 142: 2282-2292.

Terradas, J., Salvador, R., Vayreda, J., & Lloret, F. (2004). Maximal species richness: An empirical approach for evaluating woody plant forest biodiversity. *Forest Ecology and Management,* 189.1-3, 241-249.

US Geological Survey, Gap Analysis Program (GAP). May 2011. National Land Cover, Version 2

Whittaker, R. H. (1960). Vegetation of the Siskiyou Mountains, Oregon and California. *Ecological Monographs,* 30.4, 279-338.

Wiens, J. A. (1995). Habitat fragmentation: Island v landscape perspectives on bird conservation. *Ibis,* 137.s1, S97-S104.

Woollhead, J. (1994). Birds in the trophic web of Lake Esrom, Denmark. *Aquatic Birds in the Trophic Web of Lakes,* 29-38.

Xu, X., Zhou, Z., Dudley, R., Mackem, S., Chuong, C., Erickson, G. M., & Varricchio, D. J. (2014). An integrative approach to understanding bird origins. *Science,* 346.6215, 1253293-1253293.

Zhang, Q., Hou, X., Li, F.Y., Niu, J., Zhou, Y., Ding, Y., Zhao, L., Li, X., Ma, W. & Kang, S. (2014). Alpha, Beta and Gamma Diversity Differ in Response to Precipitation in the Inner Mongolia Grassland. *PLoS ONE,* 9.3.

Zimmerling, J. R., Pomeroy, A. C., Dentremont, M. V., & Francis, C. M. (2013). Canadian Estimate of Bird Mortality Due to Collisions and Direct Habitat Loss Associated with Wind Turbine Developments. *Avian Conservation and Ecology,* 8(2).

CHAPTER 5: CONCLUSIONS

Summary

In this study I sought to answer a few critical questions about β. I used simulated datasets to compare error rates across multiple well-used β indices. The results of that study indicated that popular measures like Sorensen's dissimilarity are prone to inaccuracy when used on datasets with sampling error, casting doubt on the results of some previous studies. Meanwhile, several popular indices were supported as being robust to error, namely the Bray-Curtis and Jaccard's dissimilarity. These indices were then used to identify environmental variables that may be able to predict the β of a given system. The Bray-Curtis dissimilarity was used to analyze a lake diatom dataset and found that many of the positive drivers of β may actually be harmful for α and therefore γ. It also noted a strong effect of scale on which drivers were most relevant in predicting β. Jaccard's dissimilarity was used to assess a national bird dataset and found only weak correlations between commonly used environmental variables and bird β. From this, it was inferred that the β of birds is driven more by evolutionary history and dispersal limitations than the environment. Collectively, these findings should be a useful tool for researchers looking to incorporate β into their research efforts.

Lessons from simulated error rates

The major takeaway from the simulation of error rates in β diversity is the relative robustness Jaccard's dissimilarity for presence-absence data and Bray-Curtis dissimilarity for abundance data. Additionally, it was confirmed that high error rates can have large impacts on the measurement of β, and even low error rates can be problematic if using certain measurements. Some popular measures of β were found to be especially susceptible, including

Sorensen's dissimilarity and Simpson's dissimilarity. These finding do not invalidate low-performing measures if they were used on datasets with very low sampling error, however such datasets are rare (Zhang and Zhang, 2012). If such a dataset is used the choice of β index should be based on the question being answered, and measures that were found not to be robust may become the best option. For example, indices based on min-max values were found to be highly susceptible to effects from sampling error, but they measure β independent of species richness, which is useful in highly species-dense systems where β can be conflated with α (Koleff et al., 2003). A researcher seeking to analyze β in that situation could still use one of the min-max based indices but would need to be careful to select a dataset in which he or she had a high degree of confidence. For more general questions, or for datasets with high potential for sampling error, Jaccard's or Bray-Curtis dissimilarities should be used.

Lessons from diatom β

Diatom β deviations were found to be highly predictable, especially at large neighborhood sizes. Beta deviations were distributed substantially different from Bray-Curtis dissimilarities, suggesting a possible need to reconsider the past studies based on Bray-Curtis. Additionally, though overall models were well correlated with β deviation, the components of those models varied dramatically depending on whether mean or standard deviations of environmental variables were used for the analysis and which diatom sample (plankton, top or bottom sediment) was being analyzed. It was of particular interest that many of the positive correlates for β deviation were environmental factors generally considered harmful for diversity as a whole (e.g. Carpenter et al., 1998; Anderson et al., 2002; Smith, 2003; Gilbert, 2017). Analysis of the effects of these same environmental variables on α, show the expected negative relationship. This finding serves as a useful warning about the potential dangers of focusing on only one form of diversity. Focusing only on β could cause α to drop, resulting in no improvement to overall biodiversity. Proper regional diversity management should focus on γ as its end goal and give due consideration to the effects any action will have on each of its components.

Lessons from bird β

Bird β deviations were found to be much harder to predict than those of diatoms. This finding would appear to indicate that active, long-range dispersers like birds alter community assemblage much more rapidly than passively dispersed organisms like diatoms. This is consistent with current research that suggests dispersal limitations and evolutionary history contribute most greatly to bird β (Jetz et al., 2012). This may indicate that bird populations will be in less direct danger from climate change than other organisms, but does not mean they are not vulnerable, as non-climatic factors (e.g., land use) still very much imperil them (Mortelliti et al., 2010; Zimmerling et al., 2013; Belskii, 2013; Eeva et al., 2012). A negative correlation between temperature and precipitation and β deviations was typical. This stands in contrast to current literature based on conventional measures of β that suggests a positive correlation should exist (Qian and Xiao, 2012) and indicates that the previously identified positive correlation was actually due to a positive correlation with α, which was being conflated with β. Thus, beta deviations (which shed that contribution by alpha) change existing understandings of beta diversity.

Comparing bird and diatom β

The contrast between my findings for diatom and bird β deviations drivers is striking. Both studies attempted to correlate environmental variables with β deviations across the conterminous United States, but only diatoms produced highly predictive models. Perhaps not surprisingly, diversity of different organismal groups is affected by fundamentally different forces. This finding may seem obvious to many but has been a point of contention in biogeography for many years. Some have looked at habitat filtering or related processes as the driving factor for diversity (e.g. Kraft et al., 2011; Cadotte and Tucker, 2017), while others have found that dispersal, and its limitations, are the main determinant (e.g. Condit et al., 2002; Ford and Roberts, 2018). My findings suggest that these positions are not truly contradictory. For some species we see an overwhelming effect of the environment, and for others environmental factors are only slightly relevant, depending on their general dispersal adaptations and ranges. This is not the first research to suggest that predictors vary dramatically based on taxa (e.g. Myers et al., 2012; Harbert and Cooper, 2017), however these studies do seem to imply a possible reason for the variance.

It is hardly worthwhile to enumerate all the differences between diatoms and birds; they are completely different lifeforms greatly separated on the Tree of Life. However, despite the differences between these two datasets, it is still worthwhile and reasonable to compare them. Though the birds' data had to be collapsed to a grid to make it manageable, it was still ultimately analyzed though the same moving frame system as the diatoms. Also, the data for both sets are concentrated in approximately the same geographic areas, which mirror human population distributions. Finally, many of the same environmental variables were used in model construction for the two datasets. While the extra level of summarization for bird data does introduce some extra uncertainty, that uncertainty should only require a level of caution when interpreting results; it should not preclude a comparative analysis entirely.

A comparison of these two taxonomic groups yields one major distinction: birds disperse actively over great distances, while diatoms disperse passively through their local hydrological system. As discussed in the last section, there is an existing body of work suggesting that bird diversity originates from dispersal limitation and evolution (Jetz et al., 2012), however that work mostly focuses on birds in a vacuum without a clear comparison to other species. That vacuum makes it hard to draw conclusions about birds in particular, but by comparing their diversity profile with that of a passive disperser, we see greater support for the notion that it is truly their vagility which determines their diversity. Unfortunately, since both of these studies are correlative, and one is drawing conclusions from the absence of results, it is not yet possible to say with authority that passive dispersers are affected by the environment while active dispersers are affected by dispersal limitations. It is still possible, after all, that the differences between these data are driven by sampling error or biotic interactions that were not assessed in this study. However, they may be used as an impetus to begin a more thorough examination of the viability of that argument.

Beyond differences in the degree to which each taxonomic group could be modeled, there was one other noteworthy difference. When mapping the diversity of each group, diatoms showed much clearer spatial patterns birds. This is consistent with diatoms being confined to the lakes they inhabit and thus very much beholden to spatial patterns. However, despite not being as clearly defined as in diatoms, there were some spatial patterns present within bird β deviations, at least in the years where β deviations were relatively low. It is particularly noteworthy that bird β deviations seemed to be highest in the northeast near major centers of population. This could suggest that birds are adapting to anthropogenic factors or it could be a sign that, as in diatoms, habitat fragmentation is raising β, potentially at the cost of α and γ. It may be worthwhile to do a more in-depth study of urban bird populations and their diversity.

Future directions

Evidence of causation is the loftiest goal of biogeography. Unfortunately, due to the scale at which biogeographic studies are conducted, it is also the least attainable. Nevertheless, through skilled design of field experiments and simulation studies such evidence can sometimes be found. Such evidence will be necessary in the immediate future, as conservationists continue to try and preserve diversity over broad swathes of land. A better understanding which factors to preserve to protect or restore biodiversity is essential to that endeavor, and it must be applicable to all components of biodiversity. Thus, I recommend that future studies attempt to focus on demonstrating causative relationships between ecological factors, environmental factors and biodiversity. I further recommend that special attention be paid to factors that drive β as the theory surrounding it is less developed than α at present.

One possible avenue the search for causation could take is to study the differences between active and passive dispersers. Chapters 3 and 4 taken together seem to indicate that greatly different forces drive diversity in those groups, however to more fully extrapolate this pattern to active and passive dispersers in general, more taxa are needed. Fishes and vascular plants may be taxonomic groups worth considering as there is already some research indicating their β trends (Griffiths, 2017; Giorgini et al., 2015; Oldén and Halme, 2016; Bezerra et al., 2017). Furthermore, it would greatly advance the research on this topic if experiments were constructed to support or dispute the link between method of dispersal and response to environmental variables. Diatoms may be useful to such an experiment as they are passive dispersers that can be made into “active” dispersers through careful human intervention. Results from such an experiment could provide valuable insight to conservationists who will often be called upon to conserve the diversity of both active and passive dispersers.

Another possible explanation for the lack of highly predictive models found in bird data is the possibility that their distributions are driven by biotic interactions. Another look into the eBird dataset, this time incorporating factors like food webs, may be enlightening. It is also possible that some birds are more constrained by the environment than others. A comparison of migratory and non-migratory birds may yield interesting results. If strong models are found for non-migratory birds but not for migratory birds it would suggest it is the level of dispersal experienced by a species that determines the effect of the environment, an ecologically significant result. Conversely, if strong models were only found for migratory birds it would contravene much of what is known and expected in ecology and prompt much further investigation. Furthermore, evidence was found of higher than expected bird β deviations in the northeast near major population centers. This finding is curious and suggests the need for further study of urban bird diversity and may indicate a benefit to breaking bird populations into smaller scale communities, which would reinforce the notion of scale as driving force in biogeography.

The other major area of focus I recommend going forward is β deviations. Considerable efforts have previously been made to disentangle the effects of α from β (Jost, 2007; Baselga, 2009), however the use of deviations is what truly creates a measure of β independent from differences in species richness (Myers et al., 2013). This study and others have already found significant differences in the patterns found by β deviations and conventional β measures (e.g. Qiao et al., 2015; Myers et al., 2013). A preliminary analysis using data from this dissertation reveals one possible reason for the difference: deviations correct the relationship between β and γ. Figures 5.1 and 5.3 show negative relationships between β and γ that do not make sense within the framework proposed by Whittaker (1960) (i.e. $\alpha + \beta = \gamma$). Using deviations instead of traditional measures of β returns the positive relationship predicted by Whittaker's equation (Figs. 5.2 and 5.4). Continued exploration of biological systems through the lens of β deviations, as well as reevaluations of well-studied systems, may bring to light new patterns and correlations than could not have been discovered otherwise. It could also lead to the overturning of previously accepted relationships.

The biodiversity of the world is in peril; that is no longer a serious question. The science of conservation was made specifically to respond to that peril. However, for conservation to be successful it necessary to know what is being preserved. To understand our own goals, we must be able to accurately measure biodiversity, β included. Furthermore, we must be able to understand the causes of high β if we wish to achieve it within the systems we seek to conserve or restore. It is my sincerest hope that the findings of my research may help us better understand what we are fighting to preserve and how we might do so.

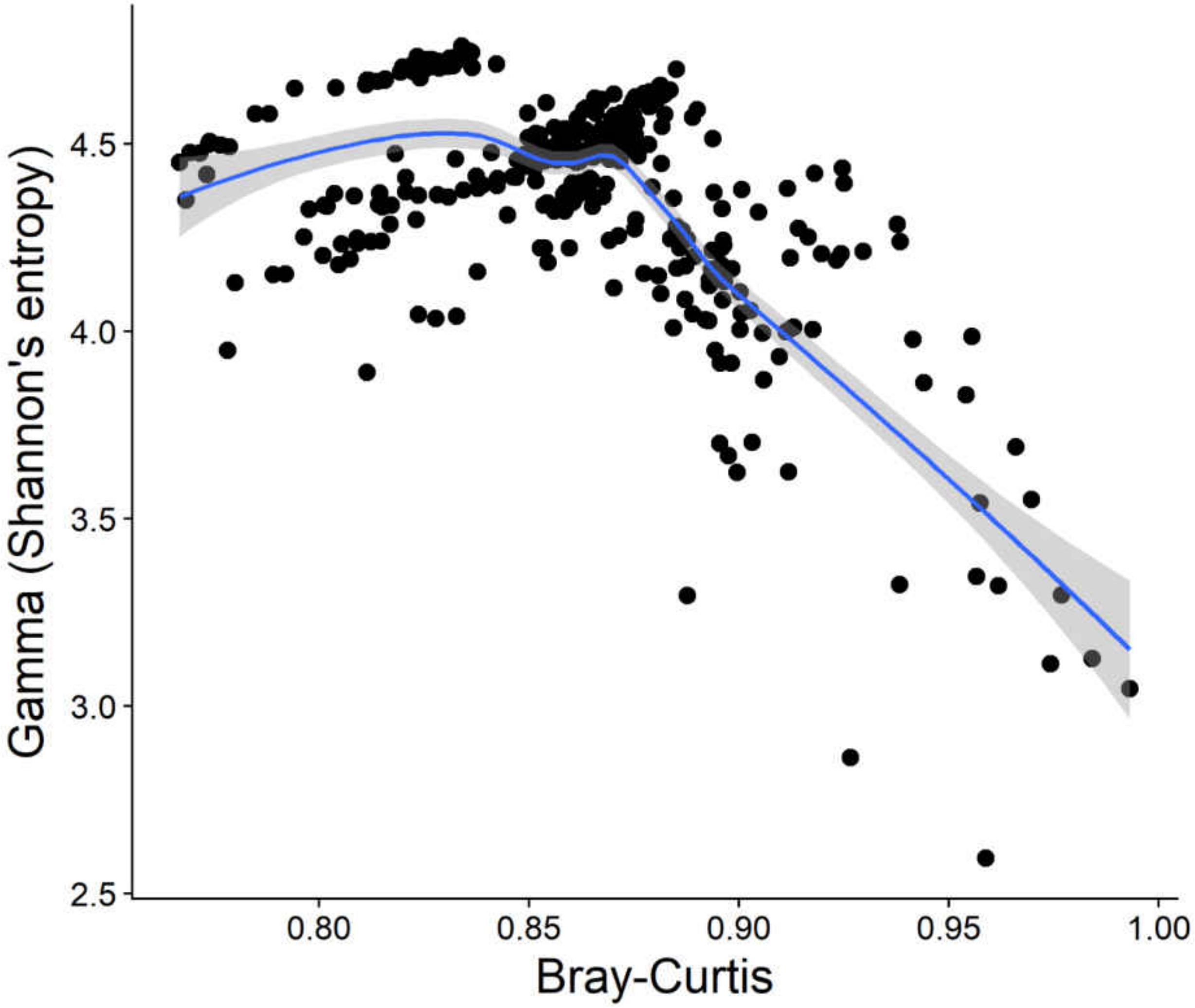

Figure 5.1 Scatterplot relating the Bray-Curtis β of each deep sediment diatom neighborhood at 400km grain size. The trendline was created through Loess regression and illustrates and overall negative relationship between β and γ.

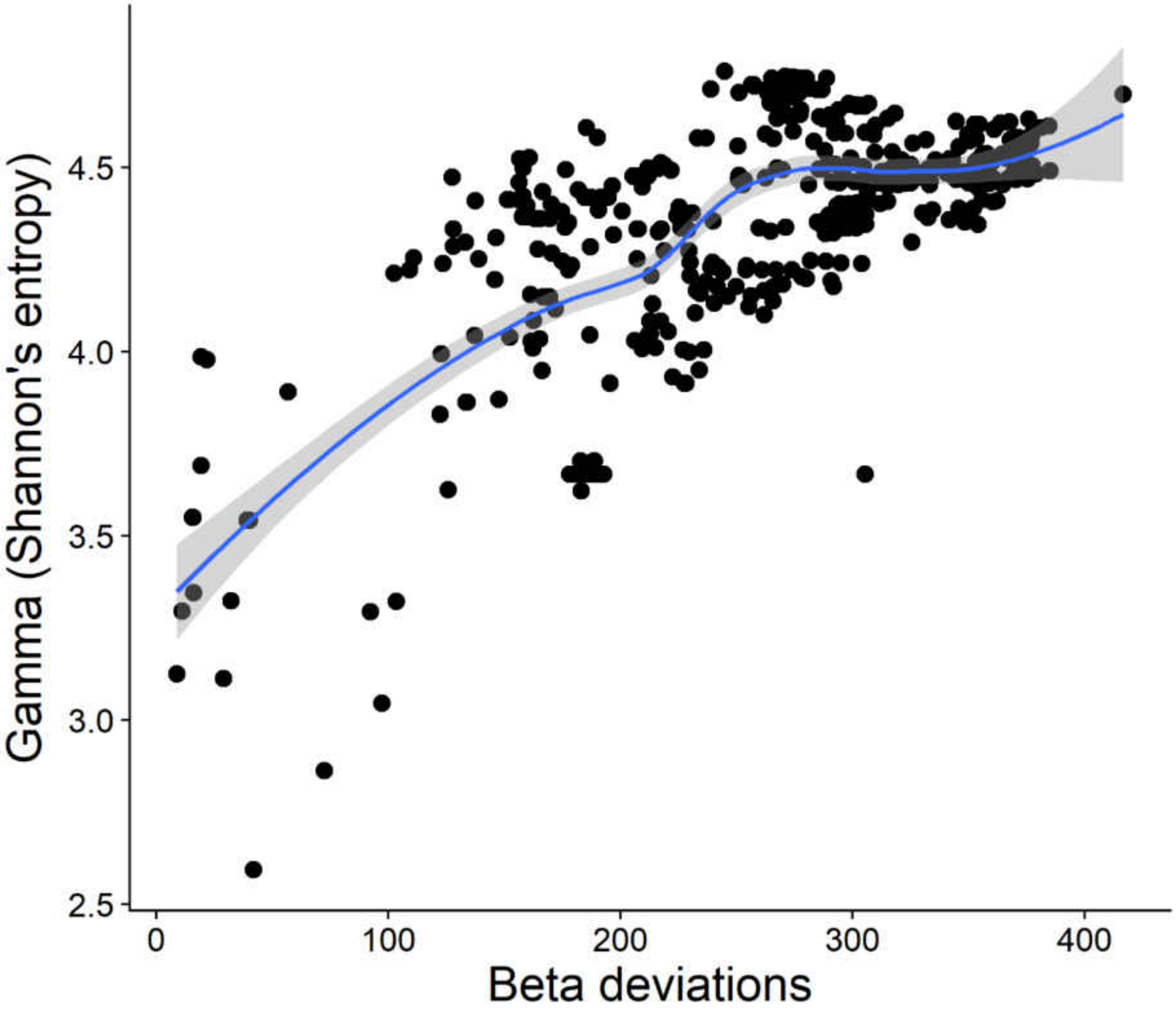

Figure 5.2 Scatterplot relating the Bray-Curtis β deviations of each deep sediment diatom neighborhood at 400km grain size. The trendline was created through Loess regression and illustrates and overall positive relationship between β and γ

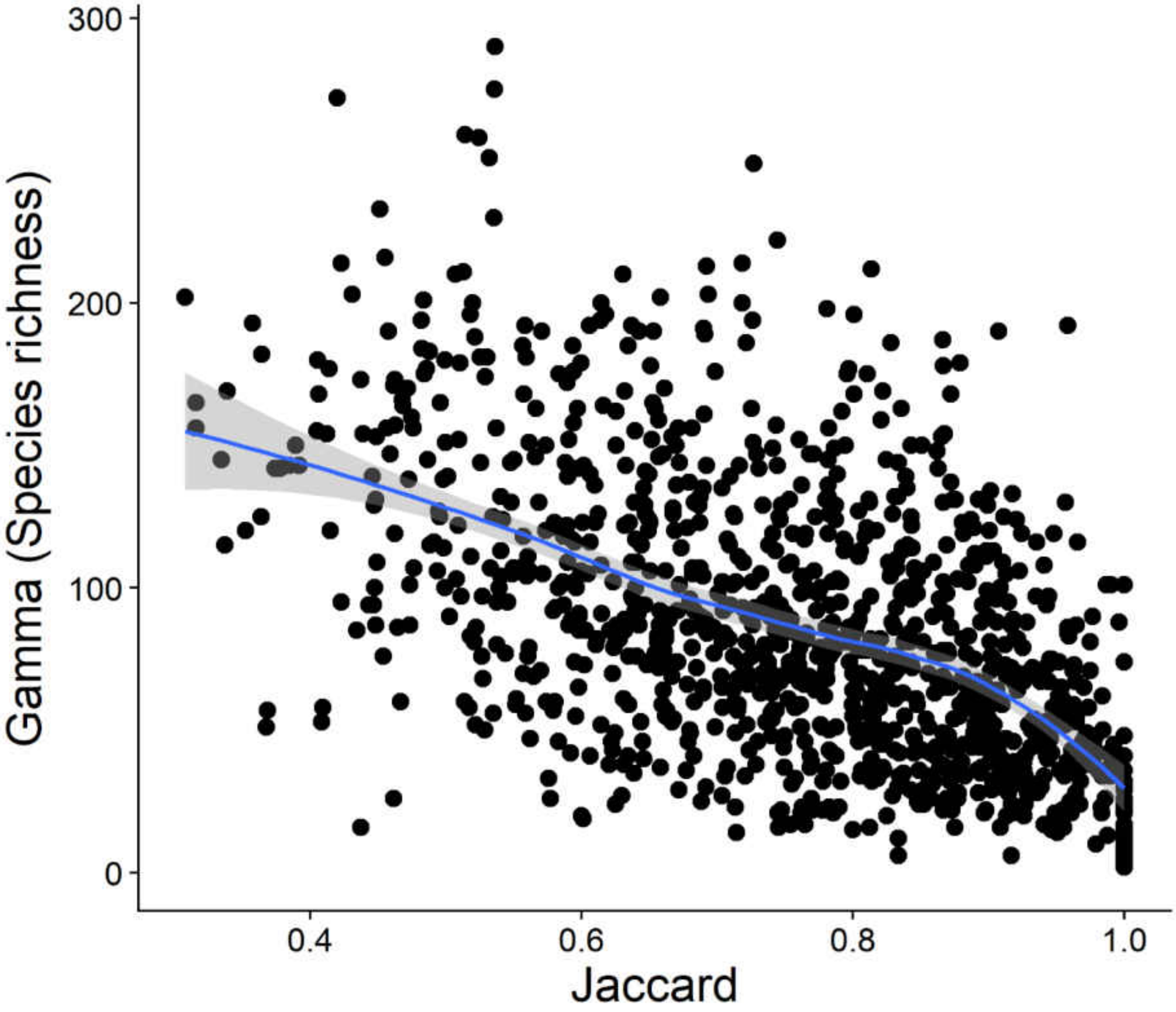

Figure 5.3 Scatterplot relating the Jaccard β of each bird neighborhood for January of 2009 with its corresponding γ. The trendline was created through Loess regression and illustrates an overall negative relationship between β and γ.

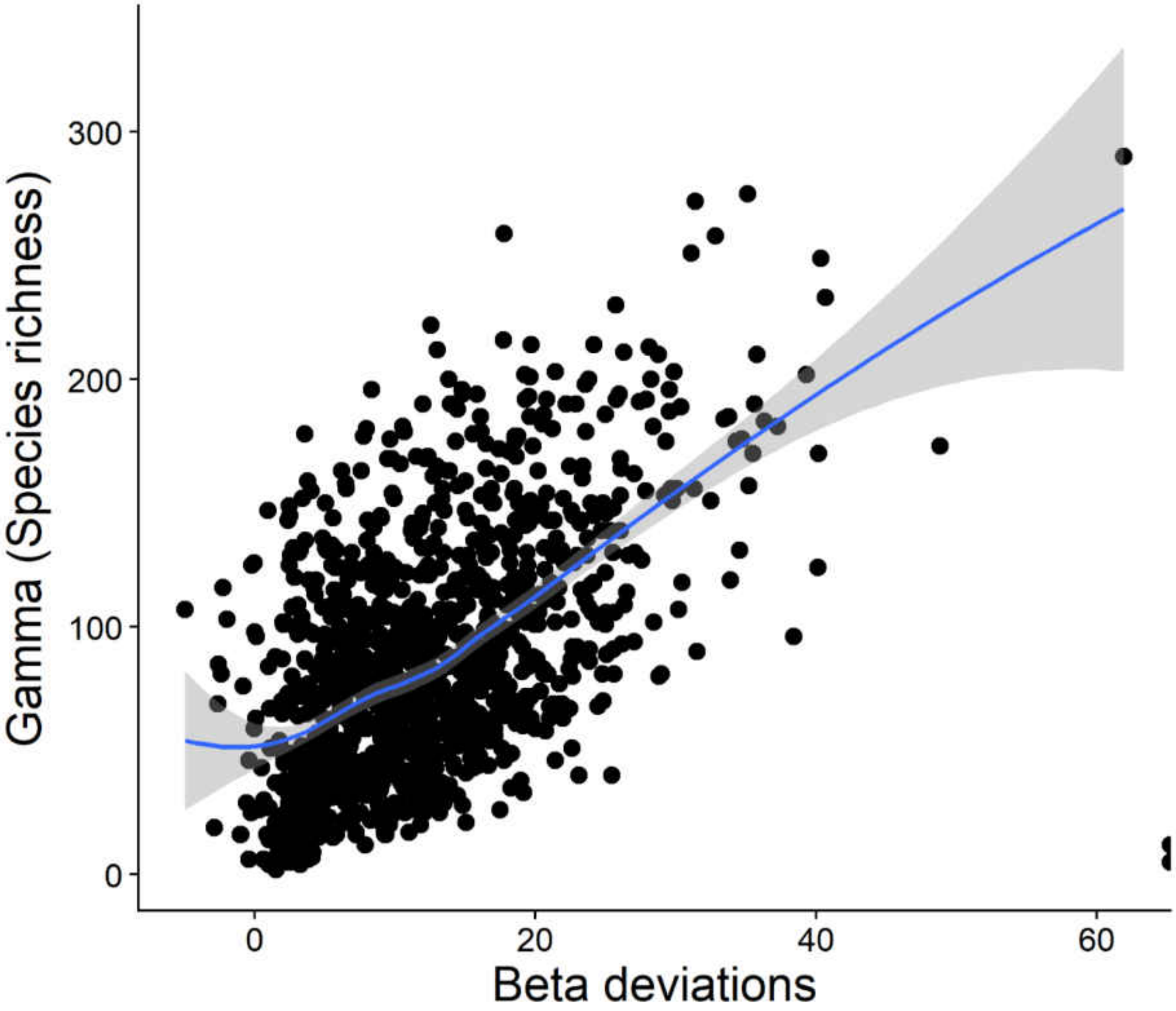

Figure 5.4 Scatterplot relating the Jaccard β deviations of each bird neighborhood for January of 2009 with its corresponding γ. The trendline was created through Loess regression and illustrates an overall positive relationship between β and γ.

References

Anderson, D. M., Glibert, P. M., & Burkholder, J. M. (2002). Harmful algal blooms and eutrophication: Nutrient sources, composition, and consequences. *Estuaries,* 25.4, 704-726.

Baselga, A. (2009). Partitioning the turnover and nestedness components of beta diversity. *Global Ecology and Biogeography,* 19.1, 134-143.

Belskii, E. A., & Belskaya, E. A. (2013). Bird population in birch forests of the Southern Urals affected by industrial pollution: Report 1. Reactions of species and the community. *Contemporary Problems of Ecology,* 6.3, 315-322.

Bezerra, L. A., Padial, A. A., Mariano, F. B., Garcez, D. S., & Sánchez-Botero, J. I. (2017). Fish diversity in tidepools: Assembling effects of environmental heterogeneity. *Environmental Biology of Fishes,* 100.5, 551-563.

Cadotte, M. W., & Tucker, C. M. (2017). Should Environmental Filtering be Abandoned? *Trends in Ecology & Evolution,* 32.6, 429-437.

Carpenter, S. R., Caraco, N. F., Correll, D. L., Howarth, R. W., Sharpley, A. N., & Smith, V. H. (1998). Nonpoint Pollution of Surface Waters with Phosphorus and Nitrogen. *Ecological Applications,* 8.3, 559.

Condit, R., Pitman, N., Leigh, E.G., Chave, J., Terborgh, J., Foster, R.B., Núnez, P., Aguilar, S., Valencia, R., Villa, G. & Muller-Landau, H.C. (2002). Beta-Diversity in Tropical Forest Trees. *Science,* 295.5555, 666-669.

Eeva, T., Belskii, E., Gilyazov, A. S., & Kozlov, M. V. (2012). Pollution impacts on bird population density and species diversity at four non-ferrous smelter sites. *Biological Conservation,* 150.1, 33-41.

Ford, B. M., & Roberts, J. D. (2018). Latitudinal gradients of dispersal and niche processes mediating neutral assembly of marine fish communities. *Marine Biology,* 165.5.

Gilbert, P. M. (2017). Eutrophication, harmful algae and biodiversity — Challenging paradigms in a world of complex nutrient changes. *Marine Pollution Bulletin,* 124.2, 591-606.

Giorgini, D., Giordani, P., Casazza, G., Amici, V., Mariotti, M. G., & Chiarucci, A. (2015). Woody species diversity as predictor of vascular plant species diversity in forest ecosystems. *Forest Ecology and Management,* 345, 50-55.

Harbert, B. L., & Cooper, D. J. (2017). Environmental drivers of subalpine and alpine fen vegetation in the Southern Rocky Mountains, Colorado, USA. *Plant Ecology,* 218.7, 885-898.

Jetz, W., Thomas, G. H., Joy, J. B., Hartmann, K., & Mooers, A. O. (2012). The global diversity of birds in space and time. *Nature,* 491.7424, 444-448.

Jost, L. (2007). Partitioning Diversity Into Independent Alpha And Beta Components. *Ecology,* 88.10, 2427-2439.

Koleff, P., Gaston, K. J., & Lennon, J. J. (2003). Measuring beta diversity for presence-absence data. *Journal of Animal Ecology,* 72.3, 367-382.

Kraft, N. J., Comita, L. S., Chase, J. M., Sanders, N. J., Swenson, N. G., Crist, T. O., . . . Myers, J. A. (2011). Disentangling the Drivers of Diversity Along Latitudinal and Elevational Gradients. *Science,* 333.6050, 1755-1758.

Mortelliti, A., Fagiani, S., Battisti, C., Capizzi, D., & Boitani, L. (2010). Independent effects of habitat loss, habitat fragmentation and structural connectivity on forest-dependent birds. *Diversity and Distributions,* 16.6, 941-951.

Myers, J. A., Chase, J. M., Jiménez, I., Jørgensen, P. M., Araujo-Murakami, A., Paniagua-Zambrana, N., & Seidel, R. (2012). Beta-diversity in temperate and tropical forests reflects dissimilar mechanisms of community assembly. *Ecology Letters,* 16.2, 151-157.

Myers, J. A., Chase, J. M., Jiménez, I., Jørgensen, P. M., Araujo-Murakami, A., Paniagua-Zambrana, N., & Seidel, R. (2013). Beta-diversity in temperate and tropical forests reflects dissimilar mechanisms of community assembly. *Ecology Letters,* 16.2, 151-157.

Oldén, A., & Halme, P. (2016). Grazers increase β-diversity of vascular plants and bryophytes in wood-pastures. *Journal of Vegetation Science,* 27.6, 1084-1093.

Qian, H., & Xiao, M. (2012). Global patterns of the beta diversity–energy relationship in terrestrial vertebrates. *Acta Oecologica,* 39, 67-71.

Qiao, X., Jabot, F., Tang, Z., Jiang, M., & Fang, J. (2015). A latitudinal gradient in tree community assembly processes evidenced in Chinese forests. *Global Ecology and Biogeography,* 24.3, 314-323.

Smith, V. H. (2003). Eutrophication of freshwater and coastal marine ecosystems a global problem. *Environmental Science and Pollution Research,* 10.2, 126-139.

Zhang, J., & Zhang, C. (2012). Sampling and sampling strategies for environmental analysis. *International Journal of Environmental Analytical Chemistry,* 92.4, 466-478.

Zimmerling, J. R., Pomeroy, A. C., Dentremont, M. V., & Francis, C. M. (2013). Canadian Estimate of Bird Mortality Due to Collisions and Direct Habitat Loss Associated with Wind Turbine Developments. *Avian Conservation and Ecology, 8*.2.

APPENDIX A: SUPPLEMENTARY FIGURES FOR CHAPTER 2

Relative abundance vs species rank

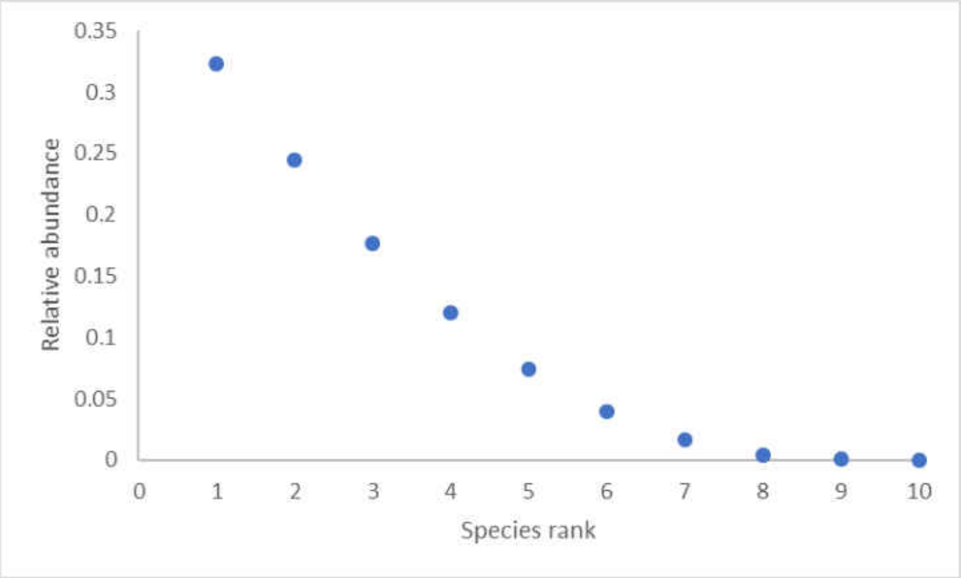

Figure A5 Species rank-abundance curve for all species in the simulation. Numbers are mean values across 1000 simulations

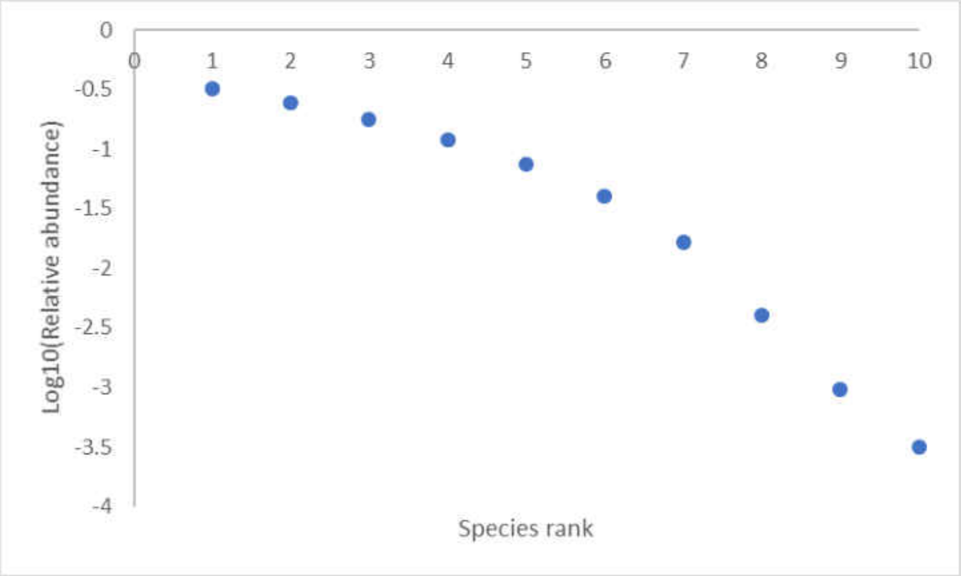

Figure A6 Logarithm-adjusted species rank-abundance curve for all species in the simulation. Numbers are mean values across 1000 simulations

Occupancy vs species rank

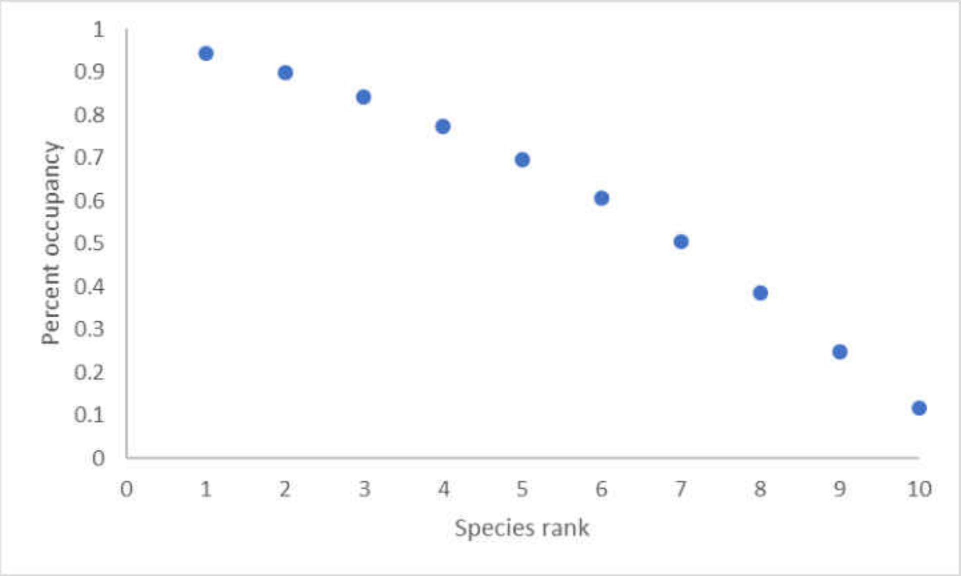

Figure A7 Rank-occupancy curve for all simulation species. Numbers are based on mean values across 1000 simulations.

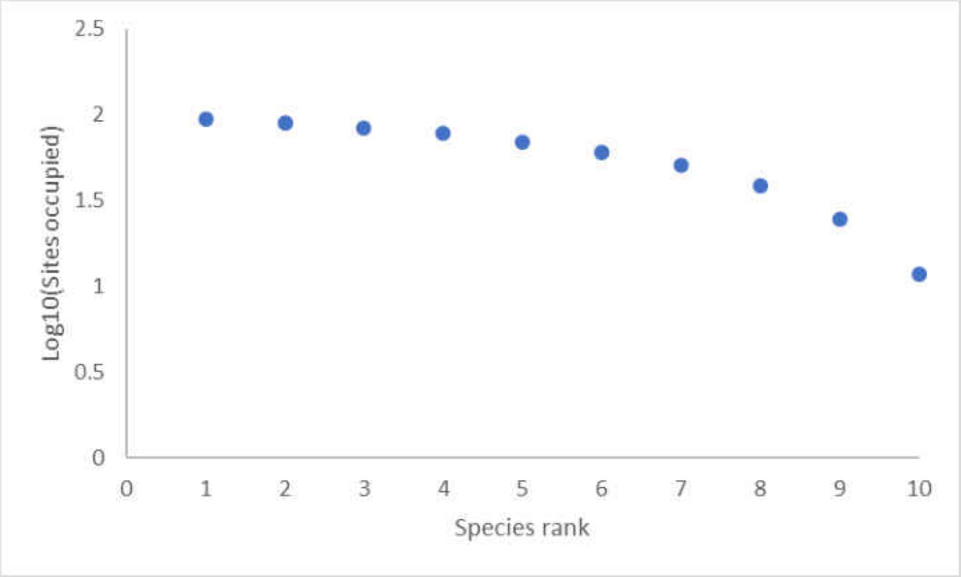

Figure A8 Logarithm-adjusted rank-occupancy curve for all simulation species. Numbers are mean values across 1000 simulations.

Small (3 x 3 x 9) landscapes

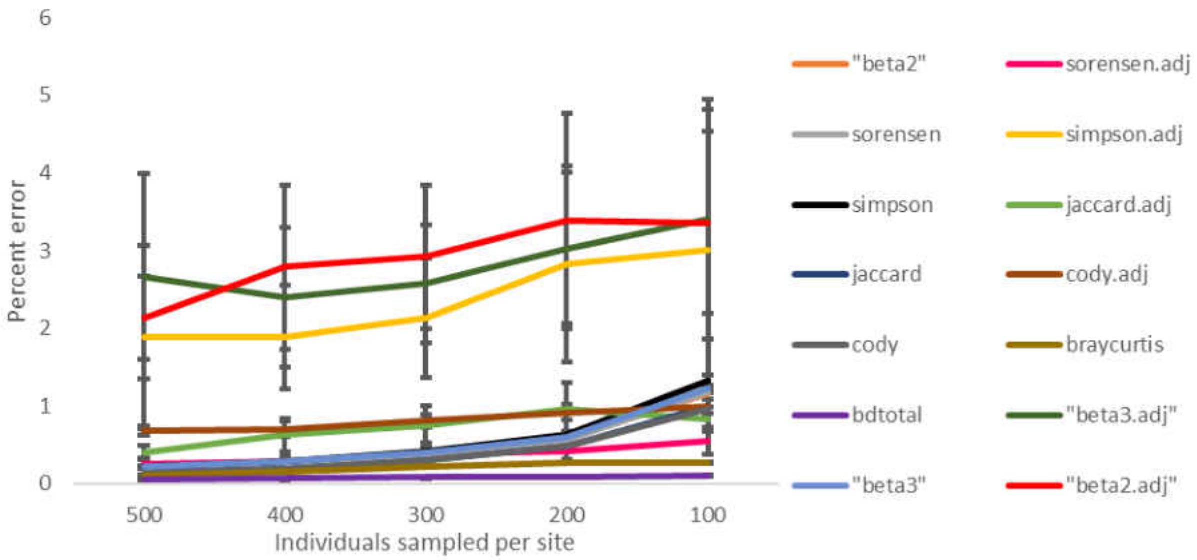

Figure A5 The percent error for five levels of numerical undersampling using presence-absence data. Errors are calculated as 100 x |estimate – known|/known.

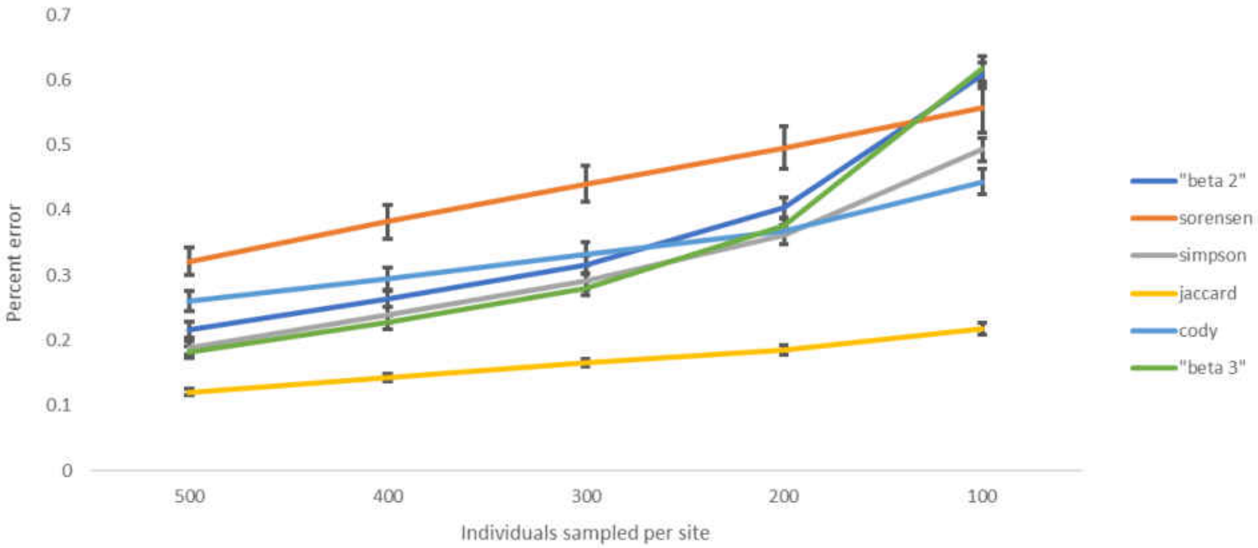

Figure A6 The percent error for five levels of numerical undersampling using presence-absence data. Calculated as in Figure S5.

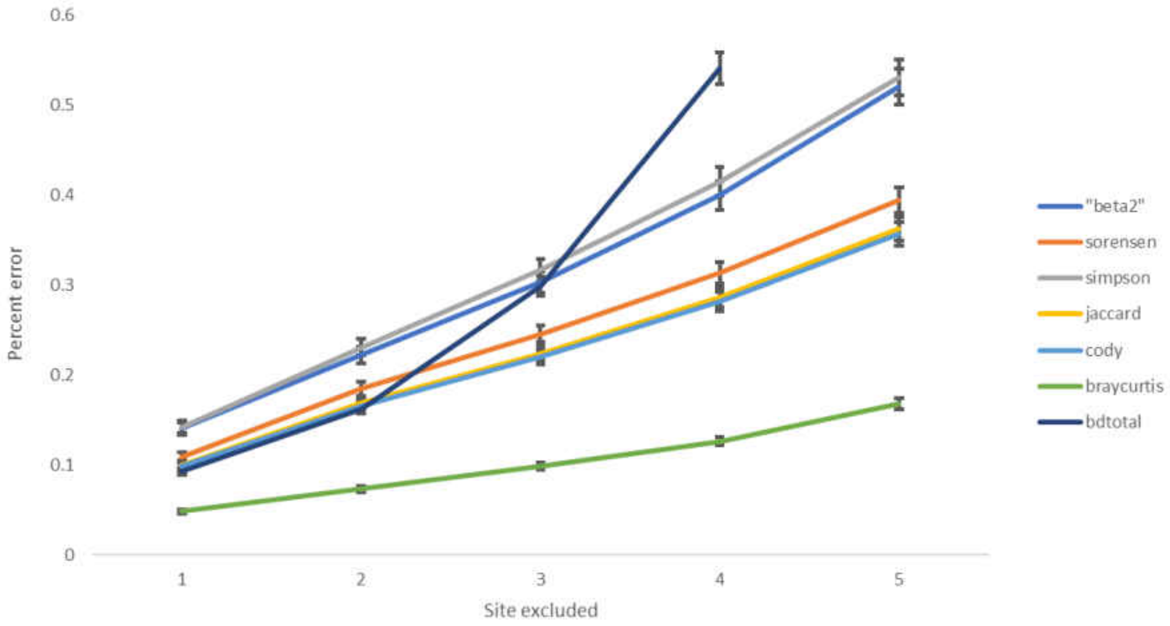

Figure A7 The percent error for five levels of geographic undersampling using abundance data. Calculated as in Figure S5.

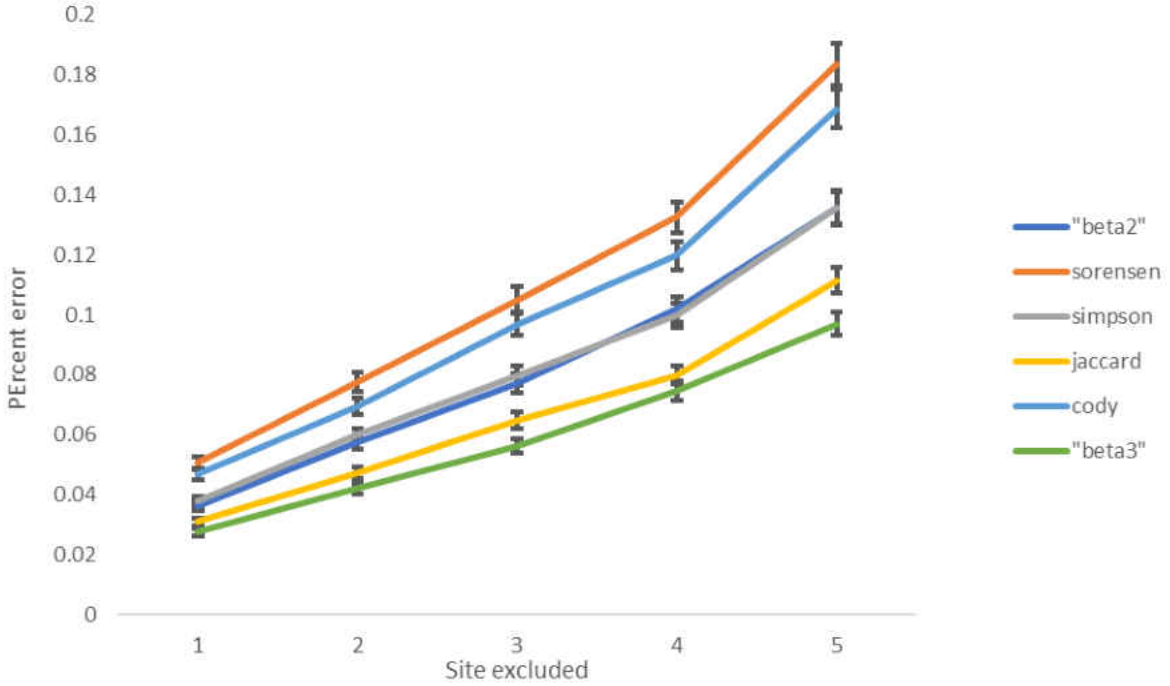

Figure A8 The percent error for five levels of geographic undersampling using presence-absence data. Calculated as in Figure S5.

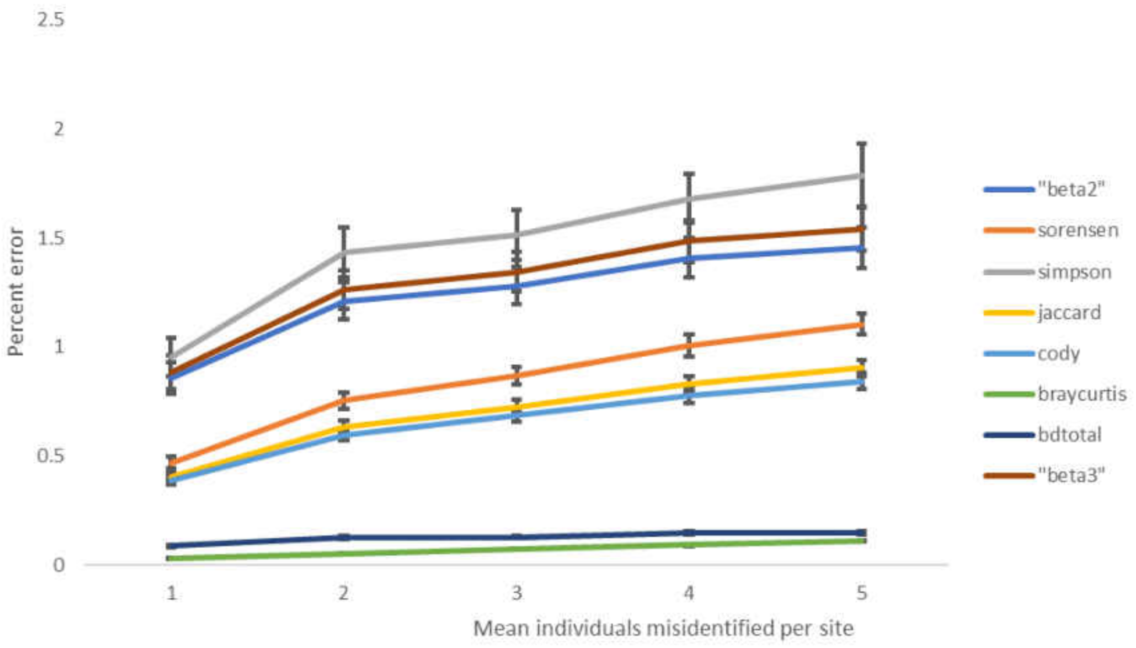

Figure A9 The percent error for five levels of taxonomic misidentification using abundance data. Calculated as in Figure S5.

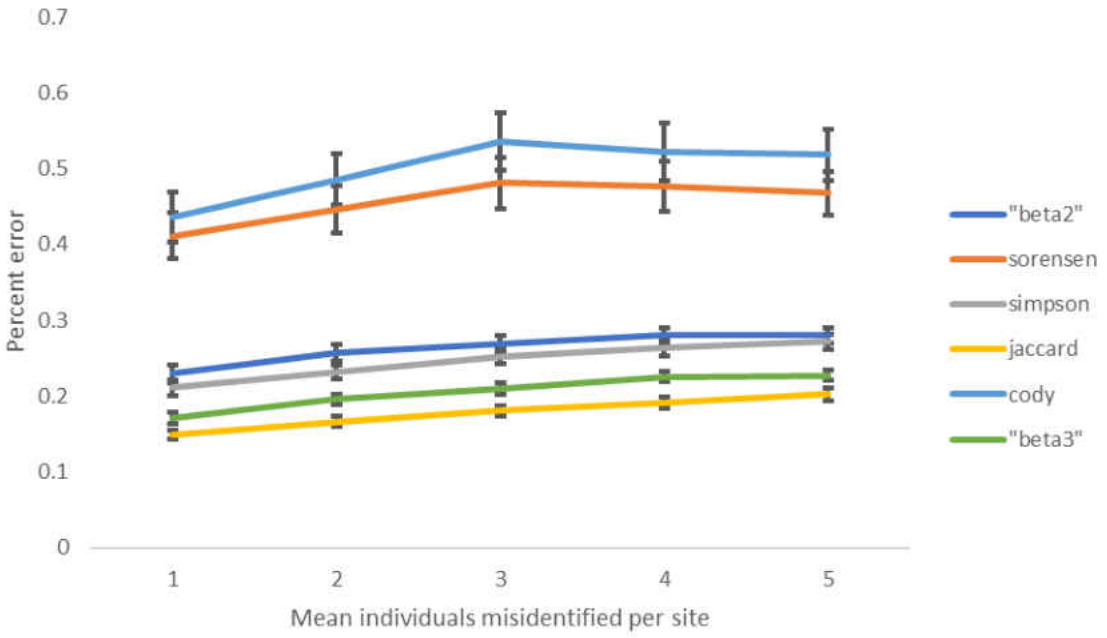

Figure A10 The percent error for five levels of taxonomic misidentification using presence-absence data. Calculated as in Figure S5.

Large (30 x 30 x 10) landscapes

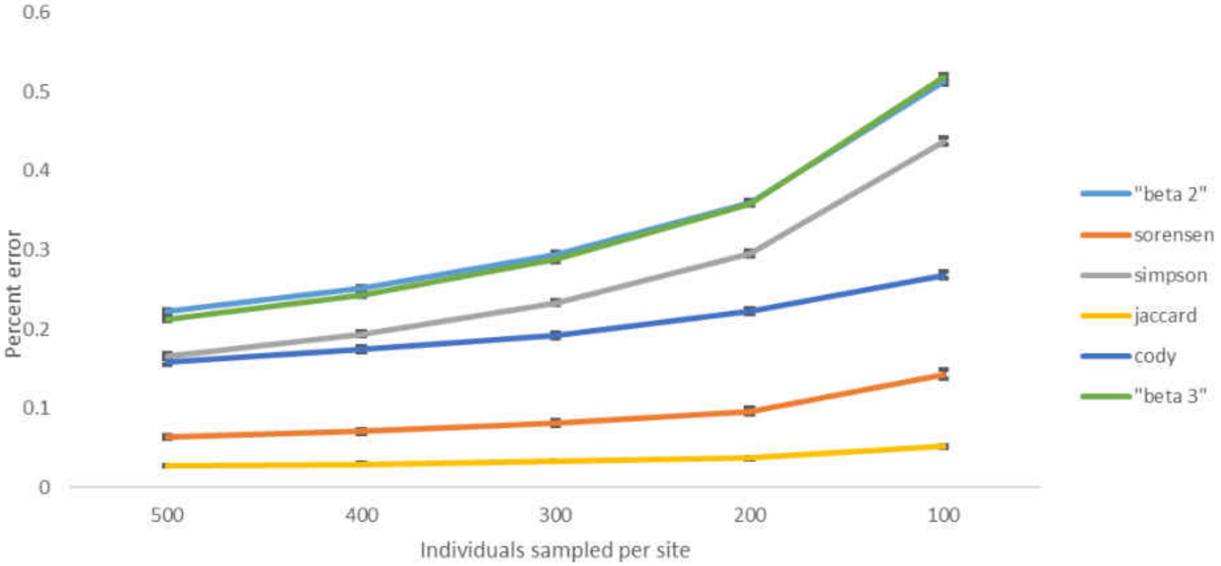

Figure A11 The percent error for five levels of numerical undersampling using presence-absence data. Calculated as in Figure S5.

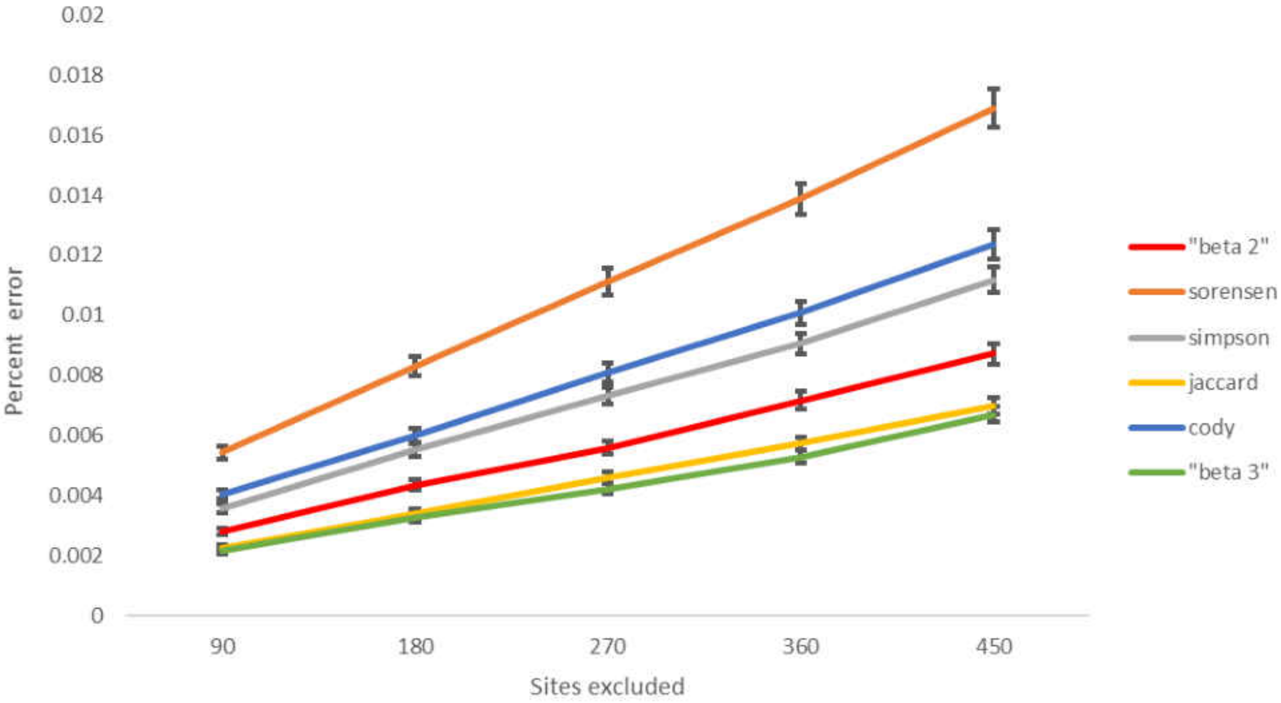

Figure A12 The percent error for five levels of geographic undersampling using presence-absence data. Calculated as in Figure S5.

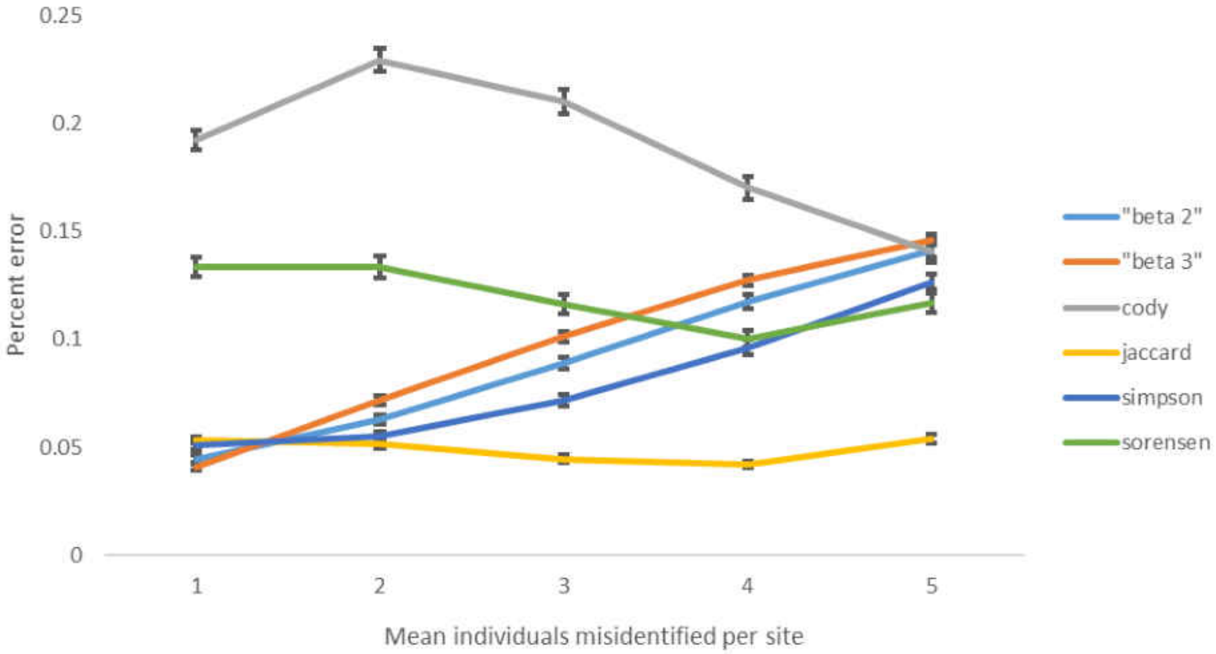

Figure A13 The percent error for five levels of numerical taxonomic misidentification using presence-absence data. Calculated as in Figure S5.

APPENDIX B: MODEL AVERAGES FOR CHAPTER 3 (R OUTPUTS)

Mean environmental variables against β deviations

Deep diatoms (100 grain)

```
Model-averaged coefficients:
(full average)
                     Estimate Std. Error Adjusted SE z value Pr(>|z|)
(Intercept)        -0.6568634  0.3625025   0.3634030   1.808 0.070679 .
Depth.x             0.1281535  0.0979318   0.0980061   1.308 0.191006
developed_basin     0.0658134  0.0989111   0.0989417   0.665 0.505939
longitude           0.2663724  0.2494085   0.2495694   1.067 0.285824
Total.N             0.3377584  0.0873731   0.0875171   3.859 0.000114 ***
Elev.pt            -0.1492733  0.1183363   0.1183932   1.261 0.207371
latitude           -0.3244599  0.2146603   0.2147467   1.511 0.130815
Lake.area          -0.0116484  0.0344466   0.0344673   0.338 0.735397
agriculture_basin  -0.0053354  0.0260138   0.0260386   0.205 0.837647
developed_buffer    0.0063058  0.0373537   0.0373884   0.169 0.866068
agriculture_buffer -0.0024330  0.0169638   0.0169841   0.143 0.886093
pH                 -0.0018522  0.0161951   0.0162235   0.114 0.909106
Total.P            -0.0003335  0.0118395   0.0118688   0.028 0.977584
SLD                -0.0002815  0.0072667   0.0072836   0.039 0.969168

(conditional average)
                   Estimate Std. Error Adjusted SE z value Pr(>|z|)
(Intercept)        -0.65686    0.36250     0.36340   1.808 0.070679 .
Depth.x             0.17774    0.06699     0.06714   2.647 0.008113 **
developed_basin     0.18475    0.07410     0.07421   2.489 0.012795 *
longitude           0.41756    0.18542     0.18576   2.248 0.024581 *
Total.N             0.33776    0.08737     0.08752   3.859 0.000114 ***
Elev.pt            -0.21877    0.07293     0.07306   2.994 0.002750 **
latitude           -0.42279    0.13591     0.13608   3.107 0.001891 **
Lake.area          -0.08897    0.04673     0.04685   1.899 0.057555 .
agriculture_basin  -0.08026    0.06455     0.06470   1.241 0.214776
developed_buffer    0.07999    0.10865     0.10881   0.735 0.462239
agriculture_buffer -0.05602    0.06020     0.06033   0.929 0.353147
pH                 -0.05036    0.06847     0.06866   0.734 0.463214
Total.P            -0.01250    0.07142     0.07161   0.175 0.861433
SLD                -0.01464    0.05035     0.05048   0.290 0.771845
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Relative variable importance:
                     Total.N latitude Depth.x Elev.pt longitude
developed_basin Lake.area developed_buffer agriculture_basin
agriculture_buffer pH   Total.P SLD
Importance:          1.00    0.77     0.72    0.68    0.64      0.36
0.13      0.08             0.07              0.04               0.04 0.03
0.02
N containing models:   58      46       39      38      38        22
10         9                7                 6                  5    4
4
```

Deep Diatoms (200 grain)

```
Model-averaged coefficients:
(full average)
                    Estimate Std. Error Adjusted SE z value Pr(>|z|)
(Intercept)       -0.4168378  0.1848764   0.1853630   2.249 0.024528 *
Depth.x            0.2264642  0.0567950   0.0569297   3.978 6.95e-05 ***
developed_basin    0.2899468  0.0744735   0.0745541   3.889 0.000101 ***
Elev.pt           -0.3280145  0.0475872   0.0477106   6.875  < 2e-16 ***
SLD               -0.2890689  0.0405194   0.0406228   7.116  < 2e-16 ***
Total.N            0.3043847  0.1157057   0.1158222   2.628 0.008588 **
Total.P            0.0621436  0.0955694   0.0956181   0.650 0.515747
longitude         -0.0055949  0.0355857   0.0356503   0.157 0.875294
developed_buffer   0.0152966  0.0718984   0.0719427   0.213 0.831622
latitude           0.0034308  0.0280365   0.0280931   0.122 0.902801
pH                 0.0005108  0.0127086   0.0127408   0.040 0.968022
agriculture_buffer  0.0003761  0.0066843   0.0066990   0.056 0.955229
agriculture_basin   0.0001516  0.0067251   0.0067425   0.022 0.982063
Lake.area         -0.0004134  0.0060004   0.0060119   0.069 0.945176

(conditional average)
                   Estimate Std. Error Adjusted SE z value Pr(>|z|)
(Intercept)       -0.416838   0.184876    0.185363   2.249 0.024528 *
Depth.x            0.226464   0.056795    0.056930   3.978 6.95e-05 ***
developed_basin    0.300805   0.049878    0.050003   6.016  < 2e-16 ***
Elev.pt           -0.328015   0.047587    0.047711   6.875  < 2e-16 ***
SLD               -0.289069   0.040519    0.040623   7.116  < 2e-16 ***
Total.N            0.321718   0.092595    0.092749   3.469 0.000523 ***
Total.P            0.167619   0.083403    0.083553   2.006 0.044843 *
longitude         -0.074927   0.108463    0.108747   0.689 0.490818
developed_buffer   0.141493   0.173092    0.173262   0.817 0.414133
latitude           0.055106   0.098883    0.099140   0.556 0.578321
pH                 0.014097   0.065314    0.065487   0.215 0.829566
agriculture_buffer  0.021169   0.045550    0.045671   0.464 0.642992
agriculture_basin   0.008564   0.049829    0.049961   0.171 0.863908
Lake.area         -0.024662   0.039368    0.039473   0.625 0.532111
---
Signif.  codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Relative variable importance:
                    Depth.x Elev.pt SLD  developed_basin Total.N Total.P
developed_buffer longitude latitude pH   agriculture_buffer
agriculture_basin Lake.area
Importance:          1.00    1.00    1.00 0.96            0.95    0.37
0.11             0.07      0.06     0.04 0.02               0.02
0.02
N containing models:   16      16      16   14              15       7
4                2         2        2    1                  1
1
```

Deep diatoms (300 grain)

```
Model-averaged coefficients:
(full average)
                     Estimate Std. Error Adjusted SE z value Pr(>|z|)
(Intercept)        -0.3494854  0.1691781   0.1696245   2.060   0.0394 *
agriculture_basin   0.3224166  0.0601188   0.0602316   5.353 1.00e-07 ***
developed_buffer    0.3431982  0.1476654   0.1477436   2.323   0.0202 *
Lake.area           0.2042689  0.0415981   0.0416978   4.899 1.00e-06 ***
latitude            0.5433589  0.0772324   0.0774010   7.020  < 2e-16 ***
SLD                -0.1815386  0.0418050   0.0418720   4.336 1.45e-05 ***
Total.P             0.1889082  0.0446944   0.0448114   4.216 2.49e-05 ***
developed_basin     0.0437564  0.1064744   0.1065110   0.411   0.6812
agriculture_buffer -0.0103807  0.0440364   0.0440877   0.235   0.8139
Elev.pt            -0.0051748  0.0221903   0.0222096   0.233   0.8158
longitude           0.0009863  0.0179563   0.0180005   0.055   0.9563
pH                 -0.0009382  0.0134266   0.0134572   0.070   0.9444
Total.N            -0.0002581  0.0134150   0.0134502   0.019   0.9847
Depth.x             0.0007462  0.0075768   0.0075891   0.098   0.9217

(conditional average)
                    Estimate Std. Error Adjusted SE z value Pr(>|z|)
(Intercept)        -0.349485   0.169178    0.169624   2.060   0.0394 *
agriculture_basin   0.322417   0.060119    0.060232   5.353 1.00e-07 ***
developed_buffer    0.391527   0.077159    0.077329   5.063 4.00e-07 ***
Lake.area           0.204269   0.041598    0.041698   4.899 1.00e-06 ***
latitude            0.543359   0.077232    0.077401   7.020  < 2e-16 ***
SLD                -0.181539   0.041805    0.041872   4.336 1.45e-05 ***
Total.P             0.188908   0.044694    0.044811   4.216 2.49e-05 ***
developed_basin     0.220426   0.134787    0.134932   1.634   0.1023
agriculture_buffer -0.115146   0.097195    0.097452   1.182   0.2374
Elev.pt            -0.068689   0.046619    0.046741   1.470   0.1417
longitude           0.024090   0.085551    0.085777   0.281   0.7788
pH                 -0.027718   0.067701    0.067880   0.408   0.6830
Total.N            -0.007671   0.072748    0.072940   0.105   0.9162
Depth.x             0.030776   0.037993    0.038093   0.808   0.4191
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Relative variable importance:
                     agriculture_basin Lake.area latitude SLD  Total.P
developed_buffer developed_basin agriculture_buffer Elev.pt longitude pH
Total.N Depth.x
Importance:          1.00              1.00      1.00     1.00 1.00
0.88             0.20            0.09               0.08    0.04      0.03
0.03    0.02
N containing models:   10                10        10       10   10
8                3               1                  2       1         1
1       1
```

Deep diatoms (400 grain)

```
Model-averaged coefficients:
(full average)
                     Estimate Std. Error Adjusted SE z value Pr(>|z|)
(Intercept)        -0.1653883  0.1590887   0.1594938   1.037 0.299756
agriculture_basin   0.4669739  0.0864970   0.0865864   5.393    1e-07 ***
developed_basin     0.5842639  0.1697399   0.1699713   3.437 0.000587 ***
developed_buffer   -0.5679569  0.2401313   0.2404017   2.363 0.018150 *
Lake.area           0.0777009  0.0736363   0.0736837   1.055 0.291645
latitude            0.2550329  0.1085490   0.1086367   2.348 0.018896 *
pH                 -0.0988833  0.1112181   0.1112853   0.889 0.374241
SLD                -0.4454672  0.0531086   0.0531853   8.376  < 2e-16 ***
Total.N             0.2238653  0.0871600   0.0872320   2.566 0.010278 *
longitude          -0.0150542  0.0501393   0.0501795   0.300 0.764172
Elev.pt            -0.0255439  0.0571899   0.0572057   0.447 0.655217
Depth.x            -0.0121058  0.0416960   0.0417099   0.290 0.771635
agriculture_buffer  0.0038499  0.0272883   0.0273257   0.141 0.887957
Total.P            -0.0001109  0.0126945   0.0127274   0.009 0.993047

(conditional average)
                    Estimate Std. Error Adjusted SE z value Pr(>|z|)
(Intercept)        -0.165388   0.159089    0.159494   1.037 0.299756
agriculture_basin   0.466974   0.086497    0.086586   5.393    1e-07 ***
developed_basin     0.584264   0.169740    0.169971   3.437 0.000587 ***
developed_buffer   -0.594589   0.211025    0.211347   2.813 0.004903 **
Lake.area           0.129669   0.048065    0.048186   2.691 0.007123 **
latitude            0.281352   0.074793    0.074933   3.755 0.000173 ***
pH                 -0.193861   0.076407    0.076598   2.531 0.011378 *
SLD                -0.445467   0.053109    0.053185   8.376  < 2e-16 ***
Total.N             0.239137   0.066807    0.066907   3.574 0.000351 ***
longitude          -0.124570   0.084617    0.084813   1.469 0.141901
Elev.pt            -0.125093   0.059701    0.059775   2.093 0.036374 *
Depth.x            -0.113630   0.069157    0.069235   1.641 0.100752
agriculture_buffer  0.072181   0.095021    0.095223   0.758 0.448440
Total.P            -0.003849   0.074681    0.074875   0.051 0.959005
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Relative variable importance:
                     agriculture_basin developed_basin SLD
developed_buffer Total.N latitude Lake.area pH   Elev.pt longitude Depth.x
agriculture_buffer Total.P
Importance:          1.00              1.00            1.00 0.96
0.94    0.91     0.60      0.51 0.20    0.12      0.11    0.05
0.03
N containing models:   32                32              32   30
29      28       18        13   10       7         7       4
```

Shallow diatoms (100 grain)

```
Model-averaged coefficients:
(full average)
                    Estimate Std. Error Adjusted SE z value Pr(>|z|)
(Intercept)       -0.1855767  0.1994985   0.1997582   0.929  0.35289
Depth.x            0.1185302  0.0447107   0.0447458   2.649  0.00807 **
developed_buffer   0.1604409  0.0343386   0.0343797   4.667 3.10e-06 ***
Elev.pt           -0.1537943  0.0471499   0.0471970   3.259  0.00112 **
longitude          0.3286716  0.1038059   0.1039095   3.163  0.00156 **
pH                 0.0657411  0.0612031   0.0612231   1.074  0.28291
SLD               -0.1706230  0.0341429   0.0341837   4.991 6.00e-07 ***
Total.N            0.1809501  0.0445307   0.0445713   4.060 4.91e-05 ***
latitude          -0.0037617  0.0210544   0.0210688   0.179  0.85829
developed_basin   -0.0015793  0.0135984   0.0136107   0.116  0.90763
Total.P            0.0024135  0.0133717   0.0133786   0.180  0.85684
Lake.area         -0.0012738  0.0088124   0.0088176   0.144  0.88513
agriculture_basin -0.0001114  0.0048018   0.0048078   0.023  0.98152

(conditional average)
                   Estimate Std. Error Adjusted SE z value Pr(>|z|)
(Intercept)       -0.185577   0.199499    0.199758   0.929 0.352886
Depth.x            0.124993   0.036059    0.036105   3.462 0.000536 ***
developed_buffer   0.160441   0.034339    0.034380   4.667 3.10e-06 ***
Elev.pt           -0.156378   0.043087    0.043139   3.625 0.000289 ***
longitude          0.333791   0.096097    0.096211   3.469 0.000522 ***
pH                 0.108372   0.039432    0.039483   2.745 0.006056 **
SLD               -0.170623   0.034143    0.034184   4.991 6.00e-07 ***
Total.N            0.180950   0.044531    0.044571   4.060 4.91e-05 ***
latitude          -0.060114   0.060798    0.060877   0.987 0.323419
developed_basin   -0.036347   0.054701    0.054771   0.664 0.506941
Total.P            0.046593   0.037327    0.037375   1.247 0.212530
Lake.area         -0.034600   0.030923    0.030963   1.117 0.263797
agriculture_basin -0.007323   0.038255    0.038304   0.191 0.848392
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Relative variable importance:
                     developed_buffer SLD  Total.N longitude Elev.pt
Depth.x pH   latitude Total.P developed_basin Lake.area agriculture_basin
Importance:          1.00             1.00 1.00    0.98      0.98    0.95
0.61 0.06     0.05    0.04             0.04      0.02
N containing models:   15               15   15      14        14      13
8    2        2       2               2         1
```

Shallow diatoms (200 grain)

```
Model-averaged coefficients:
(full average)
                     Estimate Std. Error Adjusted SE z value Pr(>|z|)
(Intercept)        -8.299e-02  1.170e-01   1.172e-01   0.708   0.4787
agriculture_basin   2.774e-01  3.450e-02   3.454e-02   8.031  < 2e-16 ***
developed_buffer    2.954e-01  7.000e-02   7.003e-02   4.218 2.47e-05 ***
latitude            2.875e-01  5.211e-02   5.217e-02   5.511  < 2e-16 ***
SLD                -9.623e-02  4.000e-02   4.003e-02   2.404   0.0162 *
Total.N             1.798e-01  3.572e-02   3.576e-02   5.027 5.00e-07 ***
developed_basin     4.282e-02  6.738e-02   6.740e-02   0.635   0.5252
Depth.x             9.507e-03  2.691e-02   2.692e-02   0.353   0.7240
longitude           1.715e-02  4.923e-02   4.925e-02   0.348   0.7277
pH                  4.151e-03  1.972e-02   1.973e-02   0.210   0.8334
Lake.area          -3.275e-03  1.405e-02   1.406e-02   0.233   0.8158
Total.P            -1.101e-03  9.334e-03   9.340e-03   0.118   0.9061
agriculture_buffer -6.864e-04  8.959e-03   8.968e-03   0.077   0.9390
Elev.pt            -9.568e-05  4.479e-03   4.484e-03   0.021   0.9830

(conditional average)
                    Estimate Std. Error Adjusted SE z value Pr(>|z|)
(Intercept)        -0.082992   0.117006    0.117152   0.708  0.47869
agriculture_basin   0.277392   0.034502    0.034538   8.031  < 2e-16 ***
developed_buffer    0.295373   0.069998    0.070033   4.218 2.47e-05 ***
latitude            0.287525   0.052107    0.052169   5.511  < 2e-16 ***
SLD                -0.103921   0.030479    0.030515   3.406  0.00066 ***
Total.N             0.179753   0.035724    0.035759   5.027 5.00e-07 ***
developed_basin     0.123570   0.055881    0.055950   2.209  0.02721 *
Depth.x             0.068033   0.034650    0.034692   1.961  0.04987 *
longitude           0.114375   0.071009    0.071092   1.609  0.10765
pH                  0.065278   0.046111    0.046165   1.414  0.15735
Lake.area          -0.047585   0.027588    0.027619   1.723  0.08490 .
Total.P            -0.037822   0.040038    0.040088   0.943  0.34543
agriculture_buffer -0.026042   0.048838    0.048899   0.533  0.59434
Elev.pt            -0.008148   0.040531    0.040582   0.201  0.84087
---
Signif.  codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Relative variable importance:
                     agriculture_basin developed_buffer latitude Total.N
SLD  developed_basin longitude Depth.x Lake.area pH   Total.P
agriculture_buffer Elev.pt
Importance:          1.00              1.00             1.00     1.00
0.93 0.35            0.15      0.14    0.07      0.06 0.03    0.03
0.01
N containing models:   22                22               22       22
19    9                5         5       4         3    2       2
```

Shallow diatoms (300 grain)

```
Model-averaged coefficients:
(full average)
                     Estimate Std. Error Adjusted SE z value Pr(>|z|)
(Intercept)        -0.0380493  0.1137831   0.1139254   0.334  0.73839
agriculture_basin   0.5622033  0.0606639   0.0606997   9.262  < 2e-16 ***
developed_buffer    0.2487168  0.0365165   0.0365534   6.804  < 2e-16 ***
Elev.pt             0.1884327  0.0381480   0.0381925   4.934    8e-07 ***
latitude            0.3998093  0.0479230   0.0479805   8.333  < 2e-16 ***
longitude           0.1582105  0.0913513   0.0913952   1.731  0.08344 .
Total.N             0.1055764  0.0358102   0.0358329   2.946  0.00322 **
agriculture_buffer -0.0197397  0.0478116   0.0478262   0.413  0.67980
developed_basin     0.0036137  0.0193897   0.0193996   0.186  0.85223
Total.P             0.0056036  0.0236213   0.0236250   0.237  0.81251
pH                  0.0009555  0.0096244   0.0096325   0.099  0.92098

(conditional average)
                   Estimate Std. Error Adjusted SE z value Pr(>|z|)
(Intercept)        -0.03805    0.11378     0.11393   0.334  0.73839
agriculture_basin   0.56220    0.06066     0.06070   9.262  < 2e-16 ***
developed_buffer    0.24872    0.03652     0.03655   6.804  < 2e-16 ***
Elev.pt             0.18843    0.03815     0.03819   4.934 8.00e-07 ***
latitude            0.39981    0.04792     0.04798   8.333  < 2e-16 ***
longitude           0.19042    0.06254     0.06261   3.041  0.00236 **
Total.N             0.11138    0.02658     0.02661   4.186 2.84e-05 ***
agriculture_buffer -0.10393    0.05732     0.05738   1.811  0.07012 .
developed_basin     0.06503    0.05265     0.05271   1.234  0.21735
Total.P             0.07574    0.04722     0.04724   1.603  0.10886
pH                  0.03272    0.04618     0.04624   0.708  0.47921
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Relative variable importance:
                     agriculture_basin developed_buffer Elev.pt latitude
Total.N longitude agriculture_buffer Total.P developed_basin pH
Importance:          1.00              1.00             1.00    1.00
0.95    0.83      0.19               0.07    0.06            0.03
N containing models:    9                 9                9       9
7       7         3                  3       1               1
```

Shallow diatoms (400 grain)

```
Model-averaged coefficients:  
(full average) 
                     Estimate Std. Error Adjusted SE z value Pr(>|z|)    
(Intercept)         0.0088930  0.1230602   0.1232148   0.072    0.942    
agriculture_basin   0.7107033  0.0564691   0.0565131  12.576  < 2e-16 ***
Depth.x            -0.1601263  0.0384491   0.0384796   4.161 3.16e-05 ***
developed_basin     0.2065325  0.0461803   0.0462116   4.469 7.80e-06 ***
Elev.pt             0.3010456  0.0445783   0.0446227   6.746  < 2e-16 ***
Lake.area          -0.1098062  0.0248914   0.0249199   4.406 1.05e-05 ***
latitude            0.3641928  0.0464259   0.0464745   7.836  < 2e-16 ***
pH                 -0.0665591  0.0758273   0.0758447   0.878    0.380    
Total.N             0.0398461  0.0573113   0.0573241   0.695    0.487    
developed_buffer   -0.0108897  0.0368357   0.0368509   0.296    0.768    
longitude           0.0015098  0.0147946   0.0148072   0.102    0.919    
agriculture_buffer  0.0008544  0.0107254   0.0107363   0.080    0.937    
SLD                -0.0003497  0.0046111   0.0046145   0.076    0.940    
Total.P             0.0001810  0.0033614   0.0033645   0.054    0.957    
 
(conditional average) 
                    Estimate Std. Error Adjusted SE z value Pr(>|z|)    
(Intercept)         0.008893   0.123060    0.123215   0.072   0.9425    
agriculture_basin   0.710703   0.056469    0.056513  12.576  < 2e-16 ***
Depth.x            -0.160126   0.038449    0.038480   4.161 3.16e-05 ***
developed_basin     0.206532   0.046180    0.046212   4.469 7.80e-06 ***
Elev.pt             0.301046   0.044578    0.044623   6.746  < 2e-16 ***
Lake.area          -0.109806   0.024891    0.024920   4.406 1.05e-05 ***
latitude            0.364193   0.046426    0.046475   7.836  < 2e-16 ***
pH                 -0.132206   0.052363    0.052413   2.522   0.0117 *  
Total.N             0.105055   0.042537    0.042582   2.467   0.0136 *  
developed_buffer   -0.091441   0.063466    0.063540   1.439   0.1501    
longitude           0.037467   0.063910    0.063982   0.586   0.5581    
agriculture_buffer  0.026493   0.053739    0.053807   0.492   0.6224    
SLD                -0.025724   0.030189    0.030226   0.851   0.3948    
Total.P             0.017172   0.027936    0.027971   0.614   0.5393    
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Relative variable importance: 
                     agriculture_basin Depth.x developed_basin Elev.pt
Lake.area latitude pH   Total.N developed_buffer longitude
agriculture_buffer SLD  Total.P
Importance:          1.00              1.00    1.00            1.00   
1.00      1.00     0.50 0.38    0.12             0.04      0.03      
0.01 0.01   
N containing models:   13                13      13              13   
13        13        6    5       3                2         2
```

Planktonic diatoms (100 grain)

```
Model-averaged coefficients:
(full average)
                     Estimate Std. Error Adjusted SE z value Pr(>|z|)
(Intercept)        -0.0397582  0.0942276   0.0944999   0.421 0.673958
Depth.x             0.2616050  0.0615734   0.0617256   4.238 2.25e-05 ***
longitude           0.3398140  0.0905779   0.0908069   3.742 0.000182 ***
pH                  0.1936435  0.0857609   0.0858833   2.255 0.024150 *
SLD                -0.2343544  0.0544524   0.0546007   4.292 1.77e-05 ***
developed_basin     0.0712798  0.1311758   0.1312282   0.543 0.587010
developed_buffer   -0.0477665  0.1076897   0.1077476   0.443 0.657535
Total.N             0.0313940  0.0737060   0.0737445   0.426 0.670317
Total.P            -0.0256107  0.0650914   0.0651283   0.393 0.694146
Elev.pt            -0.0033474  0.0208428   0.0208667   0.160 0.872550
latitude           -0.0021220  0.0174092   0.0174377   0.122 0.903147
agriculture_basin   0.0025411  0.0191457   0.0191630   0.133 0.894507
Lake.area           0.0003831  0.0071022   0.0071194   0.054 0.957083
agriculture_buffer -0.0002824  0.0069820   0.0070004   0.040 0.967823

(conditional average)
                   Estimate Std. Error Adjusted SE z value Pr(>|z|)
(Intercept)        -0.03976    0.09423     0.09450   0.421 0.673958
Depth.x             0.26161    0.06157     0.06173   4.238 2.25e-05 ***
longitude           0.33981    0.09058     0.09081   3.742 0.000182 ***
pH                  0.21150    0.06524     0.06542   3.233 0.001225 **
SLD                -0.23435    0.05445     0.05460   4.292 1.77e-05 ***
developed_basin     0.23217    0.13672     0.13689   1.696 0.089871 .
developed_buffer   -0.22090    0.12404     0.12428   1.777 0.075489 .
Total.N             0.15134    0.08965     0.08980   1.685 0.091929 .
Total.P            -0.14398    0.08232     0.08248   1.746 0.080895 .
Elev.pt            -0.08182    0.06479     0.06498   1.259 0.207974
latitude           -0.06445    0.07203     0.07224   0.892 0.372271
agriculture_basin   0.07228    0.07339     0.07352   0.983 0.325554
Lake.area           0.02200    0.04920     0.04934   0.446 0.655720
agriculture_buffer -0.01648    0.05077     0.05091   0.324 0.746252
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Relative variable importance:
                     Depth.x longitude SLD  pH   developed_basin
developed_buffer Total.N Total.P Elev.pt agriculture_basin latitude
Lake.area agriculture_buffer
Importance:          1.00    1.00      1.00 0.92 0.31            0.22
0.21    0.18    0.04    0.04              0.03     0.02      0.02
N containing models:   23      23        23   17   10               8
10       7       1       2                 1        1         1
```

Planktonic diatoms (200 grain)

```
Model-averaged coefficients:
(full average)
                     Estimate Std. Error Adjusted SE z value Pr(>|z|)
(Intercept)         0.0164325  0.1548839   0.1552849   0.106  0.91572
agriculture_basin   0.2430510  0.1809474   0.1810381   1.343  0.17942
agriculture_buffer -0.1636954  0.1581274   0.1582030   1.035  0.30080
Depth.x             0.1646104  0.0990023   0.0990744   1.661  0.09662 .
developed_basin     0.2773791  0.1028207   0.1029344   2.695  0.00704 **
Lake.area          -0.0522163  0.0638325   0.0638676   0.818  0.41360
Total.N             0.2702417  0.1539444   0.1540330   1.754  0.07936 .
Total.P            -0.1910677  0.1115035   0.1115958   1.712  0.08687 .
pH                  0.1156083  0.1234648   0.1235262   0.936  0.34932
developed_buffer   -0.0502940  0.1051251   0.1051928   0.478  0.63257
longitude           0.0294477  0.0821638   0.0822242   0.358  0.72024
latitude            0.0063854  0.0310330   0.0310652   0.206  0.83714
SLD                -0.0041140  0.0217188   0.0217370   0.189  0.84989
Elev.pt            -0.0003507  0.0128935   0.0129140   0.027  0.97833

(conditional average)
                   Estimate Std. Error Adjusted SE z value Pr(>|z|)
(Intercept)         0.01643    0.15488     0.15528   0.106  0.91572
agriculture_basin   0.32616    0.12973     0.12990   2.511  0.01204 *
agriculture_buffer -0.27404    0.10780     0.10798   2.538  0.01116 *
Depth.x             0.20249    0.06623     0.06636   3.051  0.00228 **
developed_basin     0.27738    0.10282     0.10293   2.695  0.00704 **
Lake.area          -0.11308    0.04406     0.04417   2.560  0.01046 *
Total.N             0.32534    0.10298     0.10314   3.154  0.00161 **
Total.P            -0.23260    0.07400     0.07416   3.136  0.00171 **
pH                  0.21291    0.08577     0.08593   2.478  0.01322 *
developed_buffer   -0.20218    0.11712     0.11737   1.723  0.08496 .
longitude           0.17756    0.12003     0.12028   1.476  0.13986
latitude            0.09121    0.07759     0.07777   1.173  0.24086
SLD                -0.07675    0.05679     0.05692   1.348  0.17757
Elev.pt            -0.01435    0.08124     0.08138   0.176  0.86005
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Relative variable importance:
                     developed_basin Total.N Total.P Depth.x
agriculture_basin agriculture_buffer pH   Lake.area developed_buffer
longitude latitude SLD  Elev.pt
Importance:          1.00            0.83    0.82    0.81    0.75
0.60               0.54 0.46      0.25             0.17      0.07     0.05
0.02
N containing models:  110             85      82      81      83
67                 65   46        34               27        17       12
7
```

Planktonic diatoms (300 grain)

```
Model-averaged coefficients:
(full average)
                     Estimate Std. Error Adjusted SE z value Pr(>|z|)
(Intercept)         5.740e-03  4.165e-02   4.170e-02   0.138  0.89051
Lake.area          -1.238e-01  4.304e-02   4.307e-02   2.875  0.00404 **
Elev.pt             4.030e-02  7.295e-02   7.296e-02   0.552  0.58068
longitude           1.122e-02  3.623e-02   3.624e-02   0.310  0.75684
latitude           -1.069e-03  9.423e-03   9.429e-03   0.113  0.90972
Total.P            -1.133e-03  8.795e-03   8.799e-03   0.129  0.89755
agriculture_basin   1.380e-02  5.277e-02   5.278e-02   0.261  0.79377
pH                 -6.868e-03  3.392e-02   3.392e-02   0.202  0.83954
agriculture_buffer  2.867e-03  1.614e-02   1.614e-02   0.178  0.85904
developed_buffer    1.063e-04  4.876e-03   4.881e-03   0.022  0.98262
SLD                 1.759e-05  4.476e-03   4.481e-03   0.004  0.99687
developed_basin     1.966e-05  4.332e-03   4.337e-03   0.005  0.99638
Depth.x            -3.302e-05  4.300e-03   4.305e-03   0.008  0.99388
Total.N            -1.154e-04  4.338e-03   4.342e-03   0.027  0.97880

(conditional average)
                    Estimate Std. Error Adjusted SE z value Pr(>|z|)
(Intercept)         0.005740   0.041651    0.041699   0.138 0.890513
Lake.area          -0.128985   0.035583    0.035619   3.621 0.000293 ***
Elev.pt             0.132054   0.072941    0.072973   1.810 0.070353 .
longitude           0.096269   0.055444    0.055484   1.735 0.082724 .
latitude           -0.037940   0.041857    0.041905   0.905 0.365260
Total.P            -0.040637   0.034191    0.034231   1.187 0.235166
agriculture_basin   0.137111   0.103767    0.103798   1.321 0.186524
pH                 -0.112978   0.083269    0.083303   1.356 0.175028
agriculture_buffer  0.056300   0.045898    0.045931   1.226 0.220292
developed_buffer    0.006320   0.037069    0.037112   0.170 0.864767
SLD                 0.001109   0.035520    0.035561   0.031 0.975120
developed_basin     0.001265   0.034732    0.034773   0.036 0.970970
Depth.x            -0.002131   0.034478    0.034518   0.062 0.950768
Total.N            -0.007477   0.034119    0.034159   0.219 0.826743
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Relative variable importance:
                     Lake.area Elev.pt longitude agriculture_basin pH
agriculture_buffer latitude Total.P developed_buffer SLD  developed_basin
Depth.x Total.N
Importance:          0.96      0.31    0.12      0.10              0.06
0.05               0.03     0.03    0.02             0.02 0.02
0.02    0.02
N containing models:   19         9       4         5                 3
3                  1        1       1                1    1
1       1
```

Planktonic diatoms (400 grain)

```
Model-averaged coefficients:
(full average)
                   Estimate Std. Error Adjusted SE z value Pr(>|z|)
(Intercept)         0.124619   0.205022    0.205557   0.606  0.54435
agriculture_basin   1.070511   0.151076    0.151429   7.069  < 2e-16 ***
agriculture_buffer -0.739020   0.120691    0.120964   6.109  < 2e-16 ***
developed_basin     0.505966   0.166267    0.166449   3.040  0.00237 **
developed_buffer   -0.272517   0.186648    0.186818   1.459  0.14464
Elev.pt             0.231832   0.071213    0.071356   3.249  0.00116 **
Lake.area          -0.337488   0.042060    0.042153   8.006  < 2e-16 ***
SLD                 0.199263   0.079842    0.079947   2.492  0.01269 *
Total.N             0.410713   0.080378    0.080542   5.099    3e-07 ***
Total.P            -0.240045   0.079697    0.079833   3.007  0.00264 **
Depth.x            -0.010703   0.039347    0.039379   0.272  0.78578
pH                  0.008930   0.039491    0.039538   0.226  0.82131
longitude           0.005596   0.037087    0.037154   0.151  0.88028
latitude           -0.003116   0.036190    0.036223   0.086  0.93145

(conditional average)
                   Estimate Std. Error Adjusted SE z value Pr(>|z|)
(Intercept)         0.12462    0.20502     0.20556   0.606 0.544347
agriculture_basin   1.07051    0.15108     0.15143   7.069  < 2e-16 ***
agriculture_buffer -0.73902    0.12069     0.12096   6.109  < 2e-16 ***
developed_basin     0.50597    0.16627     0.16645   3.040 0.002368 **
developed_buffer   -0.34795    0.13503     0.13533   2.571 0.010138 *
Elev.pt             0.23598    0.06468     0.06484   3.639 0.000274 ***
Lake.area          -0.33749    0.04206     0.04215   8.006  < 2e-16 ***
SLD                 0.21177    0.06423     0.06437   3.290 0.001003 **
Total.N             0.41071    0.08038     0.08054   5.099    3e-07 ***
Total.P            -0.24510    0.07243     0.07258   3.377 0.000733 ***
Depth.x            -0.11012    0.07058     0.07076   1.556 0.119664
pH                  0.10193    0.09122     0.09145   1.115 0.265045
longitude           0.07550    0.11524     0.11552   0.654 0.513427
latitude           -0.04382    0.12899     0.12912   0.339 0.734298
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Relative variable importance:
                     agriculture_basin agriculture_buffer developed_basin
Lake.area Total.N Elev.pt Total.P SLD  developed_buffer Depth.x pH
longitude latitude
Importance:          1.00              1.00               1.00
1.00      1.00    0.98    0.98    0.94 0.78             0.10    0.09 0.07
0.07
N containing models:   12                12                 12
12        12      11      11      10    7                1       2    2
3
```

Soft algae (200 grain)

```
Model-averaged coefficients:
(full average)
                     Estimate Std. Error Adjusted SE z value Pr(>|z|)
(Intercept)         3.996e-03  3.841e-02   3.846e-02   0.104   0.9172
agriculture_buffer  8.212e-02  6.553e-02   6.554e-02   1.253   0.2102
Elev.pt             1.502e-01  6.434e-02   6.437e-02   2.334   0.0196 *
longitude           1.102e-01  7.588e-02   7.590e-02   1.452   0.1464
agriculture_basin   4.856e-02  7.668e-02   7.669e-02   0.633   0.5266
latitude            6.118e-03  2.131e-02   2.131e-02   0.287   0.7741
pH                 -1.187e-02  3.719e-02   3.720e-02   0.319   0.7498
Lake.area          -5.303e-03  1.945e-02   1.946e-02   0.273   0.7852
SLD                -1.012e-03  8.144e-03   8.148e-03   0.124   0.9012
Depth.x             4.438e-04  5.628e-03   5.631e-03   0.079   0.9372
Total.N            -2.827e-04  4.313e-03   4.316e-03   0.065   0.9478
developed_buffer   -2.625e-04  4.415e-03   4.419e-03   0.059   0.9526
developed_basin    -1.011e-04  3.447e-03   3.450e-03   0.029   0.9766
Total.P             7.386e-05  3.331e-03   3.335e-03   0.022   0.9823

(conditional average)
                    Estimate Std. Error Adjusted SE z value Pr(>|z|)
(Intercept)         0.003996   0.038414    0.038457   0.104 0.917234
agriculture_buffer  0.123336   0.036960    0.036997   3.334 0.000857 ***
Elev.pt             0.164829   0.046186    0.046230   3.565 0.000363 ***
longitude           0.151654   0.040493    0.040539   3.741 0.000183 ***
agriculture_basin   0.142643   0.062072    0.062104   2.297 0.021627 *
latitude            0.063346   0.032805    0.032842   1.929 0.053753 .
pH                 -0.098992   0.054007    0.054045   1.832 0.067005 .
Lake.area          -0.060541   0.031236    0.031272   1.936 0.052878 .
SLD                -0.044968   0.031163    0.031199   1.441 0.149500
Depth.x             0.032336   0.035731    0.035772   0.904 0.366024
Total.N            -0.025306   0.032125    0.032162   0.787 0.431381
developed_buffer   -0.023578   0.034657    0.034698   0.680 0.496809
developed_basin    -0.011072   0.034352    0.034392   0.322 0.747493
Total.P             0.008238   0.034212    0.034252   0.241 0.809923
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Relative variable importance:
                     Elev.pt longitude agriculture_buffer
agriculture_basin pH   latitude Lake.area SLD  Depth.x Total.N
developed_buffer developed_basin Total.P
Importance:          0.91    0.73      0.67               0.34
0.12 0.10     0.09      0.02 0.01    0.01    0.01             0.01
0.01
N containing models:   20      15        15                 9
5    3       3         1    1       1       1                1
1
```

Soft algae (300 grain)

```
Model-averaged coefficients:
(full average)
                     Estimate Std. Error Adjusted SE z value Pr(>|z|)
(Intercept)         5.444e-03  3.924e-02   3.929e-02   0.139    0.890
agriculture_basin   1.598e-01  1.233e-01   1.233e-01   1.296    0.195
Elev.pt             1.442e-01  9.515e-02   9.517e-02   1.516    0.130
pH                 -7.700e-02  8.728e-02   8.730e-02   0.882    0.378
Lake.area          -4.520e-02  5.443e-02   5.444e-02   0.830    0.406
longitude           3.754e-02  6.268e-02   6.269e-02   0.599    0.549
agriculture_buffer  9.424e-03  3.473e-02   3.474e-02   0.271    0.786
latitude            2.969e-03  1.711e-02   1.712e-02   0.173    0.862
developed_buffer   -3.623e-04  5.172e-03   5.175e-03   0.070    0.944
Total.N            -1.287e-03  1.107e-02   1.107e-02   0.116    0.907
Total.P            -1.132e-03  9.989e-03   9.993e-03   0.113    0.910
SLD                -1.653e-04  3.734e-03   3.737e-03   0.044    0.965
Depth.x            -7.169e-05  3.741e-03   3.745e-03   0.019    0.985
developed_basin    -1.377e-04  3.640e-03   3.643e-03   0.038    0.970

(conditional average)
                    Estimate Std. Error Adjusted SE z value Pr(>|z|)
(Intercept)         0.005444   0.039242    0.039285   0.139 0.889782
agriculture_basin   0.220959   0.086629    0.086665   2.550 0.010786 *
Elev.pt             0.191182   0.055006    0.055053   3.473 0.000515 ***
pH                 -0.158549   0.052514    0.052566   3.016 0.002560 **
Lake.area          -0.097694   0.035689    0.035722   2.735 0.006241 **
longitude           0.122989   0.048606    0.048647   2.528 0.011466 *
agriculture_buffer  0.073495   0.068544    0.068573   1.072 0.283819
latitude            0.078463   0.042617    0.042666   1.839 0.065916 .
developed_buffer   -0.033149   0.036880    0.036923   0.898 0.369293
Total.N            -0.047967   0.048239    0.048276   0.994 0.320418
Total.P            -0.045936   0.044607    0.044643   1.029 0.303499
SLD                -0.019645   0.035697    0.035738   0.550 0.582533
Depth.x            -0.008615   0.040105    0.040151   0.215 0.830097
developed_basin    -0.017044   0.036763    0.036805   0.463 0.643298
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Relative variable importance:
                     Elev.pt agriculture_basin pH   Lake.area longitude
agriculture_buffer latitude Total.N Total.P developed_buffer SLD  Depth.x
developed_basin
Importance:          0.75    0.72              0.49 0.46      0.31
0.13               0.04     0.03    0.02    0.01             0.01 0.01
0.01
N containing models:   22      20                12   11         9
4                  1        3       3       1                1    1
1
```

Soft algae (400 grain)

```
Model-averaged coefficients:
(full average)
                     Estimate Std. Error Adjusted SE z value Pr(>|z|)
(Intercept)         5.740e-03  4.165e-02   4.170e-02   0.138  0.89051
Lake.area          -1.238e-01  4.304e-02   4.307e-02   2.875  0.00404 **
Elev.pt             4.030e-02  7.295e-02   7.296e-02   0.552  0.58068
longitude           1.122e-02  3.623e-02   3.624e-02   0.310  0.75684
latitude           -1.069e-03  9.423e-03   9.429e-03   0.113  0.90972
Total.P            -1.133e-03  8.795e-03   8.799e-03   0.129  0.89755
agriculture_basin   1.380e-02  5.277e-02   5.278e-02   0.261  0.79377
pH                 -6.868e-03  3.392e-02   3.392e-02   0.202  0.83954
agriculture_buffer  2.867e-03  1.614e-02   1.614e-02   0.178  0.85904
developed_buffer    1.063e-04  4.876e-03   4.881e-03   0.022  0.98262
SLD                 1.759e-05  4.476e-03   4.481e-03   0.004  0.99687
developed_basin     1.966e-05  4.332e-03   4.337e-03   0.005  0.99638
Depth.x            -3.302e-05  4.300e-03   4.305e-03   0.008  0.99388
Total.N            -1.154e-04  4.338e-03   4.342e-03   0.027  0.97880

(conditional average)
                    Estimate Std. Error Adjusted SE z value Pr(>|z|)
(Intercept)         0.005740   0.041651    0.041699   0.138 0.890513
Lake.area          -0.128985   0.035583    0.035619   3.621 0.000293 ***
Elev.pt             0.132054   0.072941    0.072973   1.810 0.070353 .
longitude           0.096269   0.055444    0.055484   1.735 0.082724 .
latitude           -0.037940   0.041857    0.041905   0.905 0.365260
Total.P            -0.040637   0.034191    0.034231   1.187 0.235166
agriculture_basin   0.137111   0.103767    0.103798   1.321 0.186524
pH                 -0.112978   0.083269    0.083303   1.356 0.175028
agriculture_buffer  0.056300   0.045898    0.045931   1.226 0.220292
developed_buffer    0.006320   0.037069    0.037112   0.170 0.864767
SLD                 0.001109   0.035520    0.035561   0.031 0.975120
developed_basin     0.001265   0.034732    0.034773   0.036 0.970970
Depth.x            -0.002131   0.034478    0.034518   0.062 0.950768
Total.N            -0.007477   0.034119    0.034159   0.219 0.826743
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Relative variable importance:
                     Lake.area Elev.pt longitude agriculture_basin pH
agriculture_buffer latitude Total.P developed_buffer SLD  developed_basin
Depth.x Total.N
Importance:          0.96      0.31    0.12      0.10              0.06
0.05               0.03     0.03    0.02             0.02 0.02
0.02    0.02
N containing models:   19        9       4         5                 3
3                  1        1       1                1    1
1       1
```

Standard deviations of environmental variables against β deviations

Deep diatoms (100 grain)

```
Model-averaged coefficients:
(full average)
                    Estimate Std. Error Adjusted SE z value Pr(>|z|)
(Intercept)        -0.746918   0.377356    0.378396   1.974   0.0484 *
agriculture_buffer  0.117998   0.087803    0.087867   1.343   0.1793
Elev.pt            -0.269079   0.055034    0.055164   4.878 1.10e-06 ***
latitude           -0.472508   0.096908    0.097129   4.865 1.10e-06 ***
SLD                 0.172015   0.043320    0.043430   3.961 7.47e-05 ***
Total.N             0.226473   0.054647    0.054777   4.134 3.56e-05 ***
agriculture_basin  -0.029234   0.060917    0.060954   0.480   0.6315
longitude           0.093305   0.164547    0.164685   0.567   0.5710
Lake.area          -0.025599   0.054446    0.054470   0.470   0.6384
Depth.x             0.020184   0.057758    0.057784   0.349   0.7269
developed_buffer    0.010120   0.032554    0.032577   0.311   0.7561
pH                  0.002313   0.015193    0.015211   0.152   0.8791
developed_basin     0.004449   0.021709    0.021730   0.205   0.8378
Total.P            -0.001323   0.012672    0.012691   0.104   0.9170

(conditional average)
                   Estimate Std. Error Adjusted SE z value Pr(>|z|)
(Intercept)        -0.74692    0.37736     0.37840   1.974   0.0484 *
agriculture_buffer  0.15785    0.06342     0.06354   2.484   0.0130 *
Elev.pt            -0.26908    0.05503     0.05516   4.878 1.10e-06 ***
latitude           -0.47251    0.09691     0.09713   4.865 1.10e-06 ***
SLD                 0.17202    0.04332     0.04343   3.961 7.47e-05 ***
Total.N             0.22647    0.05465     0.05478   4.134 3.56e-05 ***
agriculture_basin  -0.12745    0.06050     0.06066   2.101   0.0356 *
longitude           0.27811    0.17119     0.17159   1.621   0.1051
Lake.area          -0.11305    0.05661     0.05671   1.993   0.0462 *
Depth.x             0.14212    0.07848     0.07862   1.808   0.0707 .
developed_buffer    0.08745    0.04894     0.04907   1.782   0.0747 .
pH                  0.05979    0.05030     0.05044   1.185   0.2359
developed_basin     0.07235    0.05245     0.05259   1.376   0.1689
Total.P            -0.05550    0.06107     0.06124   0.906   0.3648
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Relative variable importance:
                     Elev.pt latitude SLD  Total.N agriculture_buffer
longitude agriculture_basin Lake.area Depth.x developed_buffer
developed_basin pH   Total.P
Importance:          1.00    1.00     1.00 1.00    0.75               0.34
0.23              0.23      0.14    0.12             0.06            0.04
0.02
N containing models:   38      38       38   38      28                  17
11                12        10       7                6               4
2
```

Deep diatoms (200 grain)

```
Model-averaged coefficients:
(full average)
                    Estimate Std. Error Adjusted SE z value Pr(>|z|)
(Intercept)        -0.5858094  0.2958168   0.2965982   1.975   0.0483 *
Depth.x             0.2236964  0.0529789   0.0531128   4.212 2.53e-05 ***
developed_basin     0.3506531  0.0554788   0.0555916   6.308  < 2e-16 ***
Elev.pt            -0.5041683  0.0532137   0.0533491   9.450  < 2e-16 ***
Total.N             0.3307471  0.0567994   0.0569241   5.810  < 2e-16 ***
Total.P             0.0168331  0.0431516   0.0431803   0.390   0.6967
developed_buffer   -0.0088540  0.0411132   0.0411686   0.215   0.8297
SLD                -0.0037022  0.0169124   0.0169244   0.219   0.8268
longitude          -0.0009448  0.0357400   0.0358331   0.026   0.9790
agriculture_basin  -0.0074703  0.0306450   0.0306655   0.244   0.8075
latitude            0.0017498  0.0195680   0.0196099   0.089   0.9289
Lake.area          -0.0017837  0.0116676   0.0116792   0.153   0.8786
agriculture_buffer  0.0043949  0.0242567   0.0242730   0.181   0.8563
pH                 -0.0005072  0.0080010   0.0080184   0.063   0.9496

(conditional average)
                   Estimate Std. Error Adjusted SE z value Pr(>|z|)
(Intercept)        -0.58581    0.29582     0.29660   1.975   0.0483 *
Depth.x             0.22370    0.05298     0.05311   4.212 2.53e-05 ***
developed_basin     0.35065    0.05548     0.05559   6.308  < 2e-16 ***
Elev.pt            -0.50417    0.05321     0.05335   9.450  < 2e-16 ***
Total.N             0.33075    0.05680     0.05692   5.810  < 2e-16 ***
Total.P             0.09936    0.05283     0.05297   1.876   0.0607 .
developed_buffer   -0.10286    0.09984     0.10010   1.028   0.3042
SLD                -0.06034    0.03527     0.03537   1.706   0.0880 .
longitude          -0.01369    0.13538     0.13574   0.101   0.9197
agriculture_basin  -0.08767    0.06317     0.06329   1.385   0.1660
latitude            0.04381    0.08800     0.08824   0.497   0.6195
Lake.area          -0.04948    0.03764     0.03773   1.311   0.1898
agriculture_buffer  0.08244    0.06785     0.06796   1.213   0.2251
pH                 -0.02304    0.04887     0.04900   0.470   0.6383
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Relative variable importance:
                    Depth.x developed_basin Elev.pt Total.N Total.P
developed_buffer agriculture_basin longitude SLD  agriculture_buffer
latitude Lake.area pH
Importance:          1.00    1.00            1.00    1.00    0.17    0.09
0.09             0.07      0.06 0.05              0.04     0.04
0.02
N containing models:   14      14              14      14       4       2
3                 2         1    2                 1        1         1
```

Deep diatoms (300 grain)

```
Model-averaged coefficients:
(full average)
                    Estimate Std. Error Adjusted SE z value Pr(>|z|)
(Intercept)        -0.529083   0.299566    0.300341   1.762 0.078135 .
Depth.x             0.174173   0.051778    0.051872   3.358 0.000786 ***
developed_buffer    0.331472   0.052641    0.052725   6.287  < 2e-16 ***
Elev.pt            -0.533615   0.085035    0.085125   6.269  < 2e-16 ***
Lake.area           0.206129   0.034194    0.034275   6.014  < 2e-16 ***
latitude            0.134077   0.120951    0.121027   1.108 0.267938
SLD                -0.117119   0.030172    0.030241   3.873 0.000108 ***
Total.N             0.343639   0.044485    0.044574   7.709  < 2e-16 ***
pH                 -0.021448   0.045346    0.045369   0.473 0.636399
longitude           0.030202   0.085449    0.085529   0.353 0.723998
agriculture_basin  -0.005037   0.023243    0.023268   0.216 0.828600
developed_basin     0.004005   0.026245    0.026291   0.152 0.878919
agriculture_buffer -0.001278   0.010644    0.010659   0.120 0.904557
Total.P             0.001069   0.009312    0.009325   0.115 0.908761

(conditional average)
                   Estimate Std. Error Adjusted SE z value Pr(>|z|)
(Intercept)        -0.52908    0.29957     0.30034   1.762 0.078135 .
Depth.x             0.17646    0.04808     0.04819   3.662 0.000250 ***
developed_buffer    0.33147    0.05264     0.05272   6.287  < 2e-16 ***
Elev.pt            -0.53361    0.08503     0.08513   6.269  < 2e-16 ***
Lake.area           0.20613    0.03419     0.03427   6.014  < 2e-16 ***
latitude            0.20980    0.08369     0.08386   2.502 0.012358 *
SLD                -0.11712    0.03017     0.03024   3.873 0.000108 ***
Total.N             0.34364    0.04448     0.04457   7.709  < 2e-16 ***
pH                 -0.09680    0.04457     0.04467   2.167 0.030235 *
longitude           0.17048    0.13153     0.13182   1.293 0.195907
agriculture_basin  -0.06837    0.05479     0.05494   1.244 0.213330
developed_basin     0.05993    0.08339     0.08361   0.717 0.473548
agriculture_buffer -0.04233    0.04489     0.04500   0.941 0.346849
Total.P             0.03884    0.04104     0.04115   0.944 0.345214
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Relative variable importance:
                     developed_buffer Elev.pt Lake.area SLD  Total.N
Depth.x latitude pH   longitude agriculture_basin developed_basin
agriculture_buffer Total.P
Importance:          1.00             1.00    1.00      1.00 1.00    0.99
0.64     0.22 0.18      0.07              0.07            0.03
0.03
N containing models:   20               20      20         20   20      19
13        6    5         4                 4               2
2
```

Deep diatoms (400 grain)

```
Model-averaged coefficients:
(full average)
                    Estimate Std. Error Adjusted SE z value Pr(>|z|)
(Intercept)        -0.167645   0.129311    0.129648   1.293    0.196
agriculture_basin   0.364520   0.054015    0.054154   6.731  < 2e-16 ***
Depth.x             0.218284   0.053420    0.053558   4.076 4.59e-05 ***
developed_basin     0.174242   0.036985    0.037077   4.700 2.60e-06 ***
Elev.pt            -0.315418   0.057874    0.058024   5.436 1.00e-07 ***
Lake.area           0.213268   0.032777    0.032861   6.490  < 2e-16 ***
latitude            0.270221   0.055817    0.055958   4.829 1.40e-06 ***
pH                 -0.161095   0.035348    0.035439   4.546 5.50e-06 ***
SLD                -0.345290   0.030533    0.030612  11.280  < 2e-16 ***
Total.N             0.279350   0.053934    0.054028   5.170 2.00e-07 ***
Total.P             0.034594   0.053298    0.053327   0.649    0.517
agriculture_buffer -0.007448   0.028167    0.028188   0.264    0.792
longitude           0.005378   0.031797    0.031851   0.169    0.866
developed_buffer   -0.002278   0.021115    0.021159   0.108    0.914

(conditional average)
                   Estimate Std. Error Adjusted SE z value Pr(>|z|)
(Intercept)        -0.16765    0.12931     0.12965   1.293   0.1960
agriculture_basin   0.36452    0.05402     0.05415   6.731  < 2e-16 ***
Depth.x             0.21828    0.05342     0.05356   4.076 4.59e-05 ***
developed_basin     0.17424    0.03699     0.03708   4.700 2.60e-06 ***
Elev.pt            -0.31542    0.05787     0.05802   5.436 1.00e-07 ***
Lake.area           0.21327    0.03278     0.03286   6.490  < 2e-16 ***
latitude            0.27022    0.05582     0.05596   4.829 1.40e-06 ***
pH                 -0.16110    0.03535     0.03544   4.546 5.50e-06 ***
SLD                -0.34529    0.03053     0.03061  11.280  < 2e-16 ***
Total.N             0.27935    0.05393     0.05403   5.170 2.00e-07 ***
Total.P             0.09848    0.04237     0.04248   2.318   0.0204 *
agriculture_buffer -0.07686    0.05341     0.05352   1.436   0.1510
longitude           0.06863    0.09253     0.09277   0.740   0.4594
developed_buffer   -0.03857    0.07842     0.07862   0.491   0.6237
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Relative variable importance:
                     agriculture_basin Depth.x developed_basin Elev.pt
Lake.area latitude pH   SLD  Total.N Total.P agriculture_buffer longitude
developed_buffer
Importance:          1.00              1.00    1.00            1.00
1.00      1.00     1.00 1.00 1.00    0.35    0.10               0.08
0.06
N containing models:    8                 8       8               8
8         8        8    8    8       4       2                  2
2
```

Shallow diatoms (100 grain)

```
Model-averaged coefficients:
(full average)
                     Estimate Std. Error Adjusted SE z value Pr(>|z|)
(Intercept)        -0.1896263  0.2246576   0.2249505   0.843  0.39925
agriculture_basin   0.1629426  0.0320550   0.0320955   5.077 4.00e-07 ***
Depth.x             0.1613154  0.0361735   0.0362169   4.454 8.40e-06 ***
developed_basin     0.1548058  0.0295675   0.0296051   5.229 2.00e-07 ***
Elev.pt            -0.1411931  0.0456765   0.0457148   3.089  0.00201 **
Lake.area          -0.0746862  0.0527448   0.0527606   1.416  0.15690
longitude           0.3986846  0.0922279   0.0923444   4.317 1.58e-05 ***
pH                  0.0548011  0.0489393   0.0489543   1.119  0.26295
Total.N             0.1837009  0.0364148   0.0364508   5.040 5.00e-07 ***
Total.P             0.0290844  0.0437654   0.0437771   0.664  0.50645
SLD                -0.0374200  0.0524731   0.0524834   0.713  0.47585
latitude           -0.0008049  0.0100556   0.0100653   0.080  0.93626
developed_buffer    0.0002414  0.0050571   0.0050624   0.048  0.96197
agriculture_buffer  0.0002434  0.0043633   0.0043673   0.056  0.95556

(conditional average)
                   Estimate Std. Error Adjusted SE z value Pr(>|z|)
(Intercept)        -0.18963    0.22466     0.22495   0.843 0.399246
agriculture_basin   0.16294    0.03205     0.03210   5.077 4.00e-07 ***
Depth.x             0.16132    0.03617     0.03622   4.454 8.40e-06 ***
developed_basin     0.15481    0.02957     0.02961   5.229 2.00e-07 ***
Elev.pt            -0.14423    0.04114     0.04119   3.502 0.000462 ***
Lake.area          -0.10215    0.03162     0.03166   3.227 0.001253 **
longitude           0.39868    0.09223     0.09234   4.317 1.58e-05 ***
pH                  0.08790    0.03053     0.03057   2.876 0.004033 **
Total.N             0.18370    0.03641     0.03645   5.040 5.00e-07 ***
Total.P             0.08131    0.03329     0.03334   2.439 0.014724 *
SLD                -0.09623    0.03770     0.03774   2.550 0.010769 *
latitude           -0.03365    0.05587     0.05595   0.601 0.547577
developed_buffer    0.02152    0.04268     0.04274   0.503 0.614633
agriculture_buffer  0.02359    0.03598     0.03603   0.655 0.512569
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Relative variable importance:
                     agriculture_basin Depth.x developed_basin longitude
Total.N Elev.pt Lake.area pH   SLD  Total.P latitude developed_buffer
agriculture_buffer
Importance:          1.00              1.00    1.00            1.00
1.00    0.98    0.73      0.62 0.39 0.36    0.02     0.01             0.01
N containing models:   19              19      19              19
19      17      12        11   10    8       2        1                1
```

Shallow diatoms (200 grain)

```
Model-averaged coefficients:  
(full average) 
                     Estimate Std. Error Adjusted SE z value Pr(>|z|)    
(Intercept)        -1.629e-01  1.707e-01   1.709e-01   0.953  0.34050    
agriculture_basin   1.656e-01  3.311e-02   3.315e-02   4.996 6.00e-07 ***
developed_basin     2.769e-01  4.084e-02   4.087e-02   6.775  < 2e-16 ***
latitude            2.153e-01  5.141e-02   5.148e-02   4.183 2.88e-05 ***
longitude           4.072e-01  7.775e-02   7.784e-02   5.231 2.00e-07 ***
pH                 -1.207e-01  2.859e-02   2.863e-02   4.215 2.49e-05 ***
Total.N             1.426e-01  3.354e-02   3.358e-02   4.247 2.17e-05 ***
Total.P             1.161e-01  3.699e-02   3.702e-02   3.135  0.00172 ** 
developed_buffer    1.044e-02  3.392e-02   3.393e-02   0.308  0.75833    
SLD                -4.423e-03  1.708e-02   1.709e-02   0.259  0.79578    
Elev.pt            -3.196e-03  1.670e-02   1.671e-02   0.191  0.84834    
Lake.area           9.386e-04  6.838e-03   6.842e-03   0.137  0.89089    
Depth.x            -6.854e-04  6.515e-03   6.520e-03   0.105  0.91628    
agriculture_buffer -6.969e-05  5.108e-03   5.115e-03   0.014  0.98913    
 
(conditional average) 
                    Estimate Std. Error Adjusted SE z value Pr(>|z|)    
(Intercept)        -0.162899   0.170688    0.170903   0.953 0.340504    
agriculture_basin   0.165644   0.033112    0.033153   4.996 6.00e-07 ***
developed_basin     0.276887   0.040837    0.040871   6.775  < 2e-16 ***
latitude            0.215328   0.051413    0.051475   4.183 2.88e-05 ***
longitude           0.407193   0.077745    0.077840   5.231 2.00e-07 ***
pH                 -0.120672   0.028592    0.028627   4.215 2.49e-05 ***
Total.N             0.142628   0.033543    0.033582   4.247 2.17e-05 ***
Total.P             0.119088   0.032323    0.032364   3.680 0.000234 ***
developed_buffer    0.088111   0.053536    0.053603   1.644 0.100223    
SLD                -0.053393   0.030146    0.030184   1.769 0.076910 .  
Elev.pt            -0.056062   0.043934    0.043989   1.274 0.202500    
Lake.area           0.030639   0.024830    0.024861   1.232 0.217800    
Depth.x            -0.026630   0.030958    0.030997   0.859 0.390273    
agriculture_buffer -0.003393   0.035485    0.035529   0.095 0.923921    
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Relative variable importance: 
                     agriculture_basin developed_basin latitude longitude
pH   Total.N Total.P developed_buffer SLD  Elev.pt Lake.area Depth.x
agriculture_buffer
Importance:          1.00              1.00            1.00     1.00     
1.00 1.00    0.97    0.12             0.08 0.06    0.03      0.03    0.02
N containing models:    8                 8               8        8     
8    8       7       1                1    1       1         1       1
```

Shallow diatoms (300 grain)

```
Model-averaged coefficients:
(full average)
                     Estimate Std. Error Adjusted SE z value Pr(>|z|)
(Intercept)        -0.1442381  0.1407797   0.1409564   1.023    0.306
agriculture_basin   0.0609027  0.0588050   0.0588180   1.035    0.300
Depth.x            -0.0257506  0.0388404   0.0388489   0.663    0.507
developed_buffer    0.2641735  0.0295798   0.0296087   8.922  < 2e-16 ***
Lake.area           0.1087294  0.0227139   0.0227393   4.782  1.7e-06 ***
latitude            0.3260629  0.0464595   0.0465109   7.010  < 2e-16 ***
longitude           0.4198395  0.0692559   0.0693339   6.055  < 2e-16 ***
pH                 -0.2999804  0.0297126   0.0297384  10.087  < 2e-16 ***
Total.P             0.1411734  0.0275857   0.0276161   5.112  3.0e-07 ***
agriculture_buffer  0.0489561  0.0560869   0.0560964   0.873    0.383
SLD                -0.0246254  0.0400137   0.0400224   0.615    0.538
Elev.pt            -0.0057436  0.0242832   0.0242921   0.236    0.813
developed_basin     0.0001992  0.0078658   0.0078744   0.025    0.980
Total.N            -0.0001215  0.0028146   0.0028171   0.043    0.966

(conditional average)
                    Estimate Std. Error Adjusted SE z value Pr(>|z|)
(Intercept)        -0.144238   0.140780    0.140956   1.023  0.30617
agriculture_basin   0.105663   0.035637    0.035674   2.962  0.00306 **
Depth.x            -0.073173   0.028578    0.028611   2.558  0.01054 *
developed_buffer    0.264173   0.029580    0.029609   8.922  < 2e-16 ***
Lake.area           0.108729   0.022714    0.022739   4.782  1.7e-06 ***
latitude            0.326063   0.046460    0.046511   7.010  < 2e-16 ***
longitude           0.419840   0.069256    0.069334   6.055  < 2e-16 ***
pH                 -0.299980   0.029713    0.029738  10.087  < 2e-16 ***
Total.P             0.141173   0.027586    0.027616   5.112  3.0e-07 ***
agriculture_buffer  0.101004   0.035115    0.035146   2.874  0.00406 **
SLD                -0.077017   0.031184    0.031219   2.467  0.01363 *
Elev.pt            -0.070509   0.051695    0.051746   1.363  0.17301
developed_basin     0.008439   0.050515    0.050571   0.167  0.86746
Total.N            -0.019277   0.029795    0.029833   0.646  0.51816
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Relative variable importance:
                     developed_buffer Lake.area latitude longitude pH
Total.P agriculture_basin agriculture_buffer Depth.x SLD  Elev.pt
developed_basin Total.N
Importance:          1.00             1.00      1.00     1.00      1.00
1.00    0.58              0.48               0.35    0.32 0.08    0.02
0.01
N containing models:   22               22        22       22        22
22      13                10                  9       8    6       3
1
```

Shallow diatoms (400 grain)

```
Model-averaged coefficients:
(full average)
                     Estimate Std. Error Adjusted SE z value Pr(>|z|)
(Intercept)        -7.422e-02  8.781e-02   8.792e-02   0.844   0.3985
agriculture_basin   1.747e-01  4.087e-02   4.091e-02   4.271 1.95e-05 ***
agriculture_buffer  1.617e-01  4.034e-02   4.038e-02   4.004 6.22e-05 ***
developed_buffer    1.399e-01  2.910e-02   2.913e-02   4.803 1.60e-06 ***
latitude            2.911e-01  4.562e-02   4.567e-02   6.374  < 2e-16 ***
longitude           2.809e-01  5.572e-02   5.579e-02   5.035 5.00e-07 ***
pH                 -3.200e-01  2.437e-02   2.440e-02  13.114  < 2e-16 ***
SLD                -1.581e-01  3.026e-02   3.030e-02   5.218 2.00e-07 ***
Total.P             8.690e-02  4.029e-02   4.031e-02   2.156   0.0311 *
Total.N             6.207e-03  2.073e-02   2.074e-02   0.299   0.7647
developed_basin    -3.004e-05  8.850e-03   8.861e-03   0.003   0.9973
Elev.pt             3.261e-04  7.900e-03   7.909e-03   0.041   0.9671

(conditional average)
                     Estimate Std. Error Adjusted SE z value Pr(>|z|)
(Intercept)        -0.0742246  0.0878083   0.0879184   0.844 0.398533
agriculture_basin   0.1747360  0.0408653   0.0409125   4.271 1.95e-05 ***
agriculture_buffer  0.1617157  0.0403411   0.0403839   4.004 6.22e-05 ***
developed_buffer    0.1399165  0.0290966   0.0291328   4.803 1.60e-06 ***
latitude            0.2910668  0.0456153   0.0456681   6.374  < 2e-16 ***
longitude           0.2808984  0.0557221   0.0557866   5.035 5.00e-07 ***
pH                 -0.3199988  0.0243706   0.0244010  13.114  < 2e-16 ***
SLD                -0.1581052  0.0302643   0.0303021   5.218 2.00e-07 ***
Total.P             0.0977991  0.0275823   0.0276162   3.541 0.000398 ***
Total.N             0.0572010  0.0323234   0.0323539   1.768 0.077065 .
developed_basin    -0.0008964  0.0483418   0.0484026   0.019 0.985224
Elev.pt             0.0104872  0.0435917   0.0436466   0.240 0.810118
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Relative variable importance:
                     agriculture_basin agriculture_buffer developed_buffer
latitude longitude pH   SLD  Total.P Total.N developed_basin Elev.pt
Importance:          1.00             1.00               1.00
1.00     1.00      1.00 1.00 0.89    0.11    0.03            0.03
N containing models:    6                 6                  6
6        6         6    6    4       2       1               1
```

Planktonic diatoms (100 grain)

```
Model-averaged coefficients:
(full average)
                     Estimate Std. Error Adjusted SE z value Pr(>|z|)
(Intercept)        -7.759e-02  1.239e-01   1.243e-01   0.624    0.532
developed_basin     3.712e-02  6.063e-02   6.066e-02   0.612    0.541
developed_buffer    1.491e-02  4.104e-02   4.107e-02   0.363    0.717
agriculture_basin   2.371e-02  5.364e-02   5.367e-02   0.442    0.659
longitude           3.268e-02  7.796e-02   7.802e-02   0.419    0.675
SLD                -1.825e-02  4.657e-02   4.660e-02   0.392    0.695
Depth.x             1.301e-02  4.038e-02   4.041e-02   0.322    0.747
Total.N             9.903e-03  3.940e-02   3.942e-02   0.251    0.802
Total.P            -8.239e-03  3.589e-02   3.591e-02   0.229    0.819
latitude            3.328e-04  1.377e-02   1.381e-02   0.024    0.981
agriculture_buffer -9.779e-04  1.209e-02   1.211e-02   0.081    0.936
pH                 -6.020e-04  7.869e-03   7.883e-03   0.076    0.939
Elev.pt            -6.952e-05  6.737e-03   6.756e-03   0.010    0.992
Lake.area           4.722e-05  4.965e-03   4.979e-03   0.009    0.992

(conditional average)
                    Estimate Std. Error Adjusted SE z value Pr(>|z|)
(Intercept)        -0.077586   0.123905    0.124258   0.624   0.5324
developed_basin     0.114741   0.049544    0.049684   2.309   0.0209 *
developed_buffer    0.097478   0.054425    0.054563   1.787   0.0740 .
agriculture_basin   0.116221   0.057888    0.058030   2.003   0.0452 *
longitude           0.163776   0.094821    0.095072   1.723   0.0850 .
SLD                -0.107839   0.056140    0.056274   1.916   0.0553 .
Depth.x             0.101300   0.061248    0.061381   1.650   0.0989 .
Total.N             0.112801   0.077924    0.078041   1.445   0.1483
Total.P            -0.111294   0.077038    0.077159   1.442   0.1492
latitude            0.011410   0.079835    0.080041   0.143   0.8866
agriculture_buffer -0.042981   0.067971    0.068100   0.631   0.5279
pH                 -0.037382   0.049698    0.049841   0.750   0.4532
Elev.pt            -0.004988   0.056847    0.057011   0.087   0.9303
Lake.area           0.004152   0.046376    0.046510   0.089   0.9289
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Relative variable importance:
                     developed_basin agriculture_basin longitude SLD
developed_buffer Depth.x Total.N Total.P latitude agriculture_buffer pH
Elev.pt Lake.area
Importance:          0.32            0.20              0.20      0.17 0.15
0.13    0.09    0.07    0.03     0.02                0.02 0.01    0.01
N containing models:   18              15                14        15   11
15      10       9       4        3                   2    2       2
```

Planktonic diatoms (200 grain)

```
Model-averaged coefficients:  
(full average) 
                     Estimate Std. Error Adjusted SE z value Pr(>|z|)    
(Intercept)        -0.0575783  0.1675189   0.1679483   0.343 0.731724    
agriculture_basin   0.1418554  0.0997708   0.0998571   1.421 0.155438    
agriculture_buffer -0.2532537  0.0763560   0.0764709   3.312 0.000927 ***
developed_basin     0.2901308  0.0616516   0.0617495   4.699  2.6e-06 ***
pH                 -0.1643882  0.0625436   0.0626364   2.624 0.008678 ** 
Depth.x             0.0535964  0.0751002   0.0751374   0.713 0.475653    
longitude           0.0904372  0.1349845   0.1350695   0.670 0.503138    
Total.N             0.0246829  0.0536180   0.0536417   0.460 0.645413    
latitude            0.0213552  0.0570212   0.0570587   0.374 0.708205    
Total.P             0.0135654  0.0385745   0.0385947   0.351 0.725225    
Elev.pt            -0.0103476  0.0396434   0.0396684   0.261 0.794206    
developed_buffer    0.0062176  0.0378591   0.0378823   0.164 0.869630    
SLD                 0.0004766  0.0067898   0.0067989   0.070 0.944112    
Lake.area           0.0002853  0.0048464   0.0048535   0.059 0.953129    
 
(conditional average) 
                   Estimate Std. Error Adjusted SE z value Pr(>|z|)    
(Intercept)        -0.05758    0.16752     0.16795   0.343 0.731724    
agriculture_basin   0.18763    0.06766     0.06782   2.766 0.005667 ** 
agriculture_buffer -0.25586    0.07228     0.07240   3.534 0.000410 ***
developed_basin     0.29387    0.05244     0.05256   5.591  < 2e-16 ***
pH                 -0.17267    0.05176     0.05188   3.328 0.000873 ***
Depth.x             0.13359    0.05806     0.05818   2.296 0.021676 *  
longitude           0.23483    0.11578     0.11604   2.024 0.042992 *  
Total.N             0.11633    0.05374     0.05385   2.160 0.030774 *  
latitude            0.13336    0.07326     0.07345   1.816 0.069404 .  
Total.P             0.09813    0.04965     0.04977   1.972 0.048636 *  
Elev.pt            -0.11608    0.07319     0.07334   1.583 0.113462    
developed_buffer    0.12104    0.11834     0.11849   1.022 0.307001    
SLD                 0.04727    0.04858     0.04871   0.971 0.331782    
Lake.area           0.03607    0.04097     0.04108   0.878 0.379935    
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Relative variable importance: 
                     agriculture_buffer developed_basin pH  
agriculture_basin Depth.x longitude Total.N latitude Total.P Elev.pt 
developed_buffer SLD  Lake.area
Importance:          0.99               0.99            0.95 0.76 
0.40    0.39      0.21    0.16     0.14    0.09    0.05             0.01 
0.01
N containing models:   55                 55              52   37 
27      25        16      12        10        9       7                1 
1
```

Planktonic diatoms (300 grain)

```
Model-averaged coefficients:
(full average)
                     Estimate Std. Error Adjusted SE z value Pr(>|z|)
(Intercept)        -0.2300776  0.2507173   0.2513662   0.915   0.3600
agriculture_buffer -0.2392480  0.0511870   0.0513184   4.662  3.1e-06 ***
developed_buffer    0.1310787  0.0530243   0.0531008   2.468   0.0136 *
Elev.pt             0.4654691  0.0754458   0.0756344   6.154  < 2e-16 ***
longitude           0.5669334  0.1189991   0.1193012   4.752  2.0e-06 ***
pH                 -0.3913413  0.0468940   0.0470140   8.324  < 2e-16 ***
developed_basin     0.0013266  0.0310103   0.0310413   0.043   0.9659
agriculture_basin   0.0028803  0.0180622   0.0180873   0.159   0.8735
latitude           -0.0021288  0.0177544   0.0177873   0.120   0.9047
Depth.x             0.0017448  0.0130880   0.0131078   0.133   0.8941
SLD                -0.0007118  0.0087645   0.0087823   0.081   0.9354
Lake.area          -0.0007239  0.0070537   0.0070650   0.102   0.9184
Total.P            -0.0003057  0.0066071   0.0066228   0.046   0.9632
Total.N            -0.0003036  0.0063346   0.0063495   0.048   0.9619

(conditional average)
                   Estimate Std. Error Adjusted SE z value Pr(>|z|)
(Intercept)        -0.23008    0.25072     0.25137   0.915 0.360030
agriculture_buffer -0.23925    0.05119     0.05132   4.662  3.1e-06 ***
developed_buffer    0.13983    0.04214     0.04224   3.310 0.000931 ***
Elev.pt             0.46547    0.07545     0.07563   6.154  < 2e-16 ***
longitude           0.56693    0.11900     0.11930   4.752  2.0e-06 ***
pH                 -0.39134    0.04689     0.04701   8.324  < 2e-16 ***
developed_basin     0.01467    0.10218     0.10229   0.143 0.885923
agriculture_basin   0.05556    0.05802     0.05817   0.955 0.339484
latitude           -0.04439    0.06854     0.06871   0.646 0.518232
Depth.x             0.04283    0.04945     0.04958   0.864 0.387587
SLD                -0.02411    0.04514     0.04526   0.533 0.594263
Lake.area          -0.02725    0.03392     0.03400   0.801 0.422880
Total.P            -0.01265    0.04062     0.04073   0.311 0.756126
Total.N            -0.01291    0.03929     0.03939   0.328 0.743119
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Relative variable importance:
                     agriculture_buffer Elev.pt longitude pH
developed_buffer developed_basin agriculture_basin latitude Depth.x SLD
Lake.area Total.P Total.N
Importance:          1.00               1.00    1.00      1.00 0.94
0.09            0.05              0.05     0.04    0.03 0.03      0.02
0.02
N containing models:   11                 11      11        11    9
2               1                 1        1       1    1         1
1
```

Planktonic diatoms (400 grain)

```
Model-averaged coefficients:
(full average)
                    Estimate Std. Error Adjusted SE z value Pr(>|z|)    
(Intercept)        -0.036198   0.175936    0.176390   0.205 0.837405    
agriculture_basin   0.140657   0.099724    0.099805   1.409 0.158742    
agriculture_buffer -0.310663   0.078889    0.079014   3.932 8.43e-05 ***
Depth.x            -0.226281   0.064438    0.064569   3.505 0.000458 ***
developed_basin     0.142433   0.112470    0.112507   1.266 0.205516    
Elev.pt             0.472824   0.089545    0.089723   5.270 1.00e-07 ***
Lake.area          -0.139536   0.035210    0.035292   3.954 7.69e-05 ***
latitude            0.214305   0.099417    0.099514   2.154 0.031279 *  
longitude           0.555402   0.108059    0.108330   5.127 3.00e-07 ***
pH                 -0.523606   0.047994    0.048102  10.885  < 2e-16 ***
developed_buffer    0.089962   0.114596    0.114622   0.785 0.432538    
Total.N             0.015681   0.045628    0.045647   0.344 0.731194    
Total.P             0.004702   0.021665    0.021680   0.217 0.828288    
SLD                 0.001884   0.014707    0.014726   0.128 0.898204    

(conditional average)
                   Estimate Std. Error Adjusted SE z value Pr(>|z|)    
(Intercept)        -0.03620    0.17594     0.17639   0.205 0.837405    
agriculture_basin   0.18745    0.06694     0.06710   2.793 0.005215 ** 
agriculture_buffer -0.31066    0.07889     0.07901   3.932 8.43e-05 ***
Depth.x            -0.22867    0.06041     0.06055   3.776 0.000159 ***
developed_basin     0.21403    0.06070     0.06080   3.520 0.000432 ***
Elev.pt             0.47282    0.08955     0.08972   5.270 1.00e-07 ***
Lake.area          -0.13954    0.03521     0.03529   3.954 7.69e-05 ***
latitude            0.23768    0.07353     0.07367   3.226 0.001255 ** 
longitude           0.55540    0.10806     0.10833   5.127 3.00e-07 ***
pH                 -0.52361    0.04799     0.04810  10.885  < 2e-16 ***
developed_buffer    0.21227    0.07088     0.07097   2.991 0.002782 ** 
Total.N             0.11819    0.05980     0.05990   1.973 0.048490 *  
Total.P             0.07303    0.04796     0.04806   1.520 0.128635    
SLD                 0.04566    0.05695     0.05707   0.800 0.423656    
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Relative variable importance: 
                     agriculture_buffer Elev.pt Lake.area longitude pH  
Depth.x latitude agriculture_basin developed_basin developed_buffer
Total.N Total.P SLD 
Importance:          1.00               1.00    1.00      1.00      1.00
0.99    0.90     0.75              0.67            0.42             0.13
0.06    0.04 
N containing models:   18                 18      18        18        18
17      13       12                13               7                5
3       3   
```

Soft algae (200 grain)

```
Model-averaged coefficients:
(full average)
                     Estimate Std. Error Adjusted SE z value Pr(>|z|)
(Intercept)         0.0072674  0.0491027   0.0491586   0.148    0.882
agriculture_basin   0.0482382  0.0547899   0.0548033   0.880    0.379
Depth.x             0.0070825  0.0244293   0.0244353   0.290    0.772
longitude           0.0053163  0.0212315   0.0212382   0.250    0.802
pH                 -0.0022143  0.0125934   0.0125982   0.176    0.860
agriculture_buffer  0.0006064  0.0096905   0.0096961   0.063    0.950
developed_buffer    0.0011498  0.0087085   0.0087129   0.132    0.895
latitude            0.0016200  0.0113880   0.0113941   0.142    0.887
Lake.area          -0.0012272  0.0087732   0.0087775   0.140    0.889
Elev.pt             0.0002501  0.0071087   0.0071146   0.035    0.972
developed_basin     0.0004049  0.0054913   0.0054958   0.074    0.941
Total.P             0.0004684  0.0057705   0.0057751   0.081    0.935
Total.N            -0.0002859  0.0050998   0.0051046   0.056    0.955
SLD                 0.0001238  0.0046557   0.0046608   0.027    0.979

(conditional average)
                    Estimate Std. Error Adjusted SE z value Pr(>|z|)
(Intercept)         0.007267   0.049103    0.049159   0.148   0.8825
agriculture_basin   0.095793   0.037496    0.037535   2.552   0.0107 *
Depth.x             0.070058   0.038618    0.038655   1.812   0.0699 .
longitude           0.065763   0.040012    0.040056   1.642   0.1006
pH                 -0.048258   0.035133    0.035171   1.372   0.1700
agriculture_buffer  0.018372   0.050189    0.050221   0.366   0.7145
developed_buffer    0.036954   0.033380    0.033417   1.106   0.2688
latitude            0.044375   0.040683    0.040730   1.090   0.2759
Lake.area          -0.037850   0.031428    0.031464   1.203   0.2290
Elev.pt             0.010668   0.045214    0.045253   0.236   0.8136
developed_basin     0.020220   0.033246    0.033283   0.608   0.5435
Total.P             0.022424   0.033191    0.033229   0.675   0.4998
Total.N            -0.015220   0.034016    0.034054   0.447   0.6549
SLD                 0.007055   0.034448    0.034487   0.205   0.8379
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Relative variable importance:
                    agriculture_basin Depth.x longitude pH   latitude
agriculture_buffer Lake.area developed_buffer Elev.pt Total.P
developed_basin Total.N SLD
Importance:          0.50              0.10    0.08      0.05 0.04
0.03               0.03      0.03             0.02    0.02    0.02
0.02    0.02
N containing models:   14                 3       3         2    2
2                  2         2                2       2       2
2       2
```

Soft algae (300 grain)

```
Model-averaged coefficients:
(full average)
                    Estimate Std. Error Adjusted SE z value Pr(>|z|)
(Intercept)        0.0004081  0.0331950   0.0332331   0.012  0.99020
agriculture_basin  0.1611385  0.0619110   0.0619379   2.602  0.00928 **
Elev.pt            0.2156501  0.0894054   0.0894389   2.411  0.01590 *
longitude          0.1681469  0.0745841   0.0746125   2.254  0.02422 *
pH                -0.0105218  0.0297105   0.0297180   0.354  0.72330
latitude           0.0022709  0.0121912   0.0121955   0.186  0.85228
Lake.area         -0.0034757  0.0159576   0.0159623   0.218  0.82763
developed_buffer  -0.0009165  0.0077833   0.0077877   0.118  0.90632
developed_basin   -0.0007765  0.0072111   0.0072156   0.108  0.91430
Total.N           -0.0007337  0.0069106   0.0069149   0.106  0.91550
agriculture_buffer -0.0005500  0.0076278   0.0076348   0.072  0.94257
Depth.x            0.0005498  0.0070501   0.0070562   0.078  0.93790
Total.P           -0.0004407  0.0057986   0.0058034   0.076  0.93946

(conditional average)
                    Estimate Std. Error Adjusted SE z value Pr(>|z|)
(Intercept)        0.0004081  0.0331950   0.0332331   0.012   0.9902
agriculture_basin  0.1741902  0.0432431   0.0432846   4.024 5.71e-05 ***
Elev.pt            0.2385333  0.0581647   0.0582217   4.097 4.19e-05 ***
longitude          0.1893585  0.0474125   0.0474628   3.990 6.62e-05 ***
pH                -0.0759902  0.0374183   0.0374615   2.028   0.0425 *
latitude           0.0476191  0.0309380   0.0309738   1.537   0.1242
Lake.area         -0.0550340  0.0345623   0.0345964   1.591   0.1117
developed_buffer  -0.0343180  0.0334984   0.0335372   1.023   0.3062
developed_basin   -0.0315253  0.0337910   0.0338301   0.932   0.3514
Total.N           -0.0306442  0.0328354   0.0328734   0.932   0.3512
agriculture_buffer -0.0231297  0.0438720   0.0439227   0.527   0.5985
Depth.x            0.0241943  0.0401918   0.0402383   0.601   0.5477
Total.P           -0.0220167  0.0347070   0.0347471   0.634   0.5263
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Relative variable importance:
                    agriculture_basin Elev.pt longitude pH   Lake.area
latitude developed_buffer developed_basin Total.N agriculture_buffer
Depth.x Total.P
Importance:          0.93              0.90    0.89      0.14 0.06
0.05     0.03             0.02             0.02    0.02               0.02
0.02
N containing models:   12                11      10         1    2
1        1                1                1       1                  1
1
```

Soft algae (400 grain)

```
Model-averaged coefficients:
(full average)
                     Estimate Std. Error Adjusted SE z value Pr(>|z|)
(Intercept)          0.0058340  0.0499094   0.0499666   0.117   0.9071
Lake.area           -0.1031578  0.0441929   0.0442183   2.333   0.0197 *
agriculture_basin    0.0274631  0.0605667   0.0605756   0.453   0.6503
agriculture_buffer -0.0206080  0.0527914   0.0527992   0.390   0.6963
Elev.pt              0.0256638  0.0725094   0.0725158   0.354   0.7234
longitude            0.0161488  0.0502545   0.0502608   0.321   0.7480
developed_buffer     0.0023465  0.0130396   0.0130441   0.180   0.8572
developed_basin      0.0016576  0.0109547   0.0109592   0.151   0.8798
Total.P             -0.0008573  0.0077239   0.0077282   0.111   0.9117
Total.N             -0.0005191  0.0063467   0.0063513   0.082   0.9349
latitude             0.0002098  0.0056753   0.0056813   0.037   0.9705
Depth.x              0.0002728  0.0053650   0.0053702   0.051   0.9595
SLD                 -0.0002959  0.0052625   0.0052674   0.056   0.9552
pH                   0.0003147  0.0048339   0.0048380   0.065   0.9481

(conditional average)
                    Estimate Std. Error Adjusted SE z value Pr(>|z|)
(Intercept)          0.005834   0.049909    0.049967   0.117 0.907052
Lake.area           -0.112084   0.033489    0.033525   3.343 0.000828 ***
agriculture_basin    0.135135   0.059162    0.059206   2.282 0.022464 *
agriculture_buffer -0.124236   0.062664    0.062704   1.981 0.047557 *
Elev.pt              0.169937   0.101473    0.101503   1.674 0.094091 .
longitude            0.135787   0.070643    0.070680   1.921 0.054713 .
developed_buffer     0.053188   0.033910    0.033949   1.567 0.117190
developed_basin      0.048322   0.035263    0.035304   1.369 0.171074
Total.P             -0.037315   0.035162    0.035202   1.060 0.289136
Total.N             -0.028951   0.037726    0.037770   0.767 0.443379
latitude             0.012553   0.042098    0.042147   0.298 0.765832
Depth.x              0.016968   0.038816    0.038861   0.437 0.662382
SLD                 -0.018477   0.037325    0.037368   0.494 0.620985
pH                   0.020577   0.033332    0.033371   0.617 0.537494
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Relative variable importance:
                     Lake.area agriculture_basin agriculture_buffer
Elev.pt longitude developed_buffer developed_basin Total.P Total.N
latitude Depth.x SLD  pH
Importance:          0.92      0.20              0.17               0.15
0.12      0.04             0.03            0.02    0.02    0.02     0.02
0.02 0.02
N containing models:   16         4                 2                  5
4        1                1              1       1       1        1
1    1
```

Mean environmental variables against α (Shannon’s entropy)

Deep diatoms (100 grain)

```
Model-averaged coefficients:
(full average)
                    Estimate Std. Error Adjusted SE z value Pr(>|z|)
(Intercept)       -0.2671384  0.4125451   0.4136314   0.646   0.5184
Developedbasin    -0.4363677  0.0951535   0.0953779   4.575  4.8e-06 ***
Developedbuffer    0.4538493  0.0951951   0.0954458   4.755  2.0e-06 ***
Latitude          -0.2453036  0.1128620   0.1130131   2.171   0.0300 *
pH                -0.1406284  0.0770397   0.0771272   1.823   0.0683 .
TotalN             0.3599051  0.0698805   0.0700317   5.139  3.0e-07 ***
TotalP            -0.3228948  0.0572046   0.0573538   5.630  < 2e-16 ***
SLD                0.0448200  0.0616755   0.0617046   0.726   0.4676
Lakearea          -0.0159294  0.0376859   0.0377032   0.422   0.6727
Longitude          0.0013162  0.0294766   0.0295496   0.045   0.9645
Depth             -0.0045874  0.0208585   0.0208763   0.220   0.8261
Elevation         -0.0009896  0.0097827   0.0097966   0.101   0.9195
Agriculturebuffer  0.0006173  0.0074763   0.0074886   0.082   0.9343
Agriculturebasin   0.0003819  0.0069524   0.0069675   0.055   0.9563

(conditional average)
                  Estimate Std. Error Adjusted SE z value Pr(>|z|)
(Intercept)       -0.26714    0.41255     0.41363   0.646  0.51838
Developedbasin    -0.43637    0.09515     0.09538   4.575  4.8e-06 ***
Developedbuffer    0.45385    0.09520     0.09545   4.755  2.0e-06 ***
Latitude          -0.26968    0.08620     0.08642   3.121  0.00180 **
pH                -0.16455    0.05485     0.05499   2.992  0.00277 **
TotalN             0.35991    0.06988     0.07003   5.139  3.0e-07 ***
TotalP            -0.32289    0.05720     0.05735   5.630  < 2e-16 ***
SLD                0.10953    0.04699     0.04708   2.327  0.01999 *
Lakearea          -0.08667    0.03995     0.04004   2.164  0.03044 *
Longitude          0.02169    0.11779     0.11809   0.184  0.85429
Depth             -0.06819    0.04616     0.04628   1.474  0.14061
Elevation         -0.04584    0.04876     0.04889   0.938  0.34840
Agriculturebuffer  0.03529    0.04441     0.04452   0.792  0.42808
Agriculturebasin   0.02388    0.04961     0.04974   0.480  0.63122
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Relative variable importance:
                     Developedbasin Developedbuffer TotalN TotalP Latitude
pH   SLD  Lakearea Depth Longitude Elevation Agriculturebuffer
Agriculturebasin
Importance:          1.00           1.00            1.00   1.00   0.91
0.85 0.41 0.18     0.07  0.06      0.02      0.02              0.02
N containing models:   19             19              19     19     16
15    9    5        3     3         1         1                 1
```

Deep diatoms (200 grain)

```
Model-averaged coefficients:
(full average)
                   Estimate Std. Error Adjusted SE z value Pr(>|z|)
(Intercept)       -0.472116   0.530036    0.531425   0.888  0.37433
Depth             -0.235918   0.074370    0.074447   3.169  0.00153 **
Developedbasin    -0.317341   0.055188    0.055301   5.738  < 2e-16 ***
Latitude          -0.536339   0.085030    0.085224   6.293  < 2e-16 ***
Longitude         -0.132106   0.148928    0.149032   0.886  0.37539
TotalN             0.265006   0.112943    0.113072   2.344  0.01909 *
TotalP            -0.375655   0.074729    0.074873   5.017    5e-07 ***
Agriculturebasin  -0.066472   0.123856    0.123903   0.536  0.59162
Agriculturebuffer  0.088423   0.135804    0.135846   0.651  0.51511
SLD                0.006277   0.022701    0.022716   0.276  0.78228
Developedbuffer   -0.004286   0.032852    0.032912   0.130  0.89638
pH                 0.005810   0.027535    0.027557   0.211  0.83301
Elevation          0.001701   0.014229    0.014247   0.119  0.90495

(conditional average)
                  Estimate Std. Error Adjusted SE z value Pr(>|z|)
(Intercept)       -0.47212    0.53004     0.53143   0.888 0.374328
Depth             -0.24035    0.06759     0.06768   3.551 0.000383 ***
Developedbasin    -0.31734    0.05519     0.05530   5.738  < 2e-16 ***
Latitude          -0.53634    0.08503     0.08522   6.293  < 2e-16 ***
Longitude         -0.25256    0.10945     0.10972   2.302 0.021346 *
TotalN             0.28019    0.09609     0.09625   2.911 0.003600 **
TotalP            -0.37566    0.07473     0.07487   5.017    5e-07 ***
Agriculturebasin  -0.23853    0.11834     0.11852   2.013 0.044159 *
Agriculturebuffer  0.22322    0.12833     0.12844   1.738 0.082218 .
SLD                0.06699    0.03785     0.03794   1.765 0.077489 .
Developedbuffer   -0.06299    0.11029     0.11055   0.570 0.568819
pH                 0.08401    0.06628     0.06641   1.265 0.205852
Elevation          0.04494    0.05835     0.05847   0.769 0.442140
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Relative variable importance:
                     Developedbasin Latitude TotalP Depth TotalN Longitude
Agriculturebuffer Agriculturebasin SLD  pH   Developedbuffer Elevation
Importance:          1.00           1.00     1.00   0.98  0.95   0.52
0.40              0.28             0.09 0.07 0.07            0.04
N containing models:   26             26       26     25    23     12
12                 8                4    4    4               4
```

Deep diatoms (300 grain)

```
Model-averaged coefficients:
(full average)
                  Estimate Std. Error Adjusted SE z value Pr(>|z|)
(Intercept)      -0.346845   0.502129    0.503449   0.689 0.490862
Agriculturebasin  0.632514   0.151237    0.151474   4.176 2.97e-05 ***
Agriculturebuffer -0.569144   0.142004    0.142203   4.002 6.27e-05 ***
Depth            -0.519327   0.069794    0.069884   7.431  < 2e-16 ***
Developedbuffer  -0.463696   0.170360    0.170473   2.720 0.006527 **
Elevation         0.274011   0.053962    0.054070   5.068 4.00e-07 ***
Latitude         -0.327182   0.092862    0.093054   3.516 0.000438 ***
TotalP           -0.120904   0.094036    0.094080   1.285 0.198753
TotalN           -0.085501   0.120605    0.120647   0.709 0.478519
Developedbasin    0.059123   0.126748    0.126809   0.466 0.641049
SLD              -0.031387   0.059514    0.059535   0.527 0.598053
pH               -0.005641   0.030044    0.030083   0.188 0.851257
Longitude         0.009574   0.043358    0.043416   0.221 0.825475
Lakearea         -0.001117   0.009260    0.009271   0.120 0.904107

(conditional average)
                 Estimate Std. Error Adjusted SE z value Pr(>|z|)
(Intercept)      -0.34685    0.50213     0.50345   0.689 0.490862
Agriculturebasin  0.63251    0.15124     0.15147   4.176 2.97e-05 ***
Agriculturebuffer -0.56914    0.14200     0.14220   4.002 6.27e-05 ***
Depth            -0.51933    0.06979     0.06988   7.431  < 2e-16 ***
Developedbuffer  -0.46370    0.17036     0.17047   2.720 0.006527 **
Elevation         0.27401    0.05396     0.05407   5.068 4.00e-07 ***
Latitude         -0.32718    0.09286     0.09305   3.516 0.000438 ***
TotalP           -0.17883    0.05215     0.05227   3.421 0.000623 ***
TotalN           -0.22109    0.08738     0.08753   2.526 0.011540 *
Developedbasin    0.24695    0.14394     0.14416   1.713 0.086717 .
SLD              -0.11840    0.05530     0.05539   2.138 0.032551 *
pH               -0.07854    0.08272     0.08291   0.947 0.343508
Longitude         0.10609    0.10292     0.10319   1.028 0.303911
Lakearea         -0.04001    0.03893     0.03902   1.025 0.305289
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Relative variable importance:
                     Agriculturebasin Agriculturebuffer Depth
Developedbuffer Elevation Latitude TotalP TotalN SLD  Developedbasin
Longitude pH   Lakearea
Importance:          1.00             1.00              1.00  1.00
1.00      1.00      0.68   0.39   0.27 0.24          0.09       0.07 0.03
N containing models:   18               18                18    18
18        18        11      9      7    7             3          3    2
```

Deep diatoms (400 grain)

```
Model-averaged coefficients:
(full average)
                   Estimate Std. Error Adjusted SE z value Pr(>|z|)
(Intercept)       -0.2233747  0.3486148   0.3495314   0.639    0.523
Agriculturebasin   0.8057256  0.1419828   0.1422832   5.663   <2e-16 ***
Agriculturebuffer -0.5351444  0.0941017   0.0942858   5.676   <2e-16 ***
Depth             -0.4217280  0.0627719   0.0628450   6.711   <2e-16 ***
Developedbuffer   -0.0808249  0.0713236   0.0713586   1.133    0.257
Elevation          0.4762979  0.0388424   0.0389372  12.232   <2e-16 ***
Lakearea          -0.0783709  0.0608411   0.0608812   1.287    0.198
Longitude          0.4598299  0.0825477   0.0827351   5.558   <2e-16 ***
pH                -0.4255084  0.0787721   0.0789470   5.390    1e-07 ***
Developedbasin    -0.0255886  0.0481033   0.0481252   0.532    0.595
TotalN             0.0330251  0.0775497   0.0775798   0.426    0.670
Latitude           0.0001272  0.0145475   0.0145789   0.009    0.993
TotalP             0.0007799  0.0116086   0.0116350   0.067    0.947
SLD               -0.0001739  0.0029844   0.0029890   0.058    0.954

(conditional average)
                  Estimate Std. Error Adjusted SE z value Pr(>|z|)
(Intercept)       -0.223375   0.348615    0.349531   0.639  0.52278
Agriculturebasin   0.805726   0.141983    0.142283   5.663  < 2e-16 ***
Agriculturebuffer -0.535144   0.094102    0.094286   5.676  < 2e-16 ***
Depth             -0.421728   0.062772    0.062845   6.711  < 2e-16 ***
Developedbuffer   -0.129425   0.043079    0.043172   2.998  0.00272 **
Elevation          0.476298   0.038842    0.038937  12.232  < 2e-16 ***
Lakearea          -0.112241   0.038727    0.038817   2.892  0.00383 **
Longitude          0.459830   0.082548    0.082735   5.558  < 2e-16 ***
pH                -0.425508   0.078772    0.078947   5.390    1e-07 ***
Developedbasin    -0.087131   0.050168    0.050240   1.734  0.08286 .
TotalN             0.162963   0.092200    0.092325   1.765  0.07755 .
Latitude           0.002742   0.067487    0.067633   0.041  0.96766
TotalP             0.022000   0.057746    0.057895   0.380  0.70394
SLD               -0.021581   0.025358    0.025425   0.849  0.39598
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Relative variable importance:
                     Agriculturebasin Agriculturebuffer Depth Elevation
Longitude pH   Lakearea Developedbuffer Developedbasin TotalN Latitude
TotalP SLD
Importance:          1.00             1.00              1.00  1.00
1.00      1.00 0.70     0.62            0.29           0.20   0.05
0.04   0.01
N containing models:   18               18                18    18
18        18   12       11               7              5      4        3
1
```

Shallow diatoms (100 grain)

```
Model-averaged coefficients:
(full average)
                    Estimate Std. Error Adjusted SE z value Pr(>|z|)
(Intercept)         0.0531371  0.1362198   0.1363943   0.390  0.69684
Agriculturebasin   -0.2341456  0.0307026   0.0307402   7.617  < 2e-16 ***
Depth              -0.1277072  0.0473058   0.0473302   2.698  0.00697 **
Elevation           0.0759454  0.0666987   0.0667147   1.138  0.25497
Latitude            0.0457593  0.0668361   0.0668537   0.684  0.49368
Longitude           0.2534389  0.1402405   0.1402795   1.807  0.07081 .
pH                 -0.0478738  0.0479865   0.0479990   0.997  0.31857
TotalN              0.2099040  0.0338981   0.0339386   6.185  < 2e-16 ***
TotalP             -0.1959760  0.0323551   0.0323960   6.049  < 2e-16 ***
Lakearea           -0.0150684  0.0323394   0.0323458   0.466  0.64132
Developedbuffer    -0.0007414  0.0066581   0.0066615   0.111  0.91138
SLD                -0.0005873  0.0059944   0.0059978   0.098  0.92199
Developedbasin     -0.0003922  0.0047840   0.0047870   0.082  0.93471
Agriculturebuffer   0.0001610  0.0035179   0.0035211   0.046  0.96352

(conditional average)
                  Estimate Std. Error Adjusted SE z value Pr(>|z|)
(Intercept)         0.05314    0.13622     0.13639   0.390 0.696844
Agriculturebasin   -0.23415    0.03070     0.03074   7.617  < 2e-16 ***
Depth              -0.13574    0.03590     0.03593   3.778 0.000158 ***
Elevation           0.11996    0.04179     0.04183   2.868 0.004137 **
Latitude            0.12171    0.05136     0.05142   2.367 0.017940 *
Longitude           0.30927    0.08206     0.08214   3.765 0.000167 ***
pH                 -0.08531    0.03016     0.03020   2.825 0.004725 **
TotalN              0.20990    0.03390     0.03394   6.185  < 2e-16 ***
TotalP             -0.19598    0.03236     0.03240   6.049  < 2e-16 ***
Lakearea           -0.06984    0.03197     0.03200   2.182 0.029077 *
Developedbuffer    -0.03432    0.03000     0.03003   1.143 0.253156
SLD                -0.03463    0.03066     0.03069   1.128 0.259221
Developedbasin     -0.02834    0.02936     0.02939   0.964 0.334980
Agriculturebuffer   0.02315    0.03531     0.03535   0.655 0.512675
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Relative variable importance:
                     Agriculturebasin TotalN TotalP Depth Longitude
Elevation pH   Latitude Lakearea Developedbuffer SLD  Developedbasin
Agriculturebuffer
Importance:          1.00             1.00   1.00   0.94  0.82      0.63
0.56 0.38     0.22     0.02            0.02 0.01           0.01
N containing models:   33               33     33     30    25         18
18   13       12        3               2    2              1
```

Shallow diatoms (200 grain)

```
Model-averaged coefficients:
(full average)
                   Estimate Std. Error Adjusted SE z value Pr(>|z|)
(Intercept)       -0.0401444  0.1266926   0.1268519   0.316    0.752
Agriculturebasin  -0.3128709  0.0404686   0.0405073   7.724  < 2e-16 ***
Developedbasin     0.3372171  0.0487398   0.0488005   6.910  < 2e-16 ***
Developedbuffer   -0.5235130  0.0515073   0.0515718  10.151  < 2e-16 ***
Latitude          -0.2237272  0.0451109   0.0451668   4.953 7.00e-07 ***
Longitude          0.5500882  0.0668993   0.0669814   8.213  < 2e-16 ***
pH                -0.1741795  0.0396613   0.0397110   4.386 1.15e-05 ***
TotalN             0.3217800  0.0465761   0.0466087   6.904  < 2e-16 ***
TotalP            -0.0442310  0.0523840   0.0523983   0.844    0.399
Agriculturebuffer  0.0065687  0.0243508   0.0243604   0.270    0.787
Elevation          0.0005424  0.0072921   0.0072997   0.074    0.941
SLD               -0.0002578  0.0037758   0.0037790   0.068    0.946

(conditional average)
                  Estimate Std. Error Adjusted SE z value Pr(>|z|)
(Intercept)       -0.04014    0.12669     0.12685   0.316  0.75165
Agriculturebasin  -0.31287    0.04047     0.04051   7.724  < 2e-16 ***
Developedbasin     0.33722    0.04874     0.04880   6.910  < 2e-16 ***
Developedbuffer   -0.52351    0.05151     0.05157  10.151  < 2e-16 ***
Latitude          -0.22373    0.04511     0.04517   4.953 7.00e-07 ***
Longitude          0.55009    0.06690     0.06698   8.213  < 2e-16 ***
pH                -0.17418    0.03966     0.03971   4.386 1.15e-05 ***
TotalN             0.32178    0.04658     0.04661   6.904  < 2e-16 ***
TotalP            -0.09256    0.03562     0.03567   2.595  0.00946 **
Agriculturebuffer  0.06579    0.04520     0.04525   1.454  0.14599
Elevation          0.01705    0.03728     0.03733   0.457  0.64792
SLD               -0.01852    0.02619     0.02622   0.706  0.48011
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Relative variable importance:
                     Agriculturebasin Developedbasin Developedbuffer
Latitude Longitude pH   TotalN TotalP Agriculturebuffer Elevation SLD
Importance:          1.00             1.00           1.00            1.00
1.00      1.00 1.00   0.48   0.10              0.03      0.01
N containing models:    7                7              7               7
7         7    7      3      2                 2         1
```

Shallow diatoms (300 grain)

```
Model-averaged coefficients:
(full average)
                    Estimate Std. Error Adjusted SE z value Pr(>|z|)
(Intercept)        -0.0167063  0.1297461   0.1299092   0.129   0.8977
Agriculturebasin   -0.4039055  0.0359106   0.0359457  11.237  < 2e-16 ***
Developedbasin      0.2505924  0.0561216   0.0561821   4.460  8.2e-06 ***
Developedbuffer    -0.4602799  0.0586701   0.0587340   7.837  < 2e-16 ***
Lakearea           -0.0723240  0.0330704   0.0330890   2.186   0.0288 *
Latitude           -0.3065778  0.0424209   0.0424731   7.218  < 2e-16 ***
Longitude           0.8370023  0.0627731   0.0628461  13.318  < 2e-16 ***
TotalN              0.2856138  0.0303924   0.0304223   9.388  < 2e-16 ***
pH                 -0.0146469  0.0361500   0.0361611   0.405   0.6854
Agriculturebuffer   0.0014335  0.0121941   0.0122042   0.117   0.9065
TotalP             -0.0012990  0.0095950   0.0096010   0.135   0.8924
Elevation          -0.0002633  0.0057748   0.0057814   0.046   0.9637

(conditional average)
                  Estimate Std. Error Adjusted SE z value Pr(>|z|)
(Intercept)        -0.01671    0.12975     0.12991   0.129 0.897674
Agriculturebasin   -0.40391    0.03591     0.03595  11.237  < 2e-16 ***
Developedbasin      0.25059    0.05612     0.05618   4.460  8.2e-06 ***
Developedbuffer    -0.46028    0.05867     0.05873   7.837  < 2e-16 ***
Lakearea           -0.08066    0.02339     0.02342   3.445 0.000572 ***
Latitude           -0.30658    0.04242     0.04247   7.218  < 2e-16 ***
Longitude           0.83700    0.06277     0.06285  13.318  < 2e-16 ***
TotalN              0.28561    0.03039     0.03042   9.388  < 2e-16 ***
pH                 -0.08194    0.04239     0.04244   1.931 0.053518 .
Agriculturebuffer   0.03713    0.05026     0.05032   0.738 0.460581
TotalP             -0.03672    0.03608     0.03613   1.016 0.309397
Elevation          -0.01168    0.03668     0.03673   0.318 0.750532
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Relative variable importance:
                     Agriculturebasin Developedbasin Developedbuffer
Latitude Longitude TotalN Lakearea pH   Agriculturebuffer TotalP Elevation
Importance:          1.00             1.00           1.00            1.00
1.00      1.00   0.90     0.18 0.04              0.04   0.02
N containing models:    7                7              7               7
7         7      5        2    1                 1      1
```

Shallow diatoms (400 grain)

```
Model-averaged coefficients:
(full average)
                   Estimate Std. Error Adjusted SE z value Pr(>|z|)
(Intercept)       -0.023959   0.097469    0.097592   0.246    0.806
Agriculturebasin  -0.372640   0.057930    0.057973   6.428  < 2e-16 ***
Developedbasin     0.340498   0.057013    0.057080   5.965  < 2e-16 ***
Developedbuffer   -0.385762   0.064470    0.064539   5.977  < 2e-16 ***
Lakearea          -0.149680   0.023329    0.023358   6.408  < 2e-16 ***
Latitude          -0.214945   0.040557    0.040602   5.294 1.00e-07 ***
Longitude          0.905084   0.062355    0.062424  14.499  < 2e-16 ***
pH                -0.194184   0.045404    0.045459   4.272 1.94e-05 ***
TotalN             0.370027   0.047512    0.047545   7.783  < 2e-16 ***
TotalP             0.028506   0.044909    0.044921   0.635    0.526
Agriculturebuffer  0.012117   0.037739    0.037753   0.321    0.748
Elevation         -0.003782   0.017314    0.017321   0.218    0.827
SLD                0.004600   0.018168    0.018174   0.253    0.800
Depth              0.002836   0.014177    0.014183   0.200    0.842

(conditional average)
                  Estimate Std. Error Adjusted SE z value Pr(>|z|)
(Intercept)       -0.02396    0.09747     0.09759   0.246   0.8061
Agriculturebasin  -0.37264    0.05793     0.05797   6.428  < 2e-16 ***
Developedbasin     0.34050    0.05701     0.05708   5.965  < 2e-16 ***
Developedbuffer   -0.38576    0.06447     0.06454   5.977  < 2e-16 ***
Lakearea          -0.14968    0.02333     0.02336   6.408  < 2e-16 ***
Latitude          -0.21495    0.04056     0.04060   5.294 1.00e-07 ***
Longitude          0.90508    0.06236     0.06242  14.499  < 2e-16 ***
pH                -0.19418    0.04540     0.04546   4.272 1.94e-05 ***
TotalN             0.37003    0.04751     0.04754   7.783  < 2e-16 ***
TotalP             0.08438    0.03544     0.03548   2.378   0.0174 *
Agriculturebuffer  0.09270    0.05853     0.05859   1.582   0.1136
Elevation         -0.05632    0.03880     0.03885   1.450   0.1471
SLD                0.05624    0.03364     0.03368   1.670   0.0949 .
Depth              0.04749    0.03528     0.03533   1.344   0.1789
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Relative variable importance:
                     Agriculturebasin Developedbasin Developedbuffer
Lakearea Latitude Longitude pH   TotalN TotalP Agriculturebuffer SLD
Elevation Depth
Importance:          1.00             1.00           1.00            1.00
1.00     1.00      1.00 1.00   0.34   0.13              0.08 0.07
0.06
N containing models:   11               11             11              11
11       11        11   11      5      3                 2    2          3
```

Planktonic diatoms (100 grain)

```
Model-averaged coefficients:
(full average)
                    Estimate Std. Error Adjusted SE z value Pr(>|z|)
(Intercept)       -3.084e-02  1.001e-01   1.004e-01   0.307 0.758664
Agriculturebasin  -3.190e-01  5.309e-02   5.322e-02   5.994  < 2e-16 ***
Lakearea          -1.202e-01  6.152e-02   6.160e-02   1.952 0.050937 .
TotalP             2.130e-01  5.937e-02   5.948e-02   3.581 0.000342 ***
Depth             -2.346e-02  5.019e-02   5.022e-02   0.467 0.640414
Longitude          2.035e-02  5.673e-02   5.677e-02   0.359 0.719918
Latitude           1.901e-02  5.057e-02   5.060e-02   0.376 0.707151
TotalN             1.421e-02  4.502e-02   4.504e-02   0.315 0.752425
pH                -8.529e-03  3.387e-02   3.389e-02   0.252 0.801316
Elevation         -1.106e-03  1.161e-02   1.163e-02   0.095 0.924218
Agriculturebuffer  8.130e-04  1.174e-02   1.176e-02   0.069 0.944898
SLD               -1.075e-03  1.226e-02   1.228e-02   0.088 0.930266
Developedbasin    -3.217e-04  6.214e-03   6.227e-03   0.052 0.958796
Developedbuffer   -2.235e-05  5.175e-03   5.189e-03   0.004 0.996562

(conditional average)
                   Estimate Std. Error Adjusted SE z value Pr(>|z|)
(Intercept)       -0.030835   0.100100    0.100364   0.307  0.75866
Agriculturebasin  -0.318978   0.053087    0.053215   5.994  < 2e-16 ***
Lakearea          -0.137675   0.043967    0.044082   3.123  0.00179 **
TotalP             0.215944   0.054197    0.054313   3.976 7.01e-05 ***
Depth             -0.106149   0.051193    0.051323   2.068  0.03862 *
Longitude          0.137181   0.075251    0.075444   1.818  0.06902 .
Latitude           0.114669   0.066735    0.066909   1.714  0.08657 .
TotalN             0.112760   0.070504    0.070635   1.596  0.11040
pH                -0.097969   0.066423    0.066578   1.471  0.14116
Elevation         -0.051653   0.060696    0.060857   0.849  0.39602
Agriculturebuffer  0.038736   0.071389    0.071578   0.541  0.58838
SLD               -0.043586   0.065174    0.065292   0.668  0.50442
Developedbasin    -0.023545   0.047738    0.047864   0.492  0.62278
Developedbuffer   -0.001865   0.047225    0.047351   0.039  0.96859
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Relative variable importance:
                     Agriculturebasin TotalP Lakearea Depth Latitude
Longitude TotalN pH   SLD  Elevation Agriculturebuffer Developedbasin
Developedbuffer
Importance:          1.00             0.99   0.87     0.22  0.17     0.15
0.13   0.09 0.02 0.02      0.02              0.01           0.01
N containing models:   27               26     21        7     7        5
6      4    2    1         1                 1              1
```

Planktonic diatoms (200 grain)

```
Model-averaged coefficients:
(full average)
                   Estimate Std. Error Adjusted SE z value Pr(>|z|)
(Intercept)       -0.096566   0.134175    0.134521   0.718   0.4729
Agriculturebasin  -0.643569   0.074292    0.074422   8.648   <2e-16 ***
Developedbasin    -0.271823   0.125169    0.125286   2.170   0.0300 *
Developedbuffer    0.105437   0.132460    0.132548   0.795   0.4263
Elevation         -0.146081   0.090898    0.090986   1.606   0.1084
Lakearea          -0.115974   0.066673    0.066728   1.738   0.0822 .
Longitude          0.283738   0.132057    0.132225   2.146   0.0319 *
TotalP             0.302328   0.056483    0.056590   5.342    1e-07 ***
SLD               -0.051157   0.070733    0.070769   0.723   0.4698
Agriculturebuffer -0.013778   0.046541    0.046581   0.296   0.7674
TotalN             0.012172   0.041584    0.041614   0.292   0.7699
Latitude           0.001230   0.020324    0.020355   0.060   0.9518
Depth             -0.001777   0.013791    0.013807   0.129   0.8976
pH                -0.002982   0.022521    0.022545   0.132   0.8948

(conditional average)
                  Estimate Std. Error Adjusted SE z value Pr(>|z|)
(Intercept)       -0.09657    0.13417     0.13452   0.718  0.47285
Agriculturebasin  -0.64357    0.07429     0.07442   8.648  < 2e-16 ***
Developedbasin    -0.27182    0.12517     0.12529   2.170  0.03004 *
Developedbuffer    0.22538    0.10234     0.10258   2.197  0.02802 *
Elevation         -0.18066    0.06302     0.06318   2.859  0.00424 **
Lakearea          -0.13976    0.04509     0.04519   3.093  0.00198 **
Longitude          0.31209    0.10166     0.10190   3.063  0.00219 **
TotalP             0.30233    0.05648     0.05659   5.342    1e-07 ***
SLD               -0.12676    0.05304     0.05316   2.384  0.01710 *
Agriculturebuffer -0.11666    0.07961     0.07981   1.462  0.14380
TotalN             0.10809    0.07063     0.07078   1.527  0.12673
Latitude           0.02944    0.09515     0.09530   0.309  0.75740
Depth             -0.05413    0.05440     0.05453   0.993  0.32088
pH                -0.07165    0.08523     0.08539   0.839  0.40141
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Relative variable importance:
                     Agriculturebasin Developedbasin TotalP Longitude
Lakearea Elevation Developedbuffer SLD  Agriculturebuffer TotalN Latitude
pH   Depth
Importance:          1.00             1.00           1.00   0.91      0.83
0.81      0.47            0.40 0.12              0.11   0.04     0.04 0.03
N containing models:   54               54             54     46        41
40        23              25    9                11      6        7    5
```

Planktonic diatoms (300 grain)

```
Model-averaged coefficients:
(full average)
                   Estimate Std. Error Adjusted SE z value Pr(>|z|)
(Intercept)       -0.1950132  0.2069928   0.2075274   0.940 0.347372
Agriculturebasin  -0.9956783  0.0774962   0.0776407  12.824  < 2e-16 ***
Elevation         -0.2372234  0.0662965   0.0664411   3.570 0.000356 ***
Lakearea           0.0982695  0.0557882   0.0558437   1.760 0.078454 .
Longitude          0.3542688  0.1289839   0.1292281   2.741 0.006117 **
SLD               -0.2538377  0.0499883   0.0501094   5.066    4e-07 ***
TotalP             0.2834288  0.0505740   0.0506851   5.592  < 2e-16 ***
Depth              0.0146281  0.0457888   0.0458122   0.319 0.749495
Latitude          -0.0133477  0.0453594   0.0453920   0.294 0.768717
Agriculturebuffer  0.0063217  0.0418165   0.0418554   0.151 0.879947
TotalN             0.0072544  0.0401008   0.0401231   0.181 0.856522
pH                -0.0001441  0.0119450   0.0119759   0.012 0.990398
Developedbuffer   -0.0003713  0.0074812   0.0074985   0.050 0.960508
Developedbasin     0.0002776  0.0070758   0.0070929   0.039 0.968776

(conditional average)
                  Estimate Std. Error Adjusted SE z value Pr(>|z|)
(Intercept)       -0.195013   0.206993    0.207527   0.940 0.347372
Agriculturebasin  -0.995678   0.077496    0.077641  12.824  < 2e-16 ***
Elevation         -0.237223   0.066297    0.066441   3.570 0.000356 ***
Lakearea           0.117653   0.038022    0.038120   3.086 0.002026 **
Longitude          0.365681   0.114016    0.114301   3.199 0.001378 **
SLD               -0.253838   0.049988    0.050109   5.066    4e-07 ***
TotalP             0.283429   0.050574    0.050685   5.592  < 2e-16 ***
Depth              0.110381   0.072467    0.072578   1.521 0.128296
Latitude          -0.110165   0.079470    0.079623   1.384 0.166487
Agriculturebuffer  0.102035   0.135858    0.136051   0.750 0.453268
TotalN             0.109985   0.114374    0.114493   0.961 0.336740
pH                -0.004881   0.069347    0.069527   0.070 0.944031
Developedbuffer   -0.017120   0.047895    0.048019   0.357 0.721449
Developedbasin     0.013311   0.047190    0.047313   0.281 0.778446
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Relative variable importance:
                    Agriculturebasin Elevation SLD  TotalP Longitude
Lakearea Depth Latitude TotalN Agriculturebuffer pH   Developedbuffer
Developedbasin
Importance:          1.00             1.00      1.00 1.00   0.97      0.84
0.13  0.12     0.07   0.06              0.03 0.02          0.02
N containing models:   14               14        14   14     13        11
4     4        3      2                 1    1             1
```

Planktonic diatoms (400 grain)

```
Model-averaged coefficients:
(full average)
                   Estimate Std. Error Adjusted SE z value Pr(>|z|)
(Intercept)       -0.271184   0.264732    0.265422   1.022 0.306919
Agriculturebasin  -1.070280   0.097881    0.098087  10.911  < 2e-16 ***
Depth              0.267057   0.075054    0.075189   3.552 0.000383 ***
Developedbasin     0.184625   0.111954    0.112066   1.647 0.099461 .
Elevation         -0.268271   0.067554    0.067715   3.962 7.44e-05 ***
Lakearea           0.234271   0.040274    0.040365   5.804  < 2e-16 ***
Longitude          0.696725   0.130309    0.130624   5.334 1.00e-07 ***
SLD               -0.260194   0.057914    0.058045   4.483 7.40e-06 ***
TotalN             0.131131   0.121931    0.122020   1.075 0.282527
TotalP             0.485539   0.081445    0.081565   5.953  < 2e-16 ***
Developedbuffer   -0.025326   0.098344    0.098435   0.257 0.796953
pH                 0.027149   0.071210    0.071262   0.381 0.703219
Agriculturebuffer -0.002024   0.038462    0.038537   0.053 0.958111
Latitude          -0.001959   0.025773    0.025818   0.076 0.939500

(conditional average)
                  Estimate Std. Error Adjusted SE z value Pr(>|z|)
(Intercept)       -0.27118    0.26473     0.26542   1.022 0.306919
Agriculturebasin  -1.07028    0.09788     0.09809  10.911  < 2e-16 ***
Depth              0.26706    0.07505     0.07519   3.552 0.000383 ***
Developedbasin     0.20662    0.09737     0.09752   2.119 0.034105 *
Elevation         -0.26827    0.06755     0.06772   3.962 7.44e-05 ***
Lakearea           0.23427    0.04027     0.04037   5.804  < 2e-16 ***
Longitude          0.69672    0.13031     0.13062   5.334 1.00e-07 ***
SLD               -0.26019    0.05791     0.05805   4.483 7.40e-06 ***
TotalN             0.21167    0.08337     0.08358   2.532 0.011329 *
TotalP             0.48554    0.08144     0.08157   5.953  < 2e-16 ***
Developedbuffer   -0.10622    0.17881     0.17901   0.593 0.552923
pH                 0.14911    0.09831     0.09852   1.514 0.130136
Agriculturebuffer -0.02722    0.13860     0.13888   0.196 0.844595
Latitude          -0.03541    0.10402     0.10421   0.340 0.734026
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Relative variable importance:
                     Agriculturebasin Depth Elevation Lakearea Longitude
SLD  TotalP Developedbasin TotalN Developedbuffer pH   Agriculturebuffer
Latitude
Importance:          1.00             1.00  1.00      1.00     1.00
1.00 1.00   0.89           0.62   0.24            0.18 0.07
0.06
N containing models:   20               20    20        20       20
20   20     14             10      9               6    3
3
```

APPENDIX C: MODEL AVERAGES FOR CHAPTER 4 (R OUTPUTS)

Mean environmental variables against β deviations

January 2008

```
Model-averaged coefficients:
(full average)
                     Estimate Std. Error Adjusted SE z value Pr(>|z|)
(Intercept)         0.0028012  0.0322269   0.0322664   0.087   0.9308
elevation          -0.3671145  0.0794195   0.0794455   4.621  3.8e-06 ***
Mean_temp          -0.2217875  0.1150267   0.1150517   1.928   0.0539 .
per_ag             -0.0622116  0.0493171   0.0493327   1.261   0.2073
Precip             -0.2941567  0.0451266   0.0451735   6.512  < 2e-16 ***
Precip_seasonality -0.2417365  0.0493568   0.0493959   4.894  1.0e-06 ***
Temp_seasonality   -0.6113291  0.0926123   0.0926485   6.598  < 2e-16 ***
WinAvg              0.1056041  0.0553842   0.0554014   1.906   0.0566 .
NPP                 0.0529149  0.0673335   0.0673485   0.786   0.4321
Mean_diurnal_range -0.0361774  0.0680707   0.0680820   0.531   0.5952
per_intro           0.0141920  0.0303025   0.0303099   0.468   0.6396
per_dist           -0.0001957  0.0034133   0.0034160   0.057   0.9543

(conditional average)
                    Estimate Std. Error Adjusted SE z value Pr(>|z|)
(Intercept)         0.002801   0.032227    0.032266   0.087 0.930819
elevation          -0.367115   0.079419    0.079445   4.621  3.8e-06 ***
Mean_temp          -0.261279   0.072587    0.072634   3.597 0.000322 ***
per_ag             -0.090847   0.030826    0.030862   2.944 0.003244 **
Precip             -0.294157   0.045127    0.045173   6.512  < 2e-16 ***
Precip_seasonality -0.241737   0.049357    0.049396   4.894  1.0e-06 ***
Temp_seasonality   -0.611329   0.092612    0.092649   6.598  < 2e-16 ***
WinAvg              0.125761   0.033436    0.033470   3.757 0.000172 ***
NPP                 0.119360   0.047917    0.047964   2.489 0.012828 *
Mean_diurnal_range -0.134518   0.063250    0.063295   2.125 0.033565 *
per_intro           0.065365   0.029737    0.029772   2.196 0.028127 *
per_dist           -0.021514   0.028671    0.028706   0.749 0.453585
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Relative variable importance:
                     elevation Precip Precip_seasonality Temp_seasonality
Mean_temp WinAvg per_ag NPP  Mean_diurnal_range per_intro per_dist
Importance:          1.00      1.00   1.00               1.00
0.85      0.84   0.68   0.44 0.27               0.22      0.01
N containing models:   21        21     21                 21
16        15     13     11   12                 8         1
```

January 2009

```
Model-averaged coefficients:
(full average)
                    Estimate Std. Error Adjusted SE z value Pr(>|z|)
(Intercept)        0.0042981  0.0365832   0.0366452   0.117  0.90663
elevation         -0.2976416  0.0893382   0.0893997   3.329  0.00087 ***
Mean_diurnal_range -0.1929929  0.0819576   0.0820151   2.353  0.01862 *
Mean_temp         -0.1302167  0.1075961   0.1076428   1.210  0.22639
Precip            -0.3264301  0.0560571   0.0561453   5.814  < 2e-16 ***
Precip_seasonality -0.2141373  0.0548795   0.0549541   3.897 9.75e-05 ***
Temp_seasonality  -0.4566101  0.0800803   0.0801439   5.697  < 2e-16 ***
NPP                0.0119210  0.0368765   0.0368922   0.323  0.74660
WinAvg             0.0052927  0.0227242   0.0227318   0.233  0.81589
per_intro          0.0011443  0.0087516   0.0087578   0.131  0.89604
per_dist          -0.0010271  0.0083843   0.0083907   0.122  0.90258
per_water         -0.0002972  0.0048856   0.0048921   0.061  0.95155
per_ag            -0.0002192  0.0047835   0.0047906   0.046  0.96350
per_urban         -0.0001339  0.0044246   0.0044317   0.030  0.97590

(conditional average)
                   Estimate Std. Error Adjusted SE z value Pr(>|z|)
(Intercept)        0.004298   0.036583    0.036645   0.117  0.90663
elevation         -0.297642   0.089338    0.089400   3.329  0.00087 ***
Mean_diurnal_range -0.207784   0.064486    0.064565   3.218  0.00129 **
Mean_temp         -0.188591   0.075880    0.075976   2.482  0.01306 *
Precip            -0.326430   0.056057    0.056145   5.814  < 2e-16 ***
Precip_seasonality -0.214137   0.054879    0.054954   3.897 9.75e-05 ***
Temp_seasonality  -0.456610   0.080080    0.080144   5.697  < 2e-16 ***
NPP                0.089024   0.057370    0.057445   1.550  0.12121
WinAvg             0.074348   0.046041    0.046094   1.613  0.10675
per_intro          0.040313   0.033454    0.033510   1.203  0.22898
per_dist          -0.038816   0.034495    0.034553   1.123  0.26128
per_water         -0.018413   0.033840    0.033897   0.543  0.58699
per_ag            -0.013898   0.035505    0.035566   0.391  0.69597
per_urban         -0.008972   0.035107    0.035166   0.255  0.79862
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Relative variable importance:
                    elevation Precip Precip_seasonality Temp_seasonality
Mean_diurnal_range Mean_temp NPP  WinAvg per_intro per_dist per_water
per_ag per_urban
Importance:          1.00      1.00   1.00               1.00
0.93               0.69      0.13 0.07   0.03      0.03     0.02      0.02
0.01
N containing models:   12        12     12                 12
10                 10         2    2      1         1        1         1
1
```

January 2010

```
Model-averaged coefficients:
(full average)
                     Estimate Std. Error Adjusted SE z value Pr(>|z|)
(Intercept)         2.087e-02  4.875e-02   4.884e-02   0.427   0.6692
elevation          -2.755e-01  1.349e-01   1.349e-01   2.042   0.0412 *
Mean_diurnal_range -1.229e-01  1.136e-01   1.136e-01   1.082   0.2794
Precip             -2.838e-01  6.679e-02   6.687e-02   4.244  2.2e-05 ***
Precip_seasonality -2.183e-01  8.088e-02   8.094e-02   2.697   0.0070 **
Temp_seasonality   -5.163e-01  1.247e-01   1.248e-01   4.138  3.5e-05 ***
Mean_temp          -1.668e-01  1.633e-01   1.633e-01   1.022   0.3069
WinAvg              6.839e-02  7.611e-02   7.613e-02   0.898   0.3690
NPP                -3.070e-02  6.230e-02   6.232e-02   0.493   0.6223
per_ag             -1.389e-03  1.008e-02   1.009e-02   0.138   0.8905
per_intro           2.048e-04  3.939e-03   3.944e-03   0.052   0.9586
per_urban          -6.612e-05  3.444e-03   3.450e-03   0.019   0.9847
per_dist            2.455e-04  4.819e-03   4.826e-03   0.051   0.9594

(conditional average)
                    Estimate Std. Error Adjusted SE z value Pr(>|z|)
(Intercept)         0.020865   0.048753    0.048837   0.427  0.66920
elevation          -0.288409   0.123831    0.123874   2.328  0.01990 *
Mean_diurnal_range -0.203974   0.069807    0.069872   2.919  0.00351 **
Precip             -0.283811   0.066791    0.066874   4.244  2.2e-05 ***
Precip_seasonality -0.226878   0.069625    0.069696   3.255  0.00113 **
Temp_seasonality   -0.516326   0.124717    0.124764   4.138  3.5e-05 ***
Mean_temp          -0.276833   0.117361    0.117443   2.357  0.01841 *
WinAvg              0.136662   0.047394    0.047452   2.880  0.00398 **
NPP                -0.126118   0.062532    0.062622   2.014  0.04401 *
per_ag             -0.038801   0.037231    0.037292   1.040  0.29812
per_intro           0.021142   0.034040    0.034099   0.620  0.53525
per_urban          -0.007618   0.036183    0.036245   0.210  0.83354
per_dist            0.014755   0.034373    0.034432   0.429  0.66827
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Relative variable importance:
                     Precip Temp_seasonality Precip_seasonality elevation
Mean_temp Mean_diurnal_range WinAvg NPP  per_ag per_dist per_intro
per_urban
Importance:          1.00   1.00             0.96               0.96
0.60      0.60               0.50   0.24 0.04   0.02     0.01      0.01
N containing models:   20     20               18                 18
10        14                  8      5    3      2        1         1
```

January 2011

```
Model-averaged coefficients:
(full average)
                    Estimate Std. Error Adjusted SE z value Pr(>|z|)
(Intercept)        -0.006334   0.040446    0.040516   0.156  0.87576
elevation          -0.194926   0.120228    0.120250   1.621  0.10502
per_water           0.061674   0.053949    0.053973   1.143  0.25317
Precip             -0.180241   0.069528    0.069583   2.590  0.00959 **
Precip_seasonality -0.060836   0.077276    0.077302   0.787  0.43128
Temp_seasonality   -0.278514   0.128797    0.128822   2.162  0.03062 *
WinAvg              0.031471   0.049856    0.049871   0.631  0.52801
Mean_temp           0.087893   0.144530    0.144541   0.608  0.54313
NPP                 0.073843   0.103505    0.103519   0.713  0.47564
Mean_diurnal_range -0.016021   0.043705    0.043721   0.366  0.71404
per_ag             -0.005815   0.022387    0.022395   0.260  0.79512
per_dist            0.008779   0.026349    0.026360   0.333  0.73910
per_urban           0.002191   0.013378    0.013384   0.164  0.86996
per_intro           0.005690   0.021014    0.021022   0.271  0.78666

(conditional average)
                    Estimate Std. Error Adjusted SE z value Pr(>|z|)
(Intercept)        -0.006334   0.040446    0.040516   0.156  0.87576
elevation          -0.254329   0.061254    0.061310   4.148 3.35e-05 ***
per_water           0.096804   0.034171    0.034229   2.828  0.00468 **
Precip             -0.186992   0.061260    0.061325   3.049  0.00229 **
Precip_seasonality -0.138648   0.053114    0.053198   2.606  0.00915 **
Temp_seasonality   -0.301327   0.105229    0.105262   2.863  0.00420 **
WinAvg              0.096159   0.037075    0.037135   2.589  0.00961 **
Mean_temp           0.283424   0.109273    0.109322   2.593  0.00953 **
NPP                 0.180551   0.083238    0.083281   2.168  0.03016 *
Mean_diurnal_range -0.106696   0.055196    0.055280   1.930  0.05359 .
per_ag             -0.072587   0.037536    0.037597   1.931  0.05353 .
per_dist            0.070042   0.035332    0.035392   1.979  0.04781 *
per_urban           0.059419   0.038112    0.038174   1.557  0.11958
per_intro           0.064488   0.034833    0.034890   1.848  0.06456 .
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Relative variable importance:
                     Precip Temp_seasonality elevation per_water
Precip_seasonality NPP  WinAvg Mean_temp Mean_diurnal_range per_dist
per_intro per_ag per_urban
Importance:          0.96   0.92             0.77      0.64      0.44
0.41 0.33   0.31      0.15               0.13      0.09      0.08   0.04
N containing models:  106    103              86        65        41
54   33     42        25                 23        21        14      9
```

January 2012

```
Model-averaged coefficients:
(full average)
                    Estimate Std. Error Adjusted SE z value Pr(>|z|)
(Intercept)        -9.275e-05  2.971e-02   2.974e-02   0.003    0.998
NPP                -6.165e-02  5.835e-02   5.837e-02   1.056    0.291
per_water           3.999e-02  4.546e-02   4.547e-02   0.879    0.379
Precip_seasonality -8.337e-02  5.830e-02   5.832e-02   1.430    0.153
Temp_seasonality   -2.200e-01  5.513e-02   5.516e-02   3.988 6.65e-05 ***
WinAvg             -7.161e-02  5.353e-02   5.355e-02   1.337    0.181
Mean_diurnal_range -1.097e-02  3.402e-02   3.403e-02   0.322    0.747
Mean_temp           6.494e-03  3.546e-02   3.547e-02   0.183    0.855
elevation          -6.575e-03  2.513e-02   2.513e-02   0.262    0.794
per_dist           -2.153e-03  1.186e-02   1.186e-02   0.181    0.856
per_ag              6.842e-04  6.870e-03   6.873e-03   0.100    0.921
Precip             -2.548e-04  5.840e-03   5.845e-03   0.044    0.965
per_intro           2.896e-04  4.349e-03   4.352e-03   0.067    0.947
per_urban           3.637e-05  1.837e-03   1.839e-03   0.020    0.984

(conditional average)
                    Estimate Std. Error Adjusted SE z value Pr(>|z|)
(Intercept)        -9.275e-05  2.971e-02   2.974e-02   0.003  0.99751
NPP                -9.965e-02  4.144e-02   4.148e-02   2.403  0.01628 *
per_water           8.046e-02  3.001e-02   3.005e-02   2.678  0.00741 **
Precip_seasonality -1.117e-01  3.731e-02   3.735e-02   2.991  0.00278 **
Temp_seasonality   -2.218e-01  5.156e-02   5.159e-02   4.300 1.71e-05 ***
WinAvg             -9.971e-02  3.448e-02   3.452e-02   2.889  0.00387 **
Mean_diurnal_range -9.445e-02  4.564e-02   4.569e-02   2.067  0.03870 *
Mean_temp           5.710e-02  9.036e-02   9.038e-02   0.632  0.52755
elevation          -7.587e-02  4.504e-02   4.508e-02   1.683  0.09234 .
per_dist           -4.731e-02  3.087e-02   3.090e-02   1.531  0.12582
per_ag              3.996e-02  3.445e-02   3.449e-02   1.159  0.24656
Precip             -1.807e-02  4.580e-02   4.583e-02   0.394  0.69339
per_intro           2.743e-02  3.236e-02   3.240e-02   0.847  0.39725
per_urban           1.190e-02  3.104e-02   3.108e-02   0.383  0.70169
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Relative variable importance: 
                    Temp_seasonality Precip_seasonality WinAvg NPP 
per_water Mean_diurnal_range Mean_temp elevation per_dist per_ag Precip 
per_intro per_urban
Importance:           0.99             0.75               0.72   0.62 
0.5      0.12               0.11      0.09      0.05     0.02   0.01 
0.01     <0.01    
N containing models:    55               43                 40     33 
30         6                  12         8         8        4      4      3 
1
```

January 2013

```
Model-averaged coefficients:
(full average)
                     Estimate Std. Error Adjusted SE z value Pr(>|z|)
(Intercept)        -2.821e-05  2.996e-02   2.999e-02   0.001    0.999
per_ag              1.446e-02  3.108e-02   3.109e-02   0.465    0.642
WinAvg              4.451e-03  1.702e-02   1.702e-02   0.261    0.794
Temp_seasonality    2.541e-03  1.279e-02   1.280e-02   0.199    0.843
per_water           2.096e-03  1.142e-02   1.142e-02   0.183    0.854
Precip_seasonality  2.371e-03  1.242e-02   1.243e-02   0.191    0.849
per_urban          -8.244e-04  6.989e-03   6.992e-03   0.118    0.906
NPP                -3.612e-04  4.809e-03   4.813e-03   0.075    0.940
Precip             -3.192e-04  4.603e-03   4.607e-03   0.069    0.945
Mean_temp          -2.625e-04  4.332e-03   4.335e-03   0.061    0.952
Mean_diurnal_range -2.135e-04  4.109e-03   4.113e-03   0.052    0.959

(conditional average)
                     Estimate Std. Error Adjusted SE z value Pr(>|z|)
(Intercept)        -2.821e-05  2.996e-02   2.999e-02   0.001   0.9992
per_ag              6.766e-02  3.033e-02   3.036e-02   2.228   0.0259 *
WinAvg              5.246e-02  2.990e-02   2.994e-02   1.752   0.0797 .
Temp_seasonality    4.851e-02  2.991e-02   2.995e-02   1.620   0.1053
per_water           4.251e-02  3.044e-02   3.047e-02   1.395   0.1630
Precip_seasonality  4.506e-02  3.177e-02   3.181e-02   1.417   0.1565
per_urban          -3.249e-02  2.993e-02   2.997e-02   1.084   0.2783
NPP                -2.036e-02  2.994e-02   2.998e-02   0.679   0.4971
Precip             -1.867e-02  2.994e-02   2.998e-02   0.623   0.5335
Mean_temp          -1.613e-02  2.994e-02   2.998e-02   0.538   0.5907
Mean_diurnal_range -1.366e-02  2.994e-02   2.998e-02   0.456   0.6486
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Relative variable importance:
                     per_ag WinAvg Precip_seasonality Temp_seasonality
per_water per_urban NPP  Precip Mean_temp Mean_diurnal_range
Importance:          0.21   0.08   0.05               0.05
0.05      0.03      0.02 0.02   0.02      0.02
N containing models:    4      2      2                  1
2         1         1    1      1         1
```

January 2014

```
Model-averaged coefficients:
(full average)
                     Estimate Std. Error Adjusted SE z value Pr(>|z|)
(Intercept)         1.008e-02  3.717e-02   3.722e-02   0.271  0.78652
elevation          -1.074e-01  5.111e-02   5.113e-02   2.100  0.03575 *
NPP                -1.272e-01  5.774e-02   5.776e-02   2.202  0.02767 *
Temp_seasonality   -1.667e-01  5.424e-02   5.426e-02   3.073  0.00212 **
Mean_temp           2.153e-02  6.600e-02   6.601e-02   0.326  0.74434
per_water          -3.031e-03  1.369e-02   1.370e-02   0.221  0.82490
per_dist            1.219e-03  8.415e-03   8.419e-03   0.145  0.88491
Mean_diurnal_range -6.963e-04  8.995e-03   9.003e-03   0.077  0.93835
per_intro          -5.447e-04  5.700e-03   5.704e-03   0.095  0.92393
Precip             -9.204e-05  5.240e-03   5.246e-03   0.018  0.98600

(conditional average)
                    Estimate Std. Error Adjusted SE z value Pr(>|z|)
(Intercept)         0.010080   0.037174    0.037217   0.271 0.786517
elevation          -0.123205   0.032337    0.032373   3.806 0.000141 ***
NPP                -0.145960   0.032965    0.033001   4.423  9.7e-06 ***
Temp_seasonality   -0.175774   0.038903    0.038933   4.515  6.3e-06 ***
Mean_temp           0.122253   0.111478    0.111501   1.096 0.272889
per_water          -0.047138   0.028941    0.028974   1.627 0.103757
per_dist            0.034773   0.029219    0.029253   1.189 0.234550
Mean_diurnal_range -0.022627   0.046182    0.046235   0.489 0.624554
per_intro          -0.023076   0.029267    0.029300   0.788 0.430957
Precip             -0.004332   0.035694    0.035735   0.121 0.903520
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Relative variable importance:
                     Temp_seasonality elevation NPP  Mean_temp per_water
per_dist Mean_diurnal_range per_intro Precip
Importance:          0.95             0.87      0.87 0.18      0.06
0.04     0.03               0.02      0.02
N containing models:    8                7         7    3         1
1        1                  1         1
```

July 2008

```
Model-averaged coefficients:
(full average)
                     Estimate Std. Error Adjusted SE z value Pr(>|z|)
(Intercept)        -2.218e-02  4.830e-02   4.839e-02   0.458 0.646705
elevation          -1.003e-01  1.067e-01   1.067e-01   0.940 0.347240
Mean_temp          -8.042e-02  1.091e-01   1.091e-01   0.737 0.461019
per_ag             -9.137e-02  6.285e-02   6.289e-02   1.453 0.146246
Temp_seasonality   -2.692e-01  7.797e-02   7.802e-02   3.450 0.000562 ***
NPP                 9.125e-02  8.449e-02   8.451e-02   1.080 0.280234
Precip_seasonality -2.303e-03  1.394e-02   1.395e-02   0.165 0.868867
Mean_diurnal_range  5.084e-04  1.115e-02   1.117e-02   0.046 0.963694
per_water           9.467e-04  8.513e-03   8.521e-03   0.111 0.911537
per_urban          -2.008e-04  4.507e-03   4.514e-03   0.044 0.964508
Precip              1.855e-04  6.027e-03   6.037e-03   0.031 0.975487
per_dist           -3.864e-04  5.521e-03   5.529e-03   0.070 0.944281
WinAvg             -9.863e-05  4.946e-03   4.954e-03   0.020 0.984116
per_intro           9.249e-06  3.205e-03   3.211e-03   0.003 0.997702

(conditional average)
                   Estimate Std. Error Adjusted SE z value Pr(>|z|)
(Intercept)        -0.02218    0.04830     0.04839   0.458 0.646705
elevation          -0.18629    0.07148     0.07153   2.604 0.009210 **
Mean_temp          -0.19092    0.08451     0.08461   2.257 0.024032 *
per_ag             -0.12030    0.04149     0.04156   2.895 0.003794 **
Temp_seasonality   -0.26915    0.07797     0.07802   3.450 0.000562 ***
NPP                 0.15489    0.04753     0.04759   3.255 0.001136 **
Precip_seasonality -0.05559    0.04158     0.04165   1.335 0.182003
Mean_diurnal_range  0.01510    0.05893     0.05903   0.256 0.798146
per_water           0.03165    0.03809     0.03815   0.829 0.406843
per_urban          -0.01988    0.04024     0.04031   0.493 0.621964
Precip              0.01023    0.04360     0.04368   0.234 0.814757
per_dist           -0.02217    0.03558     0.03565   0.622 0.534062
WinAvg             -0.00621    0.03876     0.03882   0.160 0.872923
per_intro           0.00116    0.03587     0.03594   0.032 0.974256
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Relative variable importance:
                     Temp_seasonality per_ag NPP  elevation Mean_temp
Precip_seasonality Mean_diurnal_range per_water Precip per_dist WinAvg
per_urban per_intro
Importance:          1.00             0.76   0.59 0.54      0.42      0.04
0.03               0.03      0.02   0.02     0.02   0.01      0.01
N containing models:   26               20     15   14        13         2
3                  3         2      2        2      1         1
```

July 2009

```
Model-averaged coefficients:
(full average)
                     Estimate Std. Error Adjusted SE z value Pr(>|z|)
(Intercept)        -0.0091725  0.0340608   0.0341022   0.269    0.788
elevation          -0.2404099  0.0462625   0.0463043   5.192  2.0e-07 ***
Mean_temp          -0.2827813  0.0525727   0.0526290   5.373  1.0e-07 ***
per_urban          -0.0595708  0.0507489   0.0507639   1.173    0.241
Temp_seasonality   -0.2229846  0.0489158   0.0489626   4.554  5.3e-06 ***
Precip_seasonality -0.0443794  0.0492898   0.0493026   0.900    0.368
per_water           0.0263352  0.0414029   0.0414120   0.636    0.525
Precip              0.0068961  0.0249522   0.0249599   0.276    0.782
NPP                -0.0030584  0.0168061   0.0168139   0.182    0.856
Mean_diurnal_range  0.0017934  0.0126281   0.0126348   0.142    0.887
WinAvg              0.0009218  0.0082962   0.0083007   0.111    0.912
per_intro           0.0004777  0.0054153   0.0054187   0.088    0.930
per_ag              0.0004154  0.0058050   0.0058084   0.072    0.943
per_dist           -0.0003089  0.0044981   0.0045016   0.069    0.945

(conditional average)
                    Estimate Std. Error Adjusted SE z value Pr(>|z|)
(Intercept)        -0.009172   0.034061    0.034102   0.269  0.78795
elevation          -0.240410   0.046263    0.046304   5.192  2.0e-07 ***
Mean_temp          -0.282781   0.052573    0.052629   5.373  1.0e-07 ***
per_urban          -0.091918   0.031633    0.031670   2.902  0.00370 **
Temp_seasonality   -0.222985   0.048916    0.048963   4.554  5.3e-06 ***
Precip_seasonality -0.087034   0.032437    0.032474   2.680  0.00736 **
per_water           0.078533   0.031821    0.031856   2.465  0.01369 *
Precip              0.070835   0.043200    0.043245   1.638  0.10142
NPP                -0.057644   0.046657    0.046710   1.234  0.21718
Mean_diurnal_range  0.050390   0.045076    0.045128   1.117  0.26417
WinAvg              0.036130   0.037758    0.037796   0.956  0.33911
per_intro           0.029318   0.030891    0.030929   0.948  0.34317
per_ag              0.028737   0.038955    0.038991   0.737  0.46111
per_dist           -0.022644   0.031264    0.031301   0.723  0.46941
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Relative variable importance:
                     elevation Mean_temp Temp_seasonality per_urban
Precip_seasonality per_water Precip NPP  Mean_diurnal_range WinAvg
per_intro per_ag per_dist
Importance:          1.00      1.00      1.00             0.65      0.51
0.34      0.10   0.05 0.04               0.03   0.02      0.01   0.01
N containing models:   31        31        31              19        17
12         6      5    3                  3      2         2      2
```

July 2010

```
Model-averaged coefficients:
(full average)
                     Estimate Std. Error Adjusted SE z value Pr(>|z|)
(Intercept)        -0.0097735  0.0437551   0.0438259   0.223  0.82353
elevation          -0.1387358  0.1015995   0.1016336   1.365  0.17223
Mean_temp          -0.4066334  0.1238790   0.1239336   3.281  0.00103 **
NPP                 0.1090477  0.0892712   0.0892991   1.221  0.22203
Precip             -0.1351445  0.0626325   0.0626747   2.156  0.03106 *
Temp_seasonality   -0.5356885  0.0814282   0.0814822   6.574  < 2e-16 ***
per_dist            0.0326732  0.0460350   0.0460500   0.710  0.47800
per_intro           0.0066494  0.0218101   0.0218185   0.305  0.76055
per_water           0.0055937  0.0198117   0.0198196   0.282  0.77777
Precip_seasonality  0.0022042  0.0138101   0.0138166   0.160  0.87325
Mean_diurnal_range -0.0008148  0.0131007   0.0131140   0.062  0.95046
per_ag              0.0007855  0.0074586   0.0074639   0.105  0.91619
per_urban           0.0015026  0.0101265   0.0101332   0.148  0.88212
WinAvg              0.0001515  0.0038965   0.0039013   0.039  0.96901

(conditional average)
                    Estimate Std. Error Adjusted SE z value Pr(>|z|)
(Intercept)        -0.009773   0.043755    0.043826   0.223  0.82353
elevation          -0.188078   0.068655    0.068724   2.737  0.00621 **
Mean_temp          -0.406633   0.123879    0.123934   3.281  0.00103 **
NPP                 0.159714   0.059833    0.059894   2.667  0.00766 **
Precip             -0.149071   0.047445    0.047506   3.138  0.00170 **
Temp_seasonality   -0.535689   0.081428    0.081482   6.574  < 2e-16 ***
per_dist            0.084517   0.033169    0.033222   2.544  0.01096 *
per_intro           0.061098   0.032313    0.032365   1.888  0.05905 .
per_water           0.058119   0.032022    0.032073   1.812  0.06998 .
Precip_seasonality  0.054791   0.043124    0.043175   1.269  0.20443
Mean_diurnal_range -0.023119   0.065984    0.066059   0.350  0.72636
per_ag              0.039916   0.035570    0.035625   1.120  0.26253
per_urban           0.040516   0.034414    0.034467   1.176  0.23979
WinAvg              0.015679   0.036432    0.036486   0.430  0.66740
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Relative variable importance:
                     Mean_temp Temp_seasonality Precip elevation NPP
per_dist per_intro per_water Precip_seasonality per_urban
Mean_diurnal_range per_ag WinAvg
Importance:          1.00      1.00             0.91   0.74      0.68 0.39
0.11     0.10      0.04               0.04      0.04              0.02
0.01
N containing models:   46        46               38     30        32   18
7        8         6                  6         5                 3
2
```

July 2011

```
Model-averaged coefficients:
(full average)
                    Estimate Std. Error Adjusted SE z value Pr(>|z|)
(Intercept)        -0.0005736  0.0327550   0.0328049   0.017    0.986
Mean_temp          -0.2327772  0.0396963   0.0397559   5.855   <2e-16 ***
Temp_seasonality   -0.3771666  0.0395900   0.0396493   9.513   <2e-16 ***
per_dist           -0.0070896  0.0227447   0.0227525   0.312    0.755
Mean_diurnal_range  0.0052533  0.0195344   0.0195416   0.269    0.788
per_water           0.0025292  0.0131387   0.0131450   0.192    0.847
per_intro          -0.0013401  0.0093191   0.0093249   0.144    0.886
WinAvg              0.0012536  0.0092237   0.0092300   0.136    0.892
elevation           0.0008820  0.0082896   0.0082972   0.106    0.915
Precip_seasonality  0.0007210  0.0072138   0.0072205   0.100    0.920
per_ag             -0.0006227  0.0068082   0.0068150   0.091    0.927
Precip             -0.0003985  0.0056158   0.0056223   0.071    0.943
NPP                -0.0003407  0.0053887   0.0053953   0.063    0.950
per_urban          -0.0002676  0.0049045   0.0049108   0.054    0.957

(conditional average)
                    Estimate Std. Error Adjusted SE z value Pr(>|z|)
(Intercept)        -0.0005736  0.0327550   0.0328049   0.017   0.9860
Mean_temp          -0.2327772  0.0396963   0.0397559   5.855   <2e-16 ***
Temp_seasonality   -0.3771666  0.0395900   0.0396493   9.513   <2e-16 ***
per_dist           -0.0635994  0.0323545   0.0324039   1.963   0.0497 *
Mean_diurnal_range  0.0604120  0.0324958   0.0325453   1.856   0.0634 .
per_water           0.0493082  0.0325402   0.0325898   1.513   0.1303
per_intro          -0.0394407  0.0324532   0.0325027   1.213   0.2250
WinAvg              0.0387727  0.0343022   0.0343545   1.129   0.2591
elevation           0.0322141  0.0387379   0.0387970   0.830   0.4064
Precip_seasonality  0.0290640  0.0356940   0.0357485   0.813   0.4162
per_ag             -0.0264676  0.0358607   0.0359154   0.737   0.4612
Precip             -0.0196982  0.0343336   0.0343859   0.573   0.5667
NPP                -0.0174203  0.0344531   0.0345057   0.505   0.6137
per_urban          -0.0146175  0.0332303   0.0332809   0.439   0.6605
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Relative variable importance:
                     Mean_temp Temp_seasonality per_dist
Mean_diurnal_range per_water per_intro WinAvg elevation Precip_seasonality
per_ag Precip NPP  per_urban
Importance:          1.00      1.00             0.11     0.09
0.05      0.03      0.03   0.03      0.02             0.02   0.02   0.02
0.02
N containing models:   12        12               1        1
1         1         1      1         1                1      1      1
1
```

July 2012

```
Model-averaged coefficients:
(full average)
                     Estimate Std. Error Adjusted SE z value Pr(>|z|)
(Intercept)        -0.0084523  0.0328048   0.0328445   0.257  0.79691
Mean_diurnal_range -0.2919568  0.0427087   0.0427520   6.829  < 2e-16 ***
Mean_temp          -0.2465547  0.0410132   0.0410597   6.005  < 2e-16 ***
Precip             -0.1406528  0.0464552   0.0464963   3.025  0.00249 **
Temp_seasonality   -0.3780571  0.0383354   0.0383802   9.850  < 2e-16 ***
per_urban          -0.0033016  0.0144385   0.0144435   0.229  0.81919
per_intro           0.0028677  0.0132491   0.0132538   0.216  0.82870
elevation           0.0025223  0.0177322   0.0177457   0.142  0.88697
WinAvg              0.0008239  0.0071970   0.0072019   0.114  0.90892
NPP                -0.0001217  0.0072722   0.0072809   0.017  0.98667
Precip_seasonality  0.0004166  0.0056864   0.0056917   0.073  0.94165
per_dist            0.0004200  0.0052468   0.0052513   0.080  0.93626
per_ag              0.0002520  0.0048976   0.0049028   0.051  0.95901

(conditional average)
                    Estimate Std. Error Adjusted SE z value Pr(>|z|)
(Intercept)        -0.008452   0.032805    0.032844   0.257 0.796914
Mean_diurnal_range -0.291957   0.042709    0.042752   6.829  < 2e-16 ***
Mean_temp          -0.246555   0.041013    0.041060   6.005  < 2e-16 ***
Precip             -0.144694   0.040440    0.040488   3.574 0.000352 ***
Temp_seasonality   -0.378057   0.038335    0.038380   9.850  < 2e-16 ***
per_urban          -0.048400   0.029553    0.029588   1.636 0.101887
per_intro           0.046012   0.028833    0.028868   1.594 0.110960
elevation           0.049040   0.061904    0.061979   0.791 0.428806
WinAvg              0.028561   0.031675    0.031714   0.901 0.367807
NPP                -0.004521   0.044105    0.044158   0.102 0.918460
Precip_seasonality  0.017991   0.032864    0.032904   0.547 0.584548
per_dist            0.018950   0.029849    0.029885   0.634 0.526020
per_ag              0.012147   0.031807    0.031846   0.381 0.702874
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Relative variable importance:
                     Mean_diurnal_range Mean_temp Temp_seasonality Precip
per_urban per_intro elevation WinAvg NPP  Precip_seasonality per_dist
per_ag
Importance:          1.00               1.00      1.00             0.97
0.07      0.06      0.05      0.03   0.03 0.02               0.02     0.02
N containing models:   10                 10        10               9
1         1         1         1      1    1                  1        1
```

July 2013

```
Model-averaged coefficients:
(full average)
                    Estimate Std. Error Adjusted SE z value Pr(>|z|)
(Intercept)         0.0031938  0.0330171   0.0330401   0.097 0.922993
elevation          -0.1672446  0.0506408   0.0506698   3.301 0.000964 ***
Mean_diurnal_range -0.1838092  0.0401891   0.0402151   4.571  4.9e-06 ***
Mean_temp          -0.3416630  0.0490927   0.0491225   6.955  < 2e-16 ***
Precip             -0.1800492  0.0332292   0.0332506   5.415  1.0e-07 ***
Temp_seasonality   -0.4491496  0.0340751   0.0340969  13.173  < 2e-16 ***
per_water           0.0250469  0.0324806   0.0324849   0.771 0.440688
per_dist            0.0043810  0.0149695   0.0149719   0.293 0.769818
NPP                -0.0020894  0.0124387   0.0124426   0.168 0.866647
Precip_seasonality  0.0016884  0.0096179   0.0096203   0.175 0.860688
per_intro          -0.0003338  0.0038123   0.0038136   0.088 0.930260

(conditional average)
                    Estimate Std. Error Adjusted SE z value Pr(>|z|)
(Intercept)         0.003194   0.033017    0.033040   0.097 0.922993
elevation          -0.169558   0.046987    0.047019   3.606 0.000311 ***
Mean_diurnal_range -0.183809   0.040189    0.040215   4.571  4.9e-06 ***
Mean_temp          -0.341663   0.049093    0.049123   6.955  < 2e-16 ***
Precip             -0.180049   0.033229    0.033251   5.415  1.0e-07 ***
Temp_seasonality   -0.449150   0.034075    0.034097  13.173  < 2e-16 ***
per_water           0.059016   0.021933    0.021948   2.689 0.007169 **
per_dist            0.043626   0.022790    0.022805   1.913 0.055755 .
NPP                -0.042110   0.037856    0.037882   1.112 0.266302
Precip_seasonality  0.036195   0.027095    0.027113   1.335 0.181889
per_intro          -0.022252   0.021937    0.021952   1.014 0.310755
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Relative variable importance:
                    Mean_diurnal_range Mean_temp Precip Temp_seasonality
elevation per_water per_dist NPP  Precip_seasonality per_intro
Importance:          1.00               1.00      1.00   1.00
0.99      0.42      0.10     0.05 0.05               0.01
N containing models:   10                 10        10     10
9         5         2        2    2                  1
```

July 2014

```
Model-averaged coefficients:
(full average)
                     Estimate Std. Error Adjusted SE z value Pr(>|z|)
(Intercept)        -0.0135379  0.0409931   0.0410417   0.330    0.742
Mean_temp          -0.2829033  0.0450044   0.0450455   6.280   <2e-16 ***
Temp_seasonality   -0.2500982  0.0420110   0.0420501   5.948   <2e-16 ***
Precip_seasonality  0.0182301  0.0363037   0.0363125   0.502    0.616
elevation          -0.0135958  0.0327223   0.0327311   0.415    0.678
per_ag             -0.0006746  0.0066160   0.0066204   0.102    0.919
Precip              0.0017083  0.0113890   0.0113936   0.150    0.881
per_intro          -0.0005001  0.0054101   0.0054139   0.092    0.926
Mean_diurnal_range -0.0003872  0.0049688   0.0049728   0.078    0.938
NPP                 0.0003568  0.0049438   0.0049480   0.072    0.943

(conditional average)
                   Estimate Std. Error Adjusted SE z value Pr(>|z|)
(Intercept)        -0.01354    0.04099     0.04104   0.330   0.7415
Mean_temp          -0.28290    0.04500     0.04505   6.280   <2e-16 ***
Temp_seasonality   -0.25010    0.04201     0.04205   5.948   <2e-16 ***
Precip_seasonality  0.07494    0.03418     0.03422   2.190   0.0285 *
elevation          -0.07436    0.03658     0.03662   2.031   0.0423 *
per_ag             -0.02870    0.03252     0.03256   0.881   0.3781
Precip              0.04173    0.03871     0.03874   1.077   0.2814
per_intro          -0.02457    0.02910     0.02913   0.843   0.3990
Mean_diurnal_range -0.02076    0.03001     0.03005   0.691   0.4897
NPP                 0.01935    0.03095     0.03099   0.624   0.5323
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Relative variable importance:
                     Mean_temp Temp_seasonality Precip_seasonality
elevation Precip per_ag per_intro Mean_diurnal_range NPP
Importance:          1.00      1.00             0.24               0.18
0.04   0.02   0.02      0.02               0.02
N containing models:   10        10                3                  2
2      1      1         1                  1
```

Standard deviations of environmental variables against β deviations

January 2008

```
Model-averaged coefficients:
(full average)
                    Estimate Std. Error Adjusted SE z value Pr(>|z|)
(Intercept)         0.002323   0.035299    0.035342   0.066  0.94759
Mean_diurnal_range  0.196276   0.040558    0.040602   4.834  1.3e-06 ***
Mean_temp          -0.071275   0.066818    0.066832   1.066  0.28621
NPP                 0.117805   0.032387    0.032424   3.633  0.00028 ***
per_ag             -0.138889   0.030455    0.030491   4.555  5.2e-06 ***
per_intro           0.032365   0.041810    0.041821   0.774  0.43899
WinAvg              0.119072   0.037713    0.037748   3.154  0.00161 **
per_urban          -0.027076   0.039591    0.039601   0.684  0.49416
elevation          -0.050693   0.065972    0.065984   0.768  0.44233
Precip_seasonality -0.009141   0.027554    0.027561   0.332  0.74014
per_water          -0.002039   0.011017    0.011022   0.185  0.85326
Precip              0.001597   0.010380    0.010385   0.154  0.87775
Temp_seasonality    0.001473   0.011166    0.011173   0.132  0.89510

(conditional average)
                    Estimate Std. Error Adjusted SE z value Pr(>|z|)
(Intercept)         0.002323   0.035299    0.035342   0.066 0.947592
Mean_diurnal_range  0.196276   0.040558    0.040602   4.834  1.3e-06 ***
Mean_temp          -0.122012   0.038111    0.038152   3.198 0.001384 **
NPP                 0.118405   0.031357    0.031396   3.771 0.000162 ***
per_ag             -0.138889   0.030455    0.030491   4.555  5.2e-06 ***
per_intro           0.075427   0.028740    0.028775   2.621 0.008760 **
WinAvg              0.121526   0.033961    0.034001   3.574 0.000351 ***
per_urban          -0.073450   0.029085    0.029121   2.522 0.011660 *
elevation          -0.119668   0.044944    0.044986   2.660 0.007811 **
Precip_seasonality -0.070957   0.038820    0.038859   1.826 0.067852 .
per_water          -0.041789   0.028757    0.028793   1.451 0.146672
Precip              0.041588   0.033792    0.033833   1.229 0.218993
Temp_seasonality    0.038732   0.042831    0.042883   0.903 0.366422
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Relative variable importance:
                     Mean_diurnal_range per_ag NPP  WinAvg Mean_temp
per_intro elevation per_urban Precip_seasonality per_water Precip
Temp_seasonality
Importance:          1.00               1.00   0.99 0.98   0.58      0.43
0.42      0.37      0.13               0.05      0.04   0.04
N containing models:   47                 47     46   44      24        20
24        20        11                  7         6      7
```

January 2009

```
Model-averaged coefficients:
(full average)
                    Estimate Std. Error Adjusted SE z value Pr(>|z|)
(Intercept)        0.0012559  0.0344834   0.0345422   0.036  0.97100
elevation         -0.1551005  0.0594594   0.0595061   2.606  0.00915 **
Mean_diurnal_range 0.0741017  0.0731724   0.0731989   1.012  0.31138
NPP                0.1594653  0.0365945   0.0366518   4.351 1.36e-05 ***
per_urban         -0.1562266  0.0339529   0.0340092   4.594 4.40e-06 ***
per_water         -0.0926141  0.0469398   0.0469745   1.972  0.04866 *
WinAvg             0.1686887  0.0410523   0.0411107   4.103 4.07e-05 ***
Temp_seasonality   0.0362903  0.0592053   0.0592223   0.613  0.54002
per_ag            -0.0072114  0.0234686   0.0234779   0.307  0.75872
Precip             0.0057217  0.0217936   0.0218035   0.262  0.79300
Mean_temp         -0.0036125  0.0303233   0.0303394   0.119  0.90522
Precip_seasonality -0.0009367  0.0087347   0.0087429   0.107  0.91468
per_dist          -0.0004311  0.0053423   0.0053470   0.081  0.93575
per_intro          0.0008060  0.0072738   0.0072797   0.111  0.91184

(conditional average)
                   Estimate Std. Error Adjusted SE z value Pr(>|z|)
(Intercept)        0.001256   0.034483    0.034542   0.036 0.970997
elevation         -0.164632   0.046728    0.046791   3.518 0.000434 ***
Mean_diurnal_range 0.130017   0.046092    0.046166   2.816 0.004858 **
NPP                0.159465   0.036595    0.036652   4.351 1.36e-05 ***
per_urban         -0.156227   0.033953    0.034009   4.594 4.40e-06 ***
per_water         -0.106022   0.033178    0.033235   3.190 0.001422 **
WinAvg             0.168689   0.041052    0.041111   4.103 4.07e-05 ***
Temp_seasonality   0.114418   0.045960    0.046030   2.486 0.012928 *
per_ag            -0.065629   0.034330    0.034388   1.908 0.056332 .
Precip             0.066166   0.038641    0.038705   1.709 0.087361 .
Mean_temp         -0.046481   0.099188    0.099252   0.468 0.639559
Precip_seasonality -0.037483   0.041028    0.041098   0.912 0.361748
per_dist          -0.032377   0.033307    0.033364   0.970 0.331835
per_intro          0.034852   0.033186    0.033242   1.048 0.294436
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Relative variable importance:
                    NPP  per_urban WinAvg elevation per_water
Mean_diurnal_range Temp_seasonality per_ag Precip Mean_temp
Precip_seasonality per_intro per_dist
Importance:          1.00 1.00      1.00   0.94      0.87      0.57
0.32             0.11   0.09   0.08      0.02                0.02      0.01
N containing models:   26   26        26     22        21        12
9                4      4      5         2                   2         1
```

January 2010

```
Model-averaged coefficients:
(full average)
                     Estimate Std. Error Adjusted SE z value Pr(>|z|)
(Intercept)         0.0091943  0.0445930   0.0446703   0.206 0.836927
Mean_diurnal_range  0.1577488  0.0887308   0.0887766   1.777 0.075582 .
NPP                 0.1257416  0.0458334   0.0458807   2.741 0.006132 **
per_urban          -0.1285112  0.0346335   0.0346910   3.704 0.000212 ***
Precip_seasonality -0.1137249  0.0574600   0.0575016   1.978 0.047955 *
Temp_seasonality    0.1477644  0.0840381   0.0840818   1.757 0.078851 .
Precip              0.0085624  0.0274956   0.0275058   0.311 0.755577
per_ag             -0.0059829  0.0219455   0.0219545   0.273 0.785226
per_dist            0.0024775  0.0135456   0.0135520   0.183 0.854944
elevation           0.0037483  0.0186241   0.0186341   0.201 0.840580
per_water          -0.0013669  0.0097810   0.0097869   0.140 0.888920
Mean_temp           0.0005790  0.0072051   0.0072133   0.080 0.936019
WinAvg              0.0004616  0.0061802   0.0061873   0.075 0.940529
per_intro           0.0003776  0.0051203   0.0051259   0.074 0.941274

(conditional average)
                    Estimate Std. Error Adjusted SE z value Pr(>|z|)
(Intercept)         0.009194   0.044593    0.044670   0.206 0.836927
Mean_diurnal_range  0.184601   0.065242    0.065314   2.826 0.004708 **
NPP                 0.131144   0.038503    0.038562   3.401 0.000672 ***
per_urban          -0.128511   0.034633    0.034691   3.704 0.000212 ***
Precip_seasonality -0.129468   0.041479    0.041544   3.116 0.001831 **
Temp_seasonality    0.173929   0.061337    0.061407   2.832 0.004620 **
Precip              0.076759   0.039277    0.039341   1.951 0.051044 .
per_ag             -0.066895   0.036195    0.036256   1.845 0.065030 .
per_dist            0.056598   0.033594    0.033652   1.682 0.092598 .
elevation           0.066290   0.044592    0.044666   1.484 0.137770
per_water          -0.047327   0.033721    0.033780   1.401 0.161202
Mean_temp           0.031907   0.043140    0.043215   0.738 0.460315
WinAvg              0.028306   0.039420    0.039489   0.717 0.473496
per_intro           0.025988   0.033745    0.033804   0.769 0.442012
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Relative variable importance:
                     per_urban NPP  Precip_seasonality Mean_diurnal_range
Temp_seasonality Precip per_ag elevation per_dist per_water Mean_temp
WinAvg per_intro
Importance:          1.00      0.96 0.88               0.85
0.85             0.11   0.09   0.06      0.04     0.03      0.02      0.02
0.01
N containing models:   22        20   19                 17
17                3      4      3         1        1         1         1
1
```

January 2011

```
Model-averaged coefficients:
(full average)
                     Estimate Std. Error Adjusted SE z value Pr(>|z|)
(Intercept)        -0.0099889  0.0422584   0.0423327   0.236 0.813462
elevation          -0.1498151  0.0803325   0.0803674   1.864 0.062304 .
Mean_diurnal_range  0.2301686  0.0462249   0.0462969   4.972    7e-07 ***
NPP                 0.1250541  0.0417653   0.0418200   2.990 0.002787 **
per_ag             -0.1334181  0.0353440   0.0354054   3.768 0.000164 ***
per_urban          -0.1247605  0.0364507   0.0365046   3.418 0.000632 ***
per_dist            0.0152428  0.0335250   0.0335373   0.455 0.649466
Mean_temp          -0.0295404  0.0652225   0.0652360   0.453 0.650676
Precip             -0.0069557  0.0243771   0.0243885   0.285 0.775489
per_intro           0.0032385  0.0151353   0.0151435   0.214 0.830663
Temp_seasonality    0.0031250  0.0180241   0.0180375   0.173 0.862453
Precip_seasonality -0.0012364  0.0100799   0.0100880   0.123 0.902451
WinAvg              0.0006936  0.0075586   0.0075665   0.092 0.926961
per_water          -0.0002695  0.0045680   0.0045740   0.059 0.953016

(conditional average)
                    Estimate Std. Error Adjusted SE z value Pr(>|z|)
(Intercept)        -0.009989   0.042258    0.042333   0.236 0.813462
elevation          -0.181326   0.045792    0.045866   3.953 7.71e-05 ***
Mean_diurnal_range  0.230169   0.046225    0.046297   4.972 7.00e-07 ***
NPP                 0.128570   0.036625    0.036689   3.504 0.000458 ***
per_ag             -0.133418   0.035344    0.035405   3.768 0.000164 ***
per_urban          -0.126425   0.033704    0.033763   3.744 0.000181 ***
per_dist            0.073646   0.033602    0.033662   2.188 0.028681 *
Mean_temp          -0.142614   0.066418    0.066482   2.145 0.031940 *
Precip             -0.069513   0.039876    0.039946   1.740 0.081828 .
per_intro           0.052212   0.033709    0.033768   1.546 0.122056
Temp_seasonality    0.062953   0.052707    0.052799   1.192 0.233144
Precip_seasonality -0.045940   0.041490    0.041563   1.105 0.269032
WinAvg              0.034126   0.040866    0.040938   0.834 0.404501
per_water          -0.019340   0.033595    0.033654   0.575 0.565504
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Relative variable importance:
                     Mean_diurnal_range per_ag per_urban NPP  elevation
Mean_temp per_dist Precip per_intro Temp_seasonality Precip_seasonality
WinAvg per_water
Importance:          1.00               1.00   0.99      0.97 0.83
0.21      0.21     0.10   0.06      0.05             0.03
0.02   0.01
N containing models:   18                 18     17        17   14
5         5        3      3         2                1                  1
1
```

January 2012

```
Model-averaged coefficients:
(full average)
                     Estimate Std. Error Adjusted SE z value Pr(>|z|)
(Intercept)         0.0001294  0.0330408   0.0330815   0.004  0.99688
Mean_diurnal_range  0.1369855  0.0430964   0.0431281   3.176  0.00149 **
Mean_temp          -0.0306751  0.0478642   0.0478758   0.641  0.52170
per_water           0.0635054  0.0487424   0.0487589   1.302  0.19277
Precip_seasonality -0.0130116  0.0327449   0.0327529   0.397  0.69117
elevation          -0.0123018  0.0333041   0.0333133   0.369  0.71192
per_urban           0.0201014  0.0360745   0.0360833   0.557  0.57747
Precip              0.0025952  0.0140589   0.0140640   0.185  0.85360
Temp_seasonality    0.0007728  0.0098001   0.0098043   0.079  0.93718
per_intro           0.0003129  0.0043576   0.0043605   0.072  0.94280
NPP                 0.0001858  0.0037160   0.0037193   0.050  0.96015
WinAvg             -0.0001472  0.0037206   0.0037244   0.040  0.96848

(conditional average)
                     Estimate Std. Error Adjusted SE z value Pr(>|z|)
(Intercept)         0.0001294  0.0330408   0.0330815   0.004 0.996880
Mean_diurnal_range  0.1396763  0.0389608   0.0389965   3.582 0.000341 ***
Mean_temp          -0.0897289  0.0374514   0.0374947   2.393 0.016706 *
per_water           0.0904621  0.0307530   0.0307902   2.938 0.003303 **
Precip_seasonality -0.0775715  0.0372064   0.0372482   2.083 0.037292 *
elevation          -0.0765198  0.0445569   0.0445995   1.716 0.086215 .
per_urban           0.0719644  0.0304417   0.0304792   2.361 0.018221 *
Precip              0.0535030  0.0367586   0.0367988   1.454 0.145965
Temp_seasonality    0.0372903  0.0572078   0.0572428   0.651 0.514762
per_intro           0.0281641  0.0304117   0.0304492   0.925 0.354991
NPP                 0.0197843  0.0328989   0.0329382   0.601 0.548074
WinAvg             -0.0158601  0.0352493   0.0352926   0.449 0.653152
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Relative variable importance:
                     Mean_diurnal_range per_water Mean_temp per_urban
Precip_seasonality elevation Precip Temp_seasonality per_intro NPP  WinAvg
Importance:          0.98               0.70      0.34      0.28      0.17
0.16      0.05   0.02             0.01      0.01 0.01
N containing models:   34                 27        14        10         8
7         6      4                2         2    2
```

January 2013

```
Model-averaged coefficients:
(full average)
                    Estimate Std. Error Adjusted SE z value Pr(>|z|)
(Intercept)        -3.515e-07  3.001e-02   3.004e-02   0.000    1.000
per_ag              3.639e-02  4.436e-02   4.437e-02   0.820    0.412
per_water           2.714e-03  1.287e-02   1.287e-02   0.211    0.833
per_urban          -1.858e-03  1.063e-02   1.064e-02   0.175    0.861
Mean_diurnal_range  4.106e-04  5.095e-03   5.098e-03   0.081    0.936
Mean_temp          -2.048e-04  3.991e-03   3.995e-03   0.051    0.959

(conditional average)
                    Estimate Std. Error Adjusted SE z value Pr(>|z|)
(Intercept)        -3.515e-07  3.001e-02   3.004e-02   0.000   1.0000
per_ag              7.897e-02  3.011e-02   3.014e-02   2.620   0.0088 **
per_water           4.247e-02  3.003e-02   3.007e-02   1.412   0.1578
per_urban          -3.720e-02  3.081e-02   3.085e-02   1.206   0.2278
Mean_diurnal_range  2.620e-02  3.131e-02   3.135e-02   0.836   0.4033
Mean_temp          -1.417e-02  3.007e-02   3.010e-02   0.471   0.6378
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Relative variable importance:
                     per_ag per_water per_urban Mean_diurnal_range
Mean_temp
Importance:          0.46   0.06      0.05      0.02               0.01
N containing models:    4      2         2         1                  1
```

January 2014

```
Model-averaged coefficients:
(full average)
                    Estimate Std. Error Adjusted SE z value Pr(>|z|)
(Intercept)         0.0109349  0.0407198   0.0407668   0.268    0.789
Temp_seasonality    0.0583623  0.0540341   0.0540466   1.080    0.280
Mean_diurnal_range  0.0212715  0.0407091   0.0407161   0.522    0.601
per_water          -0.0094341  0.0251919   0.0251980   0.374    0.708
Mean_temp          -0.0079442  0.0243930   0.0243992   0.326    0.745
NPP                -0.0059365  0.0204565   0.0204618   0.290    0.772
WinAvg              0.0045573  0.0182268   0.0182316   0.250    0.803
per_dist            0.0015846  0.0099720   0.0099756   0.159    0.874
elevation          -0.0006778  0.0068301   0.0068335   0.099    0.921
Precip_seasonality -0.0002909  0.0045034   0.0045067   0.065    0.949
Precip              0.0001346  0.0033957   0.0033990   0.040    0.968
per_ag             -0.0001547  0.0032938   0.0032967   0.047    0.963

(conditional average)
                   Estimate Std. Error Adjusted SE z value Pr(>|z|)
(Intercept)         0.01093    0.04072     0.04077   0.268  0.78852
Temp_seasonality    0.09647    0.03391     0.03394   2.842  0.00448 **
Mean_diurnal_range  0.08479    0.03493     0.03496   2.425  0.01529 *
per_water          -0.06256    0.02974     0.02978   2.101  0.03565 *
Mean_temp          -0.06608    0.03328     0.03332   1.983  0.04734 *
NPP                -0.06049    0.03105     0.03109   1.946  0.05167 .
WinAvg              0.05833    0.03340     0.03343   1.745  0.08101 .
per_dist            0.04500    0.02950     0.02953   1.524  0.12761
elevation          -0.04029    0.03431     0.03435   1.173  0.24073
Precip_seasonality -0.02601    0.03383     0.03387   0.768  0.44246
Precip              0.01507    0.03264     0.03268   0.461  0.64469
per_ag             -0.01752    0.03041     0.03044   0.576  0.56490
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Relative variable importance:
                    Temp_seasonality Mean_diurnal_range per_water
Mean_temp NPP  WinAvg per_dist elevation Precip_seasonality Precip per_ag
Importance:         0.60             0.25               0.15      0.12
0.10 0.08   0.04     0.02      0.01               0.01   0.01
N containing models:   15               7                  5         5
4    4      2        1         1                  1      1
```

July 2008

```
Model-averaged coefficients:
(full average)
                    Estimate Std. Error Adjusted SE z value Pr(>|z|)
(Intercept)       -2.699e-02  4.650e-02   4.659e-02   0.579  0.56229
Mean_diurnal_range  4.794e-02  6.062e-02   6.064e-02   0.790  0.42925
NPP                1.401e-01  4.468e-02   4.474e-02   3.131  0.00174 **
per_ag            -1.828e-01  3.784e-02   3.791e-02   4.824  1.4e-06 ***
per_urban         -8.727e-02  5.326e-02   5.329e-02   1.638  0.10152
WinAvg             3.020e-02  4.968e-02   4.970e-02   0.608  0.54342
per_water         -3.450e-02  4.865e-02   4.867e-02   0.709  0.47843
Temp_seasonality   5.866e-03  2.336e-02   2.337e-02   0.251  0.80181
Precip             3.140e-03  1.588e-02   1.589e-02   0.198  0.84333
elevation         -5.516e-04  6.800e-03   6.807e-03   0.081  0.93541
Mean_temp         -3.102e-04  5.165e-03   5.172e-03   0.060  0.95218
Precip_seasonality  2.097e-04  5.548e-03   5.556e-03   0.038  0.96989
per_intro         -1.003e-04  2.913e-03   2.917e-03   0.034  0.97258
per_dist           5.461e-05  2.584e-03   2.589e-03   0.021  0.98317

(conditional average)
                  Estimate Std. Error Adjusted SE z value Pr(>|z|)
(Intercept)       -0.02699    0.04650     0.04659   0.579 0.562287
Mean_diurnal_range  0.10757    0.04280     0.04288   2.509 0.012117 *
NPP                0.14307    0.04016     0.04023   3.556 0.000376 ***
per_ag            -0.18285    0.03784     0.03791   4.824  1.4e-06 ***
per_urban         -0.10825    0.03531     0.03537   3.060 0.002210 **
WinAvg             0.09491    0.04019     0.04026   2.357 0.018406 *
per_water         -0.08862    0.03582     0.03589   2.469 0.013546 *
Temp_seasonality   0.06564    0.04670     0.04677   1.403 0.160471
Precip             0.05566    0.03932     0.03939   1.413 0.157655
elevation         -0.03978    0.04212     0.04220   0.943 0.345800
Mean_temp         -0.02654    0.03983     0.03991   0.665 0.506026
Precip_seasonality  0.01432    0.04359     0.04366   0.328 0.742852
per_intro         -0.01893    0.03529     0.03536   0.535 0.592377
per_dist           0.01128    0.03539     0.03546   0.318 0.750487
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Relative variable importance:
                    per_ag NPP   per_urban Mean_diurnal_range per_water
WinAvg Temp_seasonality Precip Precip_seasonality elevation Mean_temp
per_intro per_dist
Importance:             1   0.98  0.81      0.45               0.39
0.32   0.09             0.06   0.01               0.01      0.01      0.01
<0.01
N containing models:    42     39    31        21                 18
14      8                6      3                  2         2         1
1
```

July 2009

```
Model-averaged coefficients:
(full average)
                     Estimate Std. Error Adjusted SE z value Pr(>|z|)
(Intercept)        -0.0161251  0.0364180   0.0364627   0.442    0.658
Mean_temp          -0.0610785  0.0730355   0.0730510   0.836    0.403
Precip              0.0818305  0.0590510   0.0590696   1.385    0.166
WinAvg              0.0892242  0.0464847   0.0465067   1.919    0.055 .
Precip_seasonality -0.0383657  0.0531584   0.0531688   0.722    0.471
elevation           0.0044936  0.0351474   0.0351610   0.128    0.898
per_urban          -0.0027219  0.0133189   0.0133237   0.204    0.838
per_ag             -0.0007618  0.0069037   0.0069074   0.110    0.912
Temp_seasonality   -0.0003527  0.0049885   0.0049919   0.071    0.944
per_water           0.0003010  0.0042681   0.0042709   0.070    0.944
Mean_diurnal_range -0.0002707  0.0046559   0.0046598   0.058    0.954
per_dist           -0.0001102  0.0029447   0.0029476   0.037    0.970

(conditional average)
                   Estimate Std. Error Adjusted SE z value Pr(>|z|)
(Intercept)        -0.01613    0.03642     0.03646   0.442  0.65832
Mean_temp          -0.12436    0.05469     0.05474   2.272  0.02309 *
Precip              0.11173    0.03769     0.03773   2.961  0.00307 **
WinAvg              0.10342    0.03220     0.03224   3.208  0.00134 **
Precip_seasonality -0.09716    0.03799     0.03803   2.555  0.01062 *
elevation           0.05377    0.11015     0.11020   0.488  0.62560
per_urban          -0.04883    0.03051     0.03055   1.599  0.10990
per_ag             -0.03598    0.03137     0.03140   1.146  0.25190
Temp_seasonality   -0.03124    0.03520     0.03525   0.886  0.37544
per_water           0.02902    0.03038     0.03042   0.954  0.34014
Mean_diurnal_range -0.02612    0.03764     0.03769   0.693  0.48817
per_dist           -0.01478    0.03075     0.03079   0.480  0.63123
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Relative variable importance: 
                     WinAvg Precip Mean_temp Precip_seasonality elevation
per_urban per_ag Temp_seasonality per_water Mean_diurnal_range per_dist
Importance:          0.86   0.73   0.49      0.39               0.08
0.06      0.02   0.01             0.01      0.01               0.01
N containing models:   21     21     14        11                  5
4         2      1                1         1                  1
```

July 2010

```
Model-averaged coefficients:
(full average)
                     Estimate Std. Error Adjusted SE z value Pr(>|z|)
(Intercept)        -0.0087237  0.0450567   0.0451308   0.193   0.8467
NPP                 0.1840932  0.0333936   0.0334468   5.504  < 2e-16 ***
per_dist            0.1092971  0.0389829   0.0390262   2.801   0.0051 **
Precip              0.1520217  0.0360214   0.0360791   4.214 2.51e-05 ***
Precip_seasonality  0.1948573  0.0362784   0.0363349   5.363 1.00e-07 ***
per_urban          -0.0100052  0.0269811   0.0269906   0.371   0.7109
Mean_diurnal_range  0.0056435  0.0214417   0.0214517   0.263   0.7925
Temp_seasonality    0.0026824  0.0145045   0.0145126   0.185   0.8534
per_ag             -0.0019158  0.0114860   0.0114926   0.167   0.8676
per_water          -0.0013953  0.0095428   0.0095489   0.146   0.8838
WinAvg              0.0012302  0.0091357   0.0091422   0.135   0.8930
Mean_temp           0.0010144  0.0092183   0.0092271   0.110   0.9125
elevation           0.0005730  0.0074809   0.0074901   0.076   0.9390
per_intro           0.0006433  0.0064402   0.0064461   0.100   0.9205

(conditional average)
                    Estimate Std. Error Adjusted SE z value Pr(>|z|)
(Intercept)        -0.008724   0.045057    0.045131   0.193 0.846726
NPP                 0.184093   0.033394    0.033447   5.504  < 2e-16 ***
per_dist            0.113800   0.032708    0.032762   3.474 0.000514 ***
Precip              0.152022   0.036021    0.036079   4.214 2.51e-05 ***
Precip_seasonality  0.194857   0.036278    0.036335   5.363 1.00e-07 ***
per_urban          -0.067293   0.032267    0.032320   2.082 0.037334 *
Mean_diurnal_range  0.063858   0.038532    0.038595   1.655 0.098018 .
Temp_seasonality    0.054579   0.038056    0.038118   1.432 0.152193
per_ag             -0.046767   0.033510    0.033566   1.393 0.163531
per_water          -0.041389   0.032341    0.032394   1.278 0.201365
WinAvg              0.039691   0.034149    0.034205   1.160 0.245894
Mean_temp           0.036134   0.041929    0.041998   0.860 0.389585
elevation           0.024643   0.042589    0.042659   0.578 0.563483
per_intro           0.028894   0.032353    0.032406   0.892 0.372596
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Relative variable importance:
                     NPP  Precip Precip_seasonality per_dist per_urban
Mean_diurnal_range Temp_seasonality per_ag per_water WinAvg Mean_temp
elevation per_intro
Importance:          1.00 1.00   1.00               0.96     0.15
0.09               0.05             0.04   0.03      0.03   0.03      0.02
0.02
N containing models:   12   12     12                 11        2
2                  1                1      1         1      1         1
1
```

July 2011

```
Model-averaged coefficients:
(full average)
                     Estimate Std. Error Adjusted SE z value Pr(>|z|)
(Intercept)        -6.381e-04  3.294e-02   3.299e-02   0.019  0.98457
per_ag             -9.874e-02  4.610e-02   4.614e-02   2.140  0.03234 *
Precip              8.664e-02  5.800e-02   5.802e-02   1.493  0.13535
Precip_seasonality  1.350e-01  4.245e-02   4.249e-02   3.178  0.00148 **
WinAvg              1.565e-01  3.538e-02   3.543e-02   4.417    1e-05 ***
Temp_seasonality    6.360e-02  6.365e-02   6.367e-02   0.999  0.31785
per_urban          -3.689e-02  4.759e-02   4.761e-02   0.775  0.43841
per_intro          -7.872e-03  2.379e-02   2.380e-02   0.331  0.74080
per_dist           -3.342e-03  1.546e-02   1.546e-02   0.216  0.82890
elevation           7.543e-04  7.779e-03   7.784e-03   0.097  0.92280
Mean_diurnal_range  1.459e-05  6.529e-03   6.536e-03   0.002  0.99822
Mean_temp           1.162e-04  3.907e-03   3.912e-03   0.030  0.97630
NPP                 1.695e-04  3.468e-03   3.472e-03   0.049  0.96106

(conditional average)
                     Estimate Std. Error Adjusted SE z value Pr(>|z|)
(Intercept)        -0.0006381  0.0329432   0.0329939   0.019 0.984571
per_ag             -0.1100839  0.0334743   0.0335242   3.284 0.001025 **
Precip              0.1131306  0.0373525   0.0374030   3.025 0.002489 **
Precip_seasonality  0.1381318  0.0376190   0.0376693   3.667 0.000246 ***
WinAvg              0.1564853  0.0353833   0.0354308   4.417    1e-05 ***
Temp_seasonality    0.1118975  0.0415168   0.0415697   2.692 0.007107 **
per_urban          -0.0854550  0.0331222   0.0331710   2.576 0.009989 **
per_intro          -0.0632168  0.0323419   0.0323908   1.952 0.050975 .
per_dist           -0.0556300  0.0326811   0.0327305   1.700 0.089200 .
elevation           0.0422942  0.0404435   0.0405046   1.044 0.296401
Mean_diurnal_range  0.0009730  0.0533159   0.0533729   0.018 0.985455
Mean_temp           0.0149649  0.0417503   0.0418145   0.358 0.720427
NPP                 0.0229896  0.0332682   0.0333194   0.690 0.490208
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Relative variable importance:
                     WinAvg Precip_seasonality per_ag Precip
Temp_seasonality per_urban per_intro per_dist elevation Mean_diurnal_range
Mean_temp NPP
Importance:          1.00   0.98               0.90   0.77   0.57
0.43      0.12      0.06     0.02      0.01               0.01      0.01
N containing models:   31     29                 25     23     18
13         6         4        2         2                  1         1
```

July 2012

```
Model-averaged coefficients:
(full average)
                     Estimate Std. Error Adjusted SE z value Pr(>|z|)
(Intercept)        -0.0288950  0.0399616   0.0400104   0.722    0.470
NPP                 0.1631316  0.0290953   0.0291305   5.600  < 2e-16 ***
per_urban          -0.1348715  0.0285459   0.0285805   4.719 2.40e-06 ***
Precip              0.1504509  0.0359803   0.0360167   4.177 2.95e-05 ***
Precip_seasonality  0.0799219  0.0622907   0.0623058   1.283    0.200
elevation           0.0715846  0.0689705   0.0689860   1.038    0.299
per_dist            0.0218902  0.0364444   0.0364530   0.601    0.548
Mean_temp           0.0073345  0.0340317   0.0340419   0.215    0.829
WinAvg              0.0015739  0.0099446   0.0099487   0.158    0.874
per_intro           0.0017732  0.0101721   0.0101765   0.174    0.862
per_water          -0.0004993  0.0053568   0.0053599   0.093    0.926
Temp_seasonality   -0.0006042  0.0069468   0.0069516   0.087    0.931
per_ag             -0.0002511  0.0038710   0.0038734   0.065    0.948
Mean_diurnal_range  0.0002567  0.0046355   0.0046399   0.055    0.956

(conditional average)
                   Estimate Std. Error Adjusted SE z value Pr(>|z|)
(Intercept)        -0.02889    0.03996     0.04001   0.722  0.47018
NPP                 0.16313    0.02910     0.02913   5.600  < 2e-16 ***
per_urban          -0.13487    0.02855     0.02858   4.719 2.40e-06 ***
Precip              0.15045    0.03598     0.03602   4.177 2.95e-05 ***
Precip_seasonality  0.11505    0.03930     0.03933   2.925  0.00345 **
elevation           0.12111    0.04528     0.04532   2.672  0.00753 **
per_dist            0.07078    0.02888     0.02892   2.448  0.01438 *
Mean_temp           0.06212    0.08004     0.08007   0.776  0.43786
WinAvg              0.04295    0.03036     0.03040   1.413  0.15768
per_intro           0.03956    0.02852     0.02856   1.385  0.16600
per_water          -0.03142    0.02888     0.02892   1.086  0.27729
Temp_seasonality   -0.02933    0.03873     0.03877   0.757  0.44934
per_ag             -0.03003    0.02997     0.03001   1.001  0.31683
Mean_diurnal_range  0.01995    0.03574     0.03578   0.558  0.57716
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Relative variable importance:
                     NPP  per_urban Precip Precip_seasonality elevation
per_dist Mean_temp per_intro WinAvg Temp_seasonality per_water
Mean_diurnal_range per_ag
Importance:          1.00 1.00      1.00   0.69               0.59
0.31     0.12      0.04      0.04   0.02             0.02      0.01
0.01
N containing models:   29   29        29     20                 17
9        7         5         3      3                2         2
1
```

July 2013

```
Model-averaged coefficients:
(full average)
                    Estimate Std. Error Adjusted SE z value Pr(>|z|)
(Intercept)        0.0007543  0.0331109   0.0331340   0.023  0.98184
NPP                0.1695641  0.0223286   0.0223438   7.589  < 2e-16 ***
per_urban         -0.0778353  0.0249618   0.0249745   3.117  0.00183 **
Precip             0.2186966  0.0235060   0.0235221   9.298  < 2e-16 ***
Precip_seasonality  0.1115123  0.0235001   0.0235159   4.742  2.1e-06 ***
per_ag            -0.0147700  0.0270405   0.0270439   0.546  0.58496
per_dist           0.0049832  0.0157453   0.0157478   0.316  0.75167
WinAvg             0.0011107  0.0073184   0.0073201   0.152  0.87940
Mean_diurnal_range  0.0008521  0.0067957   0.0067977   0.125  0.90024
Temp_seasonality   0.0003230  0.0042420   0.0042440   0.076  0.93933

(conditional average)
                    Estimate Std. Error Adjusted SE z value Pr(>|z|)
(Intercept)        0.0007543  0.0331109   0.0331340   0.023 0.981837
NPP                0.1695641  0.0223286   0.0223438   7.589  < 2e-16 ***
per_urban         -0.0799991  0.0216173   0.0216324   3.698 0.000217 ***
Precip             0.2186966  0.0235060   0.0235221   9.298  < 2e-16 ***
Precip_seasonality  0.1115123  0.0235001   0.0235159   4.742  2.1e-06 ***
per_ag            -0.0552086  0.0223726   0.0223882   2.466 0.013664 *
per_dist           0.0437219  0.0219420   0.0219572   1.991 0.046456 *
WinAvg             0.0335518  0.0230101   0.0230261   1.457 0.145084
Mean_diurnal_range  0.0318132  0.0271880   0.0272070   1.169 0.242281
Temp_seasonality   0.0189744  0.0265160   0.0265346   0.715 0.474559
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Relative variable importance:
                     NPP  Precip Precip_seasonality per_urban per_ag
per_dist WinAvg Mean_diurnal_range Temp_seasonality
Importance:          1.00 1.00   1.00               0.97      0.27   0.11
0.03   0.03               0.02
N containing models:    8    8      8                  7         2      2
1      1                  1
```

July 2014

```
Model-averaged coefficients:
(full average)
                    Estimate Std. Error Adjusted SE z value Pr(>|z|)
(Intercept)        -0.0193414  0.0428749   0.0429263   0.451   0.6523
per_ag             -0.0638334  0.0473991   0.0474155   1.346   0.1782
Precip              0.1940012  0.0317333   0.0317694   6.107   <2e-16 ***
Precip_seasonality  0.1018835  0.0417581   0.0417840   2.438   0.0148 *
Temp_seasonality   -0.0016782  0.0109135   0.0109183   0.154   0.8778
per_urban          -0.0012453  0.0084486   0.0084530   0.147   0.8829
Mean_temp           0.0026722  0.0148117   0.0148176   0.180   0.8569
per_intro          -0.0005036  0.0053717   0.0053752   0.094   0.9253
NPP                -0.0004576  0.0052489   0.0052526   0.087   0.9306
Mean_diurnal_range -0.0003008  0.0051905   0.0051956   0.058   0.9538
per_water          -0.0003513  0.0046244   0.0046280   0.076   0.9395
elevation          -0.0001642  0.0048791   0.0048846   0.034   0.9732
WinAvg              0.0003358  0.0046352   0.0046390   0.072   0.9423

(conditional average)
                   Estimate Std. Error Adjusted SE z value Pr(>|z|)
(Intercept)        -0.01934    0.04287     0.04293   0.451 0.652299
per_ag             -0.08871    0.03026     0.03029   2.929 0.003406 **
Precip              0.19400    0.03173     0.03177   6.107  < 2e-16 ***
Precip_seasonality  0.10970    0.03195     0.03198   3.430 0.000604 ***
Temp_seasonality   -0.04653    0.03486     0.03490   1.333 0.182456
per_urban          -0.03360    0.02896     0.02900   1.159 0.246610
Mean_temp           0.04776    0.04204     0.04208   1.135 0.256348
per_intro          -0.02677    0.02882     0.02885   0.928 0.353489
NPP                -0.02524    0.02990     0.02994   0.843 0.399145
Mean_diurnal_range -0.01759    0.03566     0.03570   0.493 0.622220
per_water          -0.02156    0.02925     0.02928   0.736 0.461501
elevation          -0.01009    0.03692     0.03696   0.273 0.784864
WinAvg              0.02074    0.03006     0.03010   0.689 0.490759
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Relative variable importance:
                    Precip Precip_seasonality per_ag Mean_temp per_urban
Temp_seasonality per_intro NPP  Mean_diurnal_range per_water elevation
WinAvg
Importance:          1.00   0.93               0.72   0.06      0.04
0.04             0.02      0.02 0.02               0.02      0.02
0.02
N containing models:   15     13                 12      3         2
1                1         1    1                  1         1         1
```

Mean environmental variables against β (Jaccard’s)

January 2008

```
Model-averaged coefficients:
(full average)
                   Estimate Std. Error Adjusted SE z value Pr(>|z|)
(Intercept)         0.01957    0.04441     0.04446   0.440    0.660
elevation           0.28383    0.05363     0.05366   5.290 1.00e-07 ***
NPP                -0.19043    0.04502     0.04506   4.226 2.38e-05 ***
per_ag             -0.06622    0.04907     0.04909   1.349    0.177
Precip              0.22147    0.04415     0.04420   5.011 5.00e-07 ***
Precip_seasonality  0.27174    0.04252     0.04257   6.384  < 2e-16 ***
Temp_seasonality    0.25290    0.06261     0.06265   4.037 5.42e-05 ***
WinAvg             -0.01567    0.03271     0.03272   0.479    0.632
Mean_diurnal_range  0.04054    0.06388     0.06390   0.634    0.526
per_intro          -0.01263    0.02801     0.02802   0.451    0.652
Mean_temp          -0.02653    0.06453     0.06455   0.411    0.681

(conditional average)
                   Estimate Std. Error Adjusted SE z value Pr(>|z|)
(Intercept)         0.01957    0.04441     0.04446   0.440  0.65985
elevation           0.28383    0.05363     0.05366   5.290 1.00e-07 ***
NPP                -0.19043    0.04502     0.04506   4.226 2.38e-05 ***
per_ag             -0.09235    0.03074     0.03078   3.001  0.00269 **
Precip              0.22147    0.04415     0.04420   5.011 5.00e-07 ***
Precip_seasonality  0.27174    0.04252     0.04257   6.384  < 2e-16 ***
Temp_seasonality    0.25616    0.05601     0.05605   4.570 4.90e-06 ***
WinAvg             -0.07145    0.02989     0.02993   2.387  0.01697 *
Mean_diurnal_range  0.11791    0.05241     0.05246   2.247  0.02462 *
per_intro          -0.06200    0.02812     0.02815   2.202  0.02764 *
Mean_temp          -0.13293    0.08199     0.08205   1.620  0.10522
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Relative variable importance:
                     elevation NPP  Precip Precip_seasonality
Temp_seasonality per_ag Mean_diurnal_range WinAvg per_intro Mean_temp
Importance:          1.00      1.00 1.00   1.00               0.99
0.72   0.34               0.22   0.20      0.20
N containing models:   21         21   21     21                 20
12     10                  5      8         9
```

January 2009

```
Model-averaged coefficients:
(full average)
                     Estimate Std. Error Adjusted SE z value Pr(>|z|)
(Intercept)        -0.0034314  0.0366476   0.0367094   0.093  0.92553
Mean_diurnal_range  0.2601262  0.0550256   0.0551014   4.721  2.3e-06 ***
Mean_temp          -0.3846620  0.0629766   0.0630342   6.102  < 2e-16 ***
NPP                -0.1944608  0.0603119   0.0603844   3.220  0.00128 **
per_ag             -0.1115766  0.0468308   0.0468671   2.381  0.01728 *
Precip              0.1122318  0.0776633   0.0777004   1.444  0.14862
Precip_seasonality  0.2231527  0.0536060   0.0536584   4.159  3.2e-05 ***
Temp_seasonality    0.0554963  0.0730165   0.0730431   0.760  0.44739
per_dist            0.0400885  0.0492537   0.0492702   0.814  0.41585
per_intro          -0.0084926  0.0241345   0.0241439   0.352  0.72503
elevation           0.0001960  0.0183247   0.0183412   0.011  0.99147
WinAvg              0.0006039  0.0066238   0.0066297   0.091  0.92742

(conditional average)
                    Estimate Std. Error Adjusted SE z value Pr(>|z|)
(Intercept)        -0.003431   0.036648    0.036709   0.093 0.925527
Mean_diurnal_range  0.260126   0.055026    0.055101   4.721  2.3e-06 ***
Mean_temp          -0.384662   0.062977    0.063034   6.102  < 2e-16 ***
NPP                -0.197403   0.055783    0.055863   3.534 0.000410 ***
per_ag             -0.120552   0.035882    0.035933   3.355 0.000794 ***
Precip              0.148427   0.051034    0.051109   2.904 0.003683 **
Precip_seasonality  0.223153   0.053606    0.053658   4.159  3.2e-05 ***
Temp_seasonality    0.129273   0.053680    0.053765   2.404 0.016198 *
per_dist            0.087593   0.033758    0.033810   2.591 0.009578 **
per_intro          -0.061095   0.031249    0.031301   1.952 0.050959 .
elevation           0.003796   0.080563    0.080636   0.047 0.962452
WinAvg              0.033496   0.036492    0.036551   0.916 0.359457
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Relative variable importance:
                     Mean_diurnal_range Mean_temp Precip_seasonality NPP
per_ag Precip per_dist Temp_seasonality per_intro elevation WinAvg
Importance:          1.00               1.00      1.00               0.99
0.93   0.76   0.46     0.43             0.14      0.05      0.02
N containing models:   28                 28        28                 26
23     16     16       11                8         5         2
```

January 2010

```
Model-averaged coefficients:  
(full average) 
                     Estimate Std. Error Adjusted SE z value Pr(>|z|)    
(Intercept)        -0.0020919  0.0442685   0.0443441   0.047    0.962    
Mean_diurnal_range  0.2096686  0.0419369   0.0419959   4.993    6e-07 ***
Mean_temp          -0.2362211  0.0421406   0.0422031   5.597   <2e-16 ***
elevation           0.0088487  0.0313535   0.0313703   0.282    0.778    
Precip_seasonality  0.0027385  0.0146192   0.0146284   0.187    0.851    
Temp_seasonality   -0.0004501  0.0086499   0.0086634   0.052    0.959    
NPP                -0.0004430  0.0084957   0.0085088   0.052    0.958    
per_urban           0.0005644  0.0066097   0.0066177   0.085    0.932    
Precip              0.0001365  0.0068005   0.0068120   0.020    0.984    
per_intro           0.0004711  0.0061239   0.0061318   0.077    0.939    
per_dist            0.0004261  0.0059441   0.0059520   0.072    0.943    
per_ag             -0.0004135  0.0058554   0.0058633   0.071    0.944    
per_water          -0.0003043  0.0053672   0.0053750   0.057    0.955    
WinAvg             -0.0001222  0.0051260   0.0051345   0.024    0.981    
 
(conditional average) 
                    Estimate Std. Error Adjusted SE z value Pr(>|z|)    
(Intercept)        -0.002092   0.044269    0.044344   0.047    0.962    
Mean_diurnal_range  0.209669   0.041937    0.041996   4.993    6e-07 ***
Mean_temp          -0.236221   0.042141    0.042203   5.597   <2e-16 ***
elevation           0.085012   0.054494    0.054587   1.557    0.119    
Precip_seasonality  0.052072   0.038664    0.038730   1.344    0.179    
Temp_seasonality   -0.015530   0.048449    0.048532   0.320    0.749    
NPP                -0.015470   0.047830    0.047911   0.323    0.747    
per_urban           0.022788   0.035463    0.035523   0.642    0.521    
Precip              0.005542   0.042990    0.043064   0.129    0.898    
per_intro           0.020157   0.034755    0.034814   0.579    0.563    
per_dist            0.018676   0.034751    0.034810   0.537    0.592    
per_ag             -0.018316   0.034506    0.034565   0.530    0.596    
per_water          -0.014386   0.034048    0.034106   0.422    0.673    
WinAvg             -0.005987   0.035394    0.035455   0.169    0.866    
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Relative variable importance: 
                     Mean_diurnal_range Mean_temp elevation
Precip_seasonality Temp_seasonality NPP  per_urban Precip per_intro
per_dist per_ag per_water WinAvg
Importance:          1.00               1.00      0.10      0.05
0.03             0.03 0.02      0.02   0.02      0.02     0.02   0.02
0.02
N containing models:   12                 12         1         1
1                1    1         1      1         1        1      1
1
```

January 2011

```
Model-averaged coefficients:
(full average)
                     Estimate Std. Error Adjusted SE z value Pr(>|z|)
(Intercept)         5.389e-03  3.961e-02   3.968e-02   0.136    0.892
elevation           3.306e-01  5.744e-02   5.749e-02   5.750   <2e-16 ***
per_intro          -3.762e-02  4.846e-02   4.848e-02   0.776    0.438
Temp_seasonality    1.702e-02  3.680e-02   3.681e-02   0.462    0.644
Mean_temp          -3.168e-02  6.225e-02   6.226e-02   0.509    0.611
NPP                -3.452e-02  6.126e-02   6.128e-02   0.563    0.573
Mean_diurnal_range -1.048e-02  3.612e-02   3.613e-02   0.290    0.772
per_dist            6.658e-03  2.242e-02   2.243e-02   0.297    0.767
Precip              2.099e-03  1.386e-02   1.387e-02   0.151    0.880
WinAvg              5.996e-04  6.498e-03   6.503e-03   0.092    0.927
per_urban          -5.201e-04  6.090e-03   6.096e-03   0.085    0.932
Precip_seasonality -2.077e-04  3.842e-03   3.847e-03   0.054    0.957
per_water          -1.433e-04  3.265e-03   3.269e-03   0.044    0.965
per_ag              1.718e-05  2.612e-03   2.616e-03   0.007    0.995

(conditional average)
                    Estimate Std. Error Adjusted SE z value Pr(>|z|)
(Intercept)         0.005389   0.039609    0.039677   0.136   0.8920
elevation           0.330564   0.057444    0.057488   5.750   <2e-16 ***
per_intro          -0.086766   0.033933    0.033991   2.553   0.0107 *
Temp_seasonality    0.081883   0.034711    0.034770   2.355   0.0185 *
Mean_temp          -0.128337   0.057371    0.057440   2.234   0.0255 *
NPP                -0.119207   0.053526    0.053587   2.225   0.0261 *
Mean_diurnal_range -0.101110   0.058522    0.058592   1.726   0.0844 .
per_dist            0.063859   0.034190    0.034248   1.865   0.0622 .
Precip              0.051743   0.046537    0.046605   1.110   0.2669
WinAvg              0.035077   0.035503    0.035560   0.986   0.3239
per_urban          -0.032454   0.035748    0.035809   0.906   0.3648
Precip_seasonality -0.026559   0.034467    0.034527   0.769   0.4418
per_water          -0.020884   0.033478    0.033535   0.623   0.5335
per_ag              0.002967   0.034195    0.034254   0.087   0.9310
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Relative variable importance:
                     elevation per_intro NPP  Mean_temp Temp_seasonality
per_dist Mean_diurnal_range Precip WinAvg per_urban Precip_seasonality
per_water per_ag
Importance:          1.00      0.43      0.29 0.25      0.21
0.10     0.10               0.04   0.02   0.02      0.01
0.01      0.01
N containing models:   36        16        14   10         7
6        6                  5      2      2         1                  1
1
```

January 2012

```
Model-averaged coefficients:
(full average)
                    Estimate Std. Error Adjusted SE z value Pr(>|z|)
(Intercept)       -0.0019851  0.0300726   0.0301090   0.066    0.947
elevation          0.3994221  0.0401243   0.0401608   9.946  < 2e-16 ***
NPP               -0.0704616  0.0529927   0.0530107   1.329    0.184
Precip             0.2017193  0.0451543   0.0451999   4.463 8.10e-06 ***
Precip_seasonality 0.2242390  0.0376771   0.0377214   5.945  < 2e-16 ***
Temp_seasonality   0.1793201  0.0415496   0.0415885   4.312 1.62e-05 ***
Mean_temp          0.0104295  0.0349673   0.0349780   0.298    0.766
per_ag            -0.0019820  0.0114040   0.0114086   0.174    0.862
WinAvg             0.0016948  0.0102209   0.0102250   0.166    0.868
per_urban         -0.0011534  0.0082749   0.0082789   0.139    0.889
Mean_diurnal_range 0.0010522  0.0118708   0.0118785   0.089    0.929
per_dist          -0.0002909  0.0044171   0.0044211   0.066    0.948

(conditional average)
                   Estimate Std. Error Adjusted SE z value Pr(>|z|)
(Intercept)       -0.001985   0.030073    0.030109   0.066  0.94743
elevation          0.399422   0.040124    0.040161   9.946  < 2e-16 ***
NPP               -0.099082   0.033364    0.033404   2.966  0.00302 **
Precip             0.201719   0.045154    0.045200   4.463 8.10e-06 ***
Precip_seasonality 0.224239   0.037677    0.037721   5.945  < 2e-16 ***
Temp_seasonality   0.179320   0.041550    0.041589   4.312 1.62e-05 ***
Mean_temp          0.080465   0.061628    0.061675   1.305  0.19201
per_ag            -0.045853   0.031576    0.031614   1.450  0.14695
WinAvg             0.042654   0.029701    0.029737   1.434  0.15146
per_urban         -0.037103   0.029475    0.029511   1.257  0.20866
Mean_diurnal_range 0.025789   0.053065    0.053107   0.486  0.62724
per_dist          -0.017349   0.029454    0.029490   0.588  0.55634
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Relative variable importance:
                    elevation Precip Precip_seasonality Temp_seasonality
NPP  Mean_temp per_ag Mean_diurnal_range WinAvg per_urban per_dist
Importance:          1.00      1.00   1.00               1.00
0.71 0.13      0.04   0.04               0.04   0.03      0.02
N containing models:   10        10     10                 10
7    2         1      2                  1      1         1
```

January 2013

```
Model-averaged coefficients:
(full average)
                     Estimate Std. Error Adjusted SE z value Pr(>|z|)
(Intercept)         5.789e-03  3.831e-02   3.836e-02   0.151  0.88003
elevation           1.971e-01  4.687e-02   4.693e-02   4.201 2.66e-05 ***
Mean_diurnal_range  1.873e-01  5.047e-02   5.052e-02   3.707  0.00021 ***
Mean_temp          -2.912e-01  4.627e-02   4.633e-02   6.286  < 2e-16 ***
NPP                -2.368e-01  4.148e-02   4.152e-02   5.704  < 2e-16 ***
Precip              1.796e-01  4.236e-02   4.241e-02   4.234 2.30e-05 ***
WinAvg              1.618e-01  2.973e-02   2.976e-02   5.437 1.00e-07 ***
per_dist           -1.188e-02  2.707e-02   2.707e-02   0.439  0.66074
Precip_seasonality  3.093e-03  1.416e-02   1.416e-02   0.218  0.82715
per_ag             -3.819e-03  1.514e-02   1.514e-02   0.252  0.80090
per_intro          -7.946e-04  6.514e-03   6.518e-03   0.122  0.90297
Temp_seasonality   -3.489e-06  6.930e-03   6.938e-03   0.001  0.99960

(conditional average)
                     Estimate Std. Error Adjusted SE z value Pr(>|z|)
(Intercept)         0.0057894  0.0383132   0.0383580   0.151  0.88003
elevation           0.1971323  0.0468737   0.0469278   4.201 2.66e-05 ***
Mean_diurnal_range  0.1872760  0.0504656   0.0505242   3.707  0.00021 ***
Mean_temp          -0.2911963  0.0462744   0.0463280   6.286  < 2e-16 ***
NPP                -0.2368400  0.0414756   0.0415231   5.704  < 2e-16 ***
Precip              0.1795625  0.0423621   0.0424094   4.234 2.30e-05 ***
WinAvg              0.1618243  0.0297297   0.0297643   5.437 1.00e-07 ***
per_dist           -0.0609620  0.0276839   0.0277162   2.200  0.02784 *
Precip_seasonality  0.0493205  0.0302843   0.0303197   1.627  0.10380
per_ag             -0.0468574  0.0281954   0.0282279   1.660  0.09692 .
per_intro          -0.0289431  0.0270358   0.0270675   1.069  0.28494
Temp_seasonality   -0.0001391  0.0437559   0.0438071   0.003  0.99747
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Relative variable importance:
                     elevation Mean_diurnal_range Mean_temp NPP  Precip
WinAvg per_dist per_ag Precip_seasonality per_intro Temp_seasonality
Importance:          1.00      1.00               1.00      1.00 1.00
1.00   0.19     0.08   0.06               0.03      0.03
N containing models:    7         7                  7         7    7
7      2        2      1                  1         1
```

January 2014

```
Model-averaged coefficients:
(full average)
                     Estimate Std. Error Adjusted SE z value Pr(>|z|)
(Intercept)         0.0053551  0.0391885   0.0392330   0.136 0.891430
elevation           0.3366267  0.0432463   0.0432719   7.779  < 2e-16 ***
Mean_temp           0.0800815  0.0738481   0.0738664   1.084 0.278303
Precip_seasonality  0.2114275  0.0352119   0.0352429   5.999  < 2e-16 ***
Temp_seasonality    0.2166695  0.0631775   0.0632034   3.428 0.000608 ***
WinAvg              0.0706003  0.0492187   0.0492336   1.434 0.151576
per_ag             -0.0124789  0.0287118   0.0287178   0.435 0.663901
per_intro          -0.0091274  0.0239321   0.0239375   0.381 0.702980
NPP                -0.0067156  0.0229696   0.0229744   0.292 0.770052
Mean_diurnal_range  0.0010286  0.0179888   0.0179951   0.057 0.954419
per_water           0.0040538  0.0156396   0.0156438   0.259 0.795533
per_dist            0.0019078  0.0106074   0.0106109   0.180 0.857315
per_urban           0.0008013  0.0067982   0.0068009   0.118 0.906207
Precip              0.0002336  0.0050650   0.0050693   0.046 0.963241

(conditional average)
                    Estimate Std. Error Adjusted SE z value Pr(>|z|)
(Intercept)         0.005355   0.039189    0.039233   0.136 0.891430
elevation           0.336627   0.043246    0.043272   7.779  < 2e-16 ***
Mean_temp           0.130200   0.048386    0.048431   2.688 0.007181 **
Precip_seasonality  0.211427   0.035212    0.035243   5.999  < 2e-16 ***
Temp_seasonality    0.216669   0.063178    0.063203   3.428 0.000608 ***
WinAvg              0.094570   0.031275    0.031307   3.021 0.002521 **
per_ag             -0.065527   0.029201    0.029232   2.242 0.024988 *
per_intro          -0.058658   0.027846    0.027877   2.104 0.035360 *
NPP                -0.066794   0.035138    0.035169   1.899 0.057535 .
Mean_diurnal_range  0.017803   0.072817    0.072844   0.244 0.806921
per_water           0.049922   0.026876    0.026907   1.855 0.063541 .
per_dist            0.043860   0.027328    0.027358   1.603 0.108899
per_urban           0.038188   0.027835    0.027866   1.370 0.170567
Precip              0.017805   0.040525    0.040567   0.439 0.660719
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Relative variable importance:
                     elevation Precip_seasonality Temp_seasonality WinAvg
Mean_temp per_ag per_intro NPP  per_water Mean_diurnal_range per_dist
per_urban Precip
Importance:          1.00      1.00               1.00             0.75
0.62      0.19   0.16      0.10 0.08      0.06               0.04     0.02
0.01
N containing models:   36        36                 36               26
21        9     10         6    6         5                   4       2
2
```

July 2008

```
Model-averaged coefficients:
(full average)
                    Estimate Std. Error Adjusted SE z value Pr(>|z|)
(Intercept)        1.095e-02  4.780e-02   4.789e-02   0.229  0.81911
elevation          2.499e-01  9.427e-02   9.431e-02   2.650  0.00806 **
NPP               -1.350e-01  9.771e-02   9.774e-02   1.381  0.16715
Precip_seasonality  1.494e-01  6.701e-02   6.706e-02   2.228  0.02587 *
Temp_seasonality   3.091e-01  1.065e-01   1.065e-01   2.901  0.00372 **
Mean_temp          1.205e-01  1.422e-01   1.422e-01   0.847  0.39684
Precip             4.205e-02  6.883e-02   6.886e-02   0.611  0.54136
per_dist           5.303e-03  1.998e-02   1.999e-02   0.265  0.79081
per_ag             2.716e-03  1.468e-02   1.469e-02   0.185  0.85331
Mean_diurnal_range  2.559e-04  1.183e-02   1.185e-02   0.022  0.98277
per_urban          9.934e-04  8.672e-03   8.680e-03   0.114  0.90889
WinAvg            -3.025e-04  6.528e-03   6.536e-03   0.046  0.96309
per_water         -1.457e-04  3.966e-03   3.973e-03   0.037  0.97073
per_intro         -9.722e-05  3.721e-03   3.727e-03   0.026  0.97919

(conditional average)
                   Estimate Std. Error Adjusted SE z value Pr(>|z|)
(Intercept)        0.010952   0.047799    0.047889   0.229  0.81911
elevation          0.249908   0.094269    0.094315   2.650  0.00806 **
NPP               -0.188027   0.057704    0.057768   3.255  0.00113 **
Precip_seasonality  0.161018   0.054525    0.054591   2.950  0.00318 **
Temp_seasonality   0.309063   0.106486    0.106537   2.901  0.00372 **
Mean_temp          0.246153   0.101811    0.101908   2.415  0.01572 *
Precip             0.129378   0.057240    0.057344   2.256  0.02406 *
per_dist           0.060158   0.035059    0.035125   1.713  0.08677 .
per_ag             0.053197   0.039178    0.039249   1.355  0.17530
Mean_diurnal_range  0.007657   0.064261    0.064369   0.119  0.90531
per_urban          0.037292   0.038331    0.038402   0.971  0.33151
WinAvg            -0.014944   0.043436    0.043495   0.344  0.73116
per_water         -0.013069   0.035236    0.035301   0.370  0.71123
per_intro         -0.009122   0.034879    0.034945   0.261  0.79407
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Relative variable importance:
                    elevation Temp_seasonality Precip_seasonality NPP
Mean_temp Precip per_dist per_ag Mean_diurnal_range per_urban WinAvg
per_water per_intro
Importance:          1.00      1.00             0.93               0.72
0.49      0.33   0.09     0.05   0.03              0.03      0.02   0.01
0.01
N containing models:   31        31               29                 22
16         9      5        4      4                 3         3      2
2
```

July 2009

```
Model-averaged coefficients:
(full average)
                    Estimate Std. Error Adjusted SE z value Pr(>|z|)
(Intercept)         0.004108   0.034388    0.034429   0.119    0.905
elevation           0.297521   0.052310    0.052332   5.685   <2e-16 ***
NPP                -0.035152   0.047833    0.047843   0.735    0.462
Precip_seasonality  0.257658   0.032071    0.032101   8.026   <2e-16 ***
Mean_temp           0.046106   0.075403    0.075413   0.611    0.541
Temp_seasonality    0.057565   0.079098    0.079107   0.728    0.467
per_ag             -0.019373   0.036522    0.036530   0.530    0.596
Mean_diurnal_range  0.008688   0.026993    0.026999   0.322    0.748
per_intro          -0.007146   0.021343    0.021348   0.335    0.738
WinAvg             -0.002451   0.013798    0.013802   0.178    0.859
Precip              0.003268   0.017318    0.017323   0.189    0.850

(conditional average)
                    Estimate Std. Error Adjusted SE z value Pr(>|z|)
(Intercept)         0.004108   0.034388    0.034429   0.119  0.90503
elevation           0.297521   0.052310    0.052332   5.685  < 2e-16 ***
NPP                -0.088015   0.032805    0.032838   2.680  0.00736 **
Precip_seasonality  0.257658   0.032071    0.032101   8.026  < 2e-16 ***
Mean_temp           0.145564   0.058931    0.058972   2.468  0.01357 *
Temp_seasonality    0.136225   0.063954    0.063982   2.129  0.03324 *
per_ag             -0.074923   0.031569    0.031603   2.371  0.01775 *
Mean_diurnal_range  0.075504   0.035883    0.035921   2.102  0.03556 *
per_intro          -0.056674   0.028382    0.028415   1.995  0.04610 *
WinAvg             -0.064567   0.031692    0.031730   2.035  0.04186 *
Precip              0.066361   0.043625    0.043667   1.520  0.12858
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Relative variable importance: 
                     elevation Precip_seasonality Temp_seasonality NPP
Mean_temp per_ag per_intro Mean_diurnal_range Precip WinAvg
Importance:          1.00      1.00               0.42             0.40
0.32      0.26   0.13      0.12               0.05   0.04
N containing models:   28        28                 15               12
11        11      7         4                  4      2
```

July 2010

```
Model-averaged coefficients:
(full average)
                     Estimate Std. Error Adjusted SE z value Pr(>|z|)
(Intercept)         0.0190033  0.0519808   0.0520648   0.365  0.71512
elevation           0.3184844  0.0626977   0.0627397   5.076  4.0e-07 ***
Mean_temp           0.1363203  0.0952756   0.0953189   1.430  0.15267
Precip_seasonality  0.1721322  0.0355898   0.0356443   4.829  1.4e-06 ***
Temp_seasonality    0.1983003  0.0716901   0.0717384   2.764  0.00571 **
NPP                -0.0238607  0.0476078   0.0476195   0.501  0.61632
per_intro          -0.0054644  0.0195971   0.0196050   0.279  0.78046
WinAvg             -0.0014175  0.0099781   0.0099844   0.142  0.88711
Mean_diurnal_range -0.0009320  0.0112587   0.0112727   0.083  0.93411
per_urban          -0.0010578  0.0083794   0.0083853   0.126  0.89961
per_ag              0.0009512  0.0079939   0.0079999   0.119  0.90535
Precip             -0.0004926  0.0076284   0.0076385   0.064  0.94858
per_dist            0.0003161  0.0048153   0.0048210   0.066  0.94773
per_water          -0.0002524  0.0044024   0.0044081   0.057  0.95434

(conditional average)
                   Estimate Std. Error Adjusted SE z value Pr(>|z|)
(Intercept)         0.01900    0.05198     0.05206   0.365  0.71512
elevation           0.31848    0.06270     0.06274   5.076  4.0e-07 ***
Mean_temp           0.18285    0.06057     0.06066   3.014  0.00257 **
Precip_seasonality  0.17213    0.03559     0.03564   4.829  1.4e-06 ***
Temp_seasonality    0.20252    0.06628     0.06634   3.053  0.00227 **
NPP                -0.10014    0.04328     0.04334   2.311  0.02084 *
per_intro          -0.05814    0.03199     0.03204   1.814  0.06961 .
WinAvg             -0.04414    0.03485     0.03491   1.264  0.20606
Mean_diurnal_range -0.03235    0.05816     0.05826   0.555  0.57875
per_urban          -0.03845    0.03338     0.03344   1.150  0.25013
per_ag              0.03679    0.03396     0.03401   1.082  0.27932
Precip             -0.02231    0.04635     0.04643   0.481  0.63086
per_dist            0.01927    0.03238     0.03243   0.594  0.55247
per_water          -0.01645    0.03157     0.03162   0.520  0.60292
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Relative variable importance:
                     elevation Precip_seasonality Temp_seasonality
Mean_temp NPP  per_intro WinAvg Mean_diurnal_range per_urban per_ag Precip
per_dist per_water
Importance:          1.00      1.00               0.98             0.75
0.24 0.09      0.03   0.03             0.03      0.03   0.02   0.02
0.02
N containing models:   14        14                 13               10
4    2         1      1                  1         1      1      1
1
```

July 2011

```
Model-averaged coefficients:
(full average)
                     Estimate Std. Error Adjusted SE z value Pr(>|z|)
(Intercept)        -0.0248458  0.0465231   0.0465935   0.533    0.594
elevation           0.2005950  0.0342338   0.0342813   5.851   <2e-16 ***
Precip_seasonality  0.3577474  0.0352018   0.0352535  10.148   <2e-16 ***
Temp_seasonality    0.2233733  0.0376214   0.0376741   5.929   <2e-16 ***
WinAvg             -0.0040712  0.0171618   0.0171691   0.237    0.813
Mean_diurnal_range  0.0035318  0.0171938   0.0172029   0.205    0.837
per_ag              0.0030726  0.0145636   0.0145703   0.211    0.833
Mean_temp           0.0029459  0.0167436   0.0167547   0.176    0.860
per_dist           -0.0015516  0.0098939   0.0098997   0.157    0.875
Precip             -0.0008543  0.0088587   0.0088680   0.096    0.923
per_intro          -0.0007604  0.0067112   0.0067165   0.113    0.910
NPP                -0.0004127  0.0057532   0.0057599   0.072    0.943
per_water          -0.0004706  0.0054490   0.0054545   0.086    0.931
per_urban          -0.0001818  0.0046298   0.0046362   0.039    0.969

(conditional average)
                    Estimate Std. Error Adjusted SE z value Pr(>|z|)
(Intercept)        -0.024846   0.046523    0.046594   0.533   0.5939
elevation           0.200595   0.034234    0.034281   5.851   <2e-16 ***
Precip_seasonality  0.357747   0.035202    0.035254  10.148   <2e-16 ***
Temp_seasonality    0.223373   0.037621    0.037674   5.929   <2e-16 ***
WinAvg             -0.056065   0.033778    0.033830   1.657   0.0975 .
Mean_diurnal_range  0.058258   0.041088    0.041150   1.416   0.1568
per_ag              0.051212   0.032707    0.032757   1.563   0.1180
Mean_temp           0.056587   0.048475    0.048548   1.166   0.2438
per_dist           -0.040301   0.031320    0.031367   1.285   0.1989
Precip             -0.029077   0.043016    0.043081   0.675   0.4997
per_intro          -0.029118   0.029985    0.030030   0.970   0.3322
NPP                -0.019014   0.034225    0.034277   0.555   0.5791
per_water          -0.021987   0.030236    0.030281   0.726   0.4678
per_urban          -0.009807   0.032592    0.032641   0.300   0.7638
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Relative variable importance: 
                     elevation Precip_seasonality Temp_seasonality WinAvg
Mean_diurnal_range per_ag Mean_temp per_dist Precip per_intro NPP
per_water per_urban
Importance:          1.00      1.00               1.00             0.07
0.06               0.06   0.05      0.04     0.03   0.03      0.02 0.02
0.02
N containing models:   11        11                 11                1
1                  1      1         1        1      1         1    1
1
```

July 2012

```
Model-averaged coefficients:
(full average)
                     Estimate Std. Error Adjusted SE z value Pr(>|z|)
(Intercept)        -0.0089983  0.0334211   0.0334616   0.269    0.788
elevation           0.3021801  0.0753107   0.0753323   4.011 6.04e-05 ***
NPP                -0.0850836  0.0685894   0.0686042   1.240    0.215
Precip_seasonality  0.2099979  0.0368280   0.0368563   5.698  < 2e-16 ***
Temp_seasonality    0.0729419  0.0685690   0.0685795   1.064    0.288
WinAvg             -0.0728485  0.0514655   0.0514795   1.415    0.157
Mean_diurnal_range  0.0267784  0.0536989   0.0537090   0.499    0.618
Mean_temp          -0.0684937  0.0894054   0.0894162   0.766    0.444
Precip             -0.0169478  0.0420542   0.0420621   0.403    0.687
per_urban           0.0077760  0.0224087   0.0224144   0.347    0.729
per_intro          -0.0009826  0.0075558   0.0075588   0.130    0.897
per_water           0.0001840  0.0031417   0.0031437   0.059    0.953
per_ag             -0.0001637  0.0031994   0.0032019   0.051    0.959

(conditional average)
                    Estimate Std. Error Adjusted SE z value Pr(>|z|)
(Intercept)        -0.008998   0.033421    0.033462   0.269 0.787995
elevation           0.302180   0.075311    0.075332   4.011 6.04e-05 ***
NPP                -0.121268   0.048137    0.048167   2.518 0.011815 *
Precip_seasonality  0.209998   0.036828    0.036856   5.698  < 2e-16 ***
Temp_seasonality    0.127109   0.036167    0.036201   3.511 0.000446 ***
WinAvg             -0.099080   0.031678    0.031708   3.125 0.001780 **
Mean_diurnal_range  0.108676   0.052936    0.052978   2.051 0.040233 *
Mean_temp          -0.159933   0.063564    0.063599   2.515 0.011913 *
Precip             -0.097930   0.047841    0.047881   2.045 0.040828 *
per_urban           0.058609   0.028382    0.028416   2.063 0.039154 *
per_intro          -0.039577   0.027786    0.027818   1.423 0.154814
per_water           0.024573   0.026813    0.026846   0.915 0.360020
per_ag             -0.022437   0.030055    0.030092   0.746 0.455900
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Relative variable importance:
                     elevation Precip_seasonality WinAvg NPP
Temp_seasonality Mean_temp Mean_diurnal_range Precip per_urban per_intro
per_water per_ag
Importance:          1.00      1.00               0.74   0.70 0.57
0.43      0.25              0.17   0.13      0.02      0.01      0.01
N containing models:   31        31                 21     20   18
14        10                 7      7         3         1         1
```

July 2013

```
Model-averaged coefficients:
(full average)
                     Estimate Std. Error Adjusted SE z value Pr(>|z|)
(Intercept)         0.0016288  0.0323569   0.0323794   0.050   0.9599
elevation           0.2485072  0.0353391   0.0353536   7.029  < 2e-16 ***
Mean_diurnal_range  0.1106371  0.0480796   0.0480956   2.300   0.0214 *
NPP                -0.1442460  0.0340219   0.0340384   4.238 2.26e-05 ***
Precip_seasonality  0.1994831  0.0252650   0.0252784   7.891  < 2e-16 ***
Temp_seasonality    0.0310392  0.0363613   0.0363662   0.854   0.3934
Mean_temp          -0.0080331  0.0261754   0.0261798   0.307   0.7590
WinAvg              0.0060986  0.0181489   0.0181512   0.336   0.7369
per_ag             -0.0012951  0.0081348   0.0081362   0.159   0.8735
per_urban           0.0014210  0.0080994   0.0081010   0.175   0.8608
Precip              0.0011800  0.0089626   0.0089647   0.132   0.8953
per_intro          -0.0002367  0.0030880   0.0030890   0.077   0.9389

(conditional average)
                    Estimate Std. Error Adjusted SE z value Pr(>|z|)
(Intercept)         0.001629   0.032357    0.032379   0.050 0.959881
elevation           0.248507   0.035339    0.035354   7.029  < 2e-16 ***
Mean_diurnal_range  0.120625   0.036270    0.036293   3.324 0.000889 ***
NPP                -0.144246   0.034022    0.034038   4.238 2.26e-05 ***
Precip_seasonality  0.199483   0.025265    0.025278   7.891  < 2e-16 ***
Temp_seasonality    0.064950   0.023751    0.023767   2.733 0.006281 **
Mean_temp          -0.063444   0.043540    0.043560   1.456 0.145263
WinAvg              0.049234   0.023138    0.023153   2.127 0.033462 *
per_ag             -0.040000   0.022262    0.022278   1.796 0.072570 .
per_urban           0.034405   0.021296    0.021310   1.614 0.106425
Precip              0.046079   0.032678    0.032701   1.409 0.158803
per_intro          -0.022016   0.020183    0.020197   1.090 0.275679
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Relative variable importance:
                     elevation NPP  Precip_seasonality Mean_diurnal_range
Temp_seasonality Mean_temp WinAvg per_urban per_ag Precip per_intro
Importance:          1.00      1.00 1.00               0.92
0.48             0.13      0.12   0.04      0.03   0.03   0.01
N containing models:   14        14   14                 12
8                3         3      2         1      1      1
```

July 2014

```
Model-averaged coefficients:
(full average)
                     Estimate Std. Error Adjusted SE z value Pr(>|z|)
(Intercept)         0.0236349  0.0437774   0.0438288   0.539   0.5897
elevation           0.2316875  0.0368251   0.0368554   6.286   <2e-16 ***
NPP                -0.1321071  0.0513363   0.0513570   2.572   0.0101 *
Precip_seasonality  0.2024278  0.0307442   0.0307743   6.578   <2e-16 ***
WinAvg             -0.0337163  0.0414468   0.0414561   0.813   0.4160
Mean_diurnal_range  0.0338009  0.0613283   0.0613381   0.551   0.5816
per_ag             -0.0029680  0.0136094   0.0136142   0.218   0.8274
Precip             -0.0007982  0.0075331   0.0075370   0.106   0.9157
per_intro          -0.0013425  0.0085434   0.0085472   0.157   0.8752
Mean_temp           0.0004570  0.0071010   0.0071075   0.064   0.9487
Temp_seasonality    0.0002030  0.0040707   0.0040744   0.050   0.9603
per_urban           0.0004424  0.0051000   0.0051037   0.087   0.9309

(conditional average)
                   Estimate Std. Error Adjusted SE z value Pr(>|z|)
(Intercept)         0.02363    0.04378     0.04383   0.539 0.589711
elevation           0.23169    0.03683     0.03686   6.286  < 2e-16 ***
NPP                -0.14247    0.03696     0.03699   3.852 0.000117 ***
Precip_seasonality  0.20243    0.03074     0.03077   6.578  < 2e-16 ***
WinAvg             -0.07471    0.02727     0.02730   2.737 0.006209 **
Mean_diurnal_range  0.11841    0.05619     0.05623   2.106 0.035223 *
per_ag             -0.04636    0.02969     0.02972   1.560 0.118803
Precip             -0.04056    0.03565     0.03569   1.136 0.255843
per_intro          -0.03434    0.02709     0.02712   1.266 0.205380
Mean_temp           0.01929    0.04201     0.04206   0.459 0.646497
Temp_seasonality    0.01794    0.03386     0.03390   0.529 0.596626
per_urban           0.02239    0.02872     0.02876   0.779 0.436210
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Relative variable importance:
                     elevation Precip_seasonality NPP  WinAvg
Mean_diurnal_range per_ag per_intro Mean_temp per_urban Precip
Temp_seasonality
Importance:          1.00      1.00               0.93 0.45   0.29
0.06   0.04      0.02      0.02      0.02   0.01
N containing models:   17        17                 16    8      5
3      3         2         2         1      1
```

Standard deviations of environmental variables against β (Jaccard's)

January 2008

```
Model-averaged coefficients:
(full average)
                     Estimate Std. Error Adjusted SE z value Pr(>|z|)
(Intercept)         0.0261176  0.0441333   0.0441877   0.591 0.554479
elevation           0.1422442  0.0476185   0.0476555   2.985 0.002837 **
NPP                -0.1835773  0.0291774   0.0292127   6.284  < 2e-16 ***
per_urban           0.1370189  0.0286281   0.0286633   4.780  1.8e-06 ***
per_water           0.0992577  0.0339438   0.0339723   2.922 0.003481 **
Precip_seasonality  0.1314499  0.0351130   0.0351546   3.739 0.000185 ***
Mean_temp          -0.0067044  0.0296560   0.0296713   0.226 0.821235
Precip              0.0061169  0.0222330   0.0222388   0.275 0.783275
WinAvg             -0.0035482  0.0153979   0.0154032   0.230 0.817817
per_ag              0.0016402  0.0099764   0.0099809   0.164 0.869471
Mean_diurnal_range  0.0003111  0.0058540   0.0058604   0.053 0.957667
per_dist           -0.0004373  0.0051055   0.0051096   0.086 0.931802
Temp_seasonality    0.0001279  0.0050233   0.0050293   0.025 0.979712

(conditional average)
                   Estimate Std. Error Adjusted SE z value Pr(>|z|)
(Intercept)         0.02612    0.04413     0.04419   0.591 0.554479
elevation           0.14497    0.04377     0.04381   3.309 0.000935 ***
NPP                -0.18358    0.02918     0.02921   6.284  < 2e-16 ***
per_urban           0.13702    0.02863     0.02866   4.780  1.8e-06 ***
per_water           0.10292    0.02860     0.02863   3.594 0.000325 ***
Precip_seasonality  0.13145    0.03511     0.03515   3.739 0.000185 ***
Mean_temp          -0.08314    0.06746     0.06755   1.231 0.218402
Precip              0.06510    0.03769     0.03773   1.725 0.084439 .
WinAvg             -0.05171    0.03106     0.03110   1.663 0.096407 .
per_ag              0.04003    0.02987     0.02991   1.338 0.180736
Mean_diurnal_range  0.01405    0.03680     0.03685   0.381 0.703049
per_dist           -0.02091    0.02861     0.02864   0.730 0.465279
Temp_seasonality    0.00642    0.03502     0.03506   0.183 0.854712
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Relative variable importance:
                     NPP  per_urban Precip_seasonality elevation per_water
Precip Mean_temp WinAvg per_ag Mean_diurnal_range per_dist
Temp_seasonality
Importance:          1.00 1.00      1.00               0.98      0.96
0.09   0.08      0.07   0.04   0.02               0.02     0.02
N containing models:   10   10        10                 9         9
2      1         1      1      1                  1        1
```

January 2009

```
Model-averaged coefficients:
(full average)
                     Estimate Std. Error Adjusted SE z value Pr(>|z|)
(Intercept)         0.0007627  0.0379650   0.0380294   0.020  0.98400
elevation           0.1884172  0.0703380   0.0703768   2.677  0.00742 **
NPP                -0.1372668  0.0346481   0.0347043   3.955 7.64e-05 ***
per_urban           0.1422364  0.0333609   0.0334166   4.256 2.08e-05 ***
per_water           0.1293546  0.0330013   0.0330566   3.913 9.11e-05 ***
Precip_seasonality  0.1031808  0.0595453   0.0595823   1.732  0.08332 .
WinAvg             -0.1671556  0.0364473   0.0365064   4.579 4.70e-06 ***
Temp_seasonality    0.0209422  0.0449724   0.0449871   0.466  0.64156
per_ag             -0.0023771  0.0129834   0.0129904   0.183  0.85481
Mean_temp           0.0146735  0.0519498   0.0519617   0.282  0.77764
per_dist            0.0011795  0.0088113   0.0088176   0.134  0.89359
Mean_diurnal_range  0.0010041  0.0095830   0.0095930   0.105  0.91664
per_intro          -0.0006693  0.0065808   0.0065868   0.102  0.91906
Precip              0.0003688  0.0058584   0.0058663   0.063  0.94987

(conditional average)
                     Estimate Std. Error Adjusted SE z value Pr(>|z|)
(Intercept)         0.0007627  0.0379650   0.0380294   0.020  0.98400
elevation           0.2039198  0.0468315   0.0468947   4.348 1.37e-05 ***
NPP                -0.1372668  0.0346481   0.0347043   3.955 7.64e-05 ***
per_urban           0.1422364  0.0333609   0.0334166   4.256 2.08e-05 ***
per_water           0.1293546  0.0330013   0.0330566   3.913 9.11e-05 ***
Precip_seasonality  0.1245366  0.0402482   0.0403143   3.089  0.00201 **
WinAvg             -0.1671556  0.0364473   0.0365064   4.579 4.70e-06 ***
Temp_seasonality    0.0957710  0.0456373   0.0457032   2.095  0.03613 *
per_ag             -0.0509813  0.0337250   0.0337822   1.509  0.13127
Mean_temp           0.1297908  0.0944995   0.0945573   1.373  0.16987
per_dist            0.0395184  0.0329578   0.0330138   1.197  0.23130
Mean_diurnal_range  0.0363315  0.0451594   0.0452361   0.803  0.42189
per_intro          -0.0301987  0.0325904   0.0326457   0.925  0.35494
Precip              0.0193256  0.0378439   0.0379081   0.510  0.61019
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Relative variable importance:
                     NPP  per_urban per_water WinAvg elevation
Precip_seasonality Temp_seasonality Mean_temp per_ag per_dist
Mean_diurnal_range per_intro Precip
Importance:          1.00 1.00      1.00      1.00   0.92      0.83
0.22               0.11      0.05   0.03     0.03              0.02
0.02
N containing models:   13   13        13        13     10        10
4                  4         1      1        1                 1        1
```

January 2010

```
Model-averaged coefficients:
(full average)
                     Estimate Std. Error Adjusted SE z value Pr(>|z|)
(Intercept)         2.029e-03  4.386e-02   4.393e-02   0.046  0.96316
NPP                -1.791e-01  3.462e-02   3.468e-02   5.165    2e-07 ***
per_urban           1.794e-01  3.448e-02   3.454e-02   5.194    2e-07 ***
Precip_seasonality  1.562e-01  4.873e-02   4.877e-02   3.203  0.00136 **
Mean_temp           1.363e-02  3.855e-02   3.856e-02   0.353  0.72378
per_water           3.701e-03  1.645e-02   1.646e-02   0.225  0.82211
elevation           1.707e-03  1.181e-02   1.182e-02   0.144  0.88518
per_ag              1.236e-03  9.355e-03   9.363e-03   0.132  0.89502
Temp_seasonality    7.977e-04  8.159e-03   8.168e-03   0.098  0.92221
per_intro           8.396e-04  7.570e-03   7.578e-03   0.111  0.91177
Mean_diurnal_range  2.458e-04  6.587e-03   6.598e-03   0.037  0.97028
Precip              1.740e-04  5.291e-03   5.300e-03   0.033  0.97382
per_dist           -2.885e-04  5.233e-03   5.241e-03   0.055  0.95610
WinAvg              9.695e-05  5.278e-03   5.287e-03   0.018  0.98537

(conditional average)
                    Estimate Std. Error Adjusted SE z value Pr(>|z|)
(Intercept)         0.002029   0.043856    0.043932   0.046   0.9632
NPP                -0.179147   0.034624    0.034684   5.165 2.00e-07 ***
per_urban           0.179379   0.034479    0.034538   5.194 2.00e-07 ***
Precip_seasonality  0.162155   0.038772    0.038830   4.176 2.97e-05 ***
Mean_temp           0.094213   0.051786    0.051842   1.817   0.0692 .
per_water           0.055577   0.034375    0.034434   1.614   0.1065
elevation           0.044313   0.041646    0.041719   1.062   0.2881
per_ag              0.037755   0.035997    0.036059   1.047   0.2951
Temp_seasonality    0.029111   0.040066    0.040136   0.725   0.4683
per_intro           0.030962   0.034362    0.034422   0.899   0.3684
Mean_diurnal_range  0.010726   0.042205    0.042278   0.254   0.7997
Precip              0.008787   0.036586    0.036649   0.240   0.8105
per_dist           -0.014605   0.034314    0.034373   0.425   0.6709
WinAvg              0.004909   0.037243    0.037307   0.132   0.8953
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Relative variable importance:
                     NPP  per_urban Precip_seasonality Mean_temp per_water
elevation per_ag Temp_seasonality per_intro Mean_diurnal_range Precip
per_dist WinAvg
Importance:          1.00 1.00      0.96               0.14      0.07
0.04      0.03   0.03             0.03      0.02               0.02   0.02
0.02
N containing models:   12   12        11                 2         1
1         1      1                1         1                  1      1
1
```

January 2011

```
Model-averaged coefficients:
(full average)
                    Estimate Std. Error Adjusted SE z value Pr(>|z|)
(Intercept)         8.686e-03  4.227e-02   4.235e-02   0.205    0.837
NPP                -1.623e-01  3.509e-02   3.515e-02   4.617 3.90e-06 ***
per_urban           1.351e-01  3.423e-02   3.429e-02   3.938 8.21e-05 ***
Precip_seasonality  2.201e-01  4.397e-02   4.403e-02   4.999 6.00e-07 ***
elevation           4.553e-02  7.081e-02   7.083e-02   0.643    0.520
Temp_seasonality   -7.844e-03  2.743e-02   2.744e-02   0.286    0.775
Mean_temp          -5.319e-03  4.105e-02   4.108e-02   0.129    0.897
per_intro          -1.408e-03  9.747e-03   9.755e-03   0.144    0.885
per_water           1.231e-03  9.109e-03   9.117e-03   0.135    0.893
Precip              6.101e-04  6.718e-03   6.725e-03   0.091    0.928
Mean_diurnal_range  3.646e-04  6.174e-03   6.182e-03   0.059    0.953
per_dist            3.153e-04  4.929e-03   4.935e-03   0.064    0.949
WinAvg             -1.171e-07  4.414e-03   4.421e-03   0.000    1.000
per_ag              1.332e-04  4.307e-03   4.314e-03   0.031    0.975

(conditional average)
                    Estimate Std. Error Adjusted SE z value Pr(>|z|)
(Intercept)         8.686e-03  4.227e-02   4.235e-02   0.205   0.8375
NPP                -1.623e-01  3.509e-02   3.515e-02   4.617 3.90e-06 ***
per_urban           1.351e-01  3.423e-02   3.429e-02   3.938 8.21e-05 ***
Precip_seasonality  2.201e-01  4.397e-02   4.403e-02   4.999 6.00e-07 ***
elevation           1.177e-01  6.681e-02   6.687e-02   1.761   0.0783 .
Temp_seasonality   -7.478e-02  4.655e-02   4.662e-02   1.604   0.1087
Mean_temp          -4.962e-02  1.163e-01   1.164e-01   0.426   0.6698
per_intro          -3.782e-02  3.428e-02   3.434e-02   1.101   0.2708
per_water           3.552e-02  3.429e-02   3.435e-02   1.034   0.3011
Precip              3.092e-02  3.675e-02   3.681e-02   0.840   0.4010
Mean_diurnal_range  2.056e-02  4.164e-02   4.172e-02   0.493   0.6221
per_dist            2.051e-02  3.415e-02   3.421e-02   0.599   0.5489
WinAvg             -8.339e-06  3.725e-02   3.731e-02   0.000   0.9998
per_ag              9.630e-03  3.535e-02   3.542e-02   0.272   0.7857
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Relative variable importance:
                    NPP  per_urban Precip_seasonality elevation Mean_temp
Temp_seasonality per_intro per_water Precip Mean_diurnal_range per_dist
WinAvg per_ag
Importance:          1.00 1.00      1.00               0.39      0.11
0.10             0.04      0.03      0.02   0.02               0.02
0.01   0.01
N containing models:   16   16        16                 6         3
3                2         2         1      1                  1        1
1
```

January 2012

```
Model-averaged coefficients:
(full average)
                     Estimate Std. Error Adjusted SE z value Pr(>|z|)
(Intercept)        -0.0002620  0.0311031   0.0311413   0.008  0.99329
elevation           0.0939712  0.0699142   0.0699316   1.344  0.17903
NPP                -0.1339624  0.0314199   0.0314548   4.259 2.05e-05 ***
per_urban           0.1025547  0.0337035   0.0337338   3.040  0.00236 **
Precip_seasonality  0.1679856  0.0376673   0.0377085   4.455 8.40e-06 ***
Mean_temp           0.0348721  0.0599874   0.0599971   0.581  0.56109
Mean_diurnal_range -0.0100350  0.0295205   0.0295281   0.340  0.73397
WinAvg             -0.0098165  0.0268444   0.0268508   0.366  0.71467
Temp_seasonality   -0.0062545  0.0229859   0.0229925   0.272  0.78560
per_intro           0.0013582  0.0090861   0.0090900   0.149  0.88123
Precip              0.0025817  0.0140669   0.0140715   0.183  0.85443
per_water           0.0006789  0.0063659   0.0063690   0.107  0.91511
per_dist           -0.0003650  0.0046154   0.0046184   0.079  0.93701

(conditional average)
                    Estimate Std. Error Adjusted SE z value Pr(>|z|)
(Intercept)        -0.000262   0.031103    0.031141   0.008 0.993286
elevation           0.133809   0.040367    0.040410   3.311 0.000929 ***
NPP                -0.133962   0.031420    0.031455   4.259 2.05e-05 ***
per_urban           0.105443   0.029382    0.029418   3.584 0.000338 ***
Precip_seasonality  0.167986   0.037667    0.037708   4.455 8.40e-06 ***
Mean_temp           0.118980   0.047649    0.047691   2.495 0.012603 *
Mean_diurnal_range -0.078037   0.038344    0.038389   2.033 0.042072 *
WinAvg             -0.068609   0.031667    0.031706   2.164 0.030471 *
Temp_seasonality   -0.070242   0.037936    0.037981   1.849 0.064398 .
per_intro           0.041021   0.029436    0.029472   1.392 0.163966
Precip              0.054409   0.036748    0.036785   1.479 0.139114
per_water           0.036889   0.029433    0.029469   1.252 0.210647
per_dist           -0.027767   0.029323    0.029358   0.946 0.344259
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Relative variable importance:
                     NPP  Precip_seasonality per_urban elevation Mean_temp
WinAvg Mean_diurnal_range Temp_seasonality Precip per_intro per_water
per_dist
Importance:          1.00 1.00               0.97      0.70      0.29
0.14   0.13               0.09             0.05   0.03      0.02      0.01
N containing models:   19   19                 17        11         7
3      2                  2                3      2         1         1
```

January 2013

```
Model-averaged coefficients:
(full average)
                     Estimate Std. Error Adjusted SE z value Pr(>|z|)
(Intercept)        -0.0005909  0.0340541   0.0340943   0.017  0.98617
elevation           0.1823736  0.0680254   0.0680602   2.680  0.00737 **
NPP                -0.1760068  0.0297939   0.0298259   5.901  < 2e-16 ***
per_urban           0.0910864  0.0359310   0.0359548   2.533  0.01130 *
Precip_seasonality  0.2367131  0.0370961   0.0371329   6.375  < 2e-16 ***
WinAvg             -0.0314066  0.0442761   0.0442855   0.709  0.47821
per_dist           -0.0335161  0.0415468   0.0415567   0.807  0.41995
Mean_diurnal_range -0.0224028  0.0439845   0.0439943   0.509  0.61060
Temp_seasonality   -0.0113715  0.0310751   0.0310826   0.366  0.71448
Mean_temp          -0.0293461  0.0649099   0.0649293   0.452  0.65129
per_water           0.0049550  0.0177039   0.0177089   0.280  0.77963
per_intro           0.0021269  0.0113429   0.0113467   0.187  0.85131
per_ag              0.0001024  0.0024907   0.0024926   0.041  0.96722
Precip             -0.0000365  0.0021135   0.0021158   0.017  0.98624

(conditional average)
                     Estimate Std. Error Adjusted SE z value Pr(>|z|)
(Intercept)        -0.0005909  0.0340541   0.0340943   0.017 0.986172
elevation           0.1823736  0.0680254   0.0680602   2.680 0.007371 **
NPP                -0.1760068  0.0297939   0.0298259   5.901  < 2e-16 ***
per_urban           0.0970715  0.0281938   0.0282262   3.439 0.000584 ***
Precip_seasonality  0.2367130  0.0370961   0.0371329   6.375  < 2e-16 ***
WinAvg             -0.0819556  0.0311901   0.0312248   2.625 0.008673 **
per_dist           -0.0744354  0.0280661   0.0280987   2.649 0.008072 **
Mean_diurnal_range -0.0911678  0.0400478   0.0400914   2.274 0.022966 *
Temp_seasonality   -0.0777195  0.0379922   0.0380340   2.043 0.041011 *
Mean_temp          -0.1342303  0.0720633   0.0721432   1.861 0.062799 .
per_water           0.0528763  0.0284740   0.0285068   1.855 0.063615 .
per_intro           0.0456944  0.0278108   0.0278436   1.641 0.100775
per_ag              0.0220449  0.0291749   0.0292093   0.755 0.450416
Precip             -0.0090900  0.0320974   0.0321353   0.283 0.777279
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Relative variable importance:
                     elevation NPP   Precip_seasonality per_urban per_dist
WinAvg Mean_diurnal_range Mean_temp Temp_seasonality per_water per_intro
per_ag Precip
Importance:              1         1     1               0.94      0.45
0.38   0.25               0.22      0.15             0.09      0.05
<0.01  <0.01
N containing models:    48        48    48                41        22
16     16                 14        10                12         6
1      1
```

January 2014

```
Model-averaged coefficients:
(full average)
                     Estimate Std. Error Adjusted SE z value Pr(>|z|)
(Intercept)         0.0092608  0.0372179   0.0372606   0.249 0.803715
elevation           0.1296882  0.0417561   0.0417925   3.103 0.001915 **
per_urban           0.1970041  0.0269409   0.0269716   7.304  < 2e-16 ***
per_water           0.1479361  0.0272156   0.0272466   5.430    1e-07 ***
Precip             -0.1233433  0.0355963   0.0356286   3.462 0.000536 ***
Precip_seasonality  0.2757472  0.0325231   0.0325598   8.469  < 2e-16 ***
WinAvg             -0.0820497  0.0415227   0.0415420   1.975 0.048257 *
NPP                -0.0101064  0.0256236   0.0256290   0.394 0.693333
per_ag              0.0028380  0.0131059   0.0131099   0.216 0.828615
Mean_temp          -0.0023398  0.0171000   0.0171117   0.137 0.891241
per_dist            0.0009689  0.0072615   0.0072649   0.133 0.893899
per_intro           0.0007635  0.0063733   0.0063766   0.120 0.904694
Temp_seasonality    0.0006338  0.0064823   0.0064868   0.098 0.922166
Mean_diurnal_range  0.0001385  0.0047731   0.0047783   0.029 0.976869

(conditional average)
                    Estimate Std. Error Adjusted SE z value Pr(>|z|)
(Intercept)         0.009261   0.037218    0.037261   0.249 0.803715
elevation           0.131906   0.038482    0.038522   3.424 0.000617 ***
per_urban           0.197004   0.026941    0.026972   7.304  < 2e-16 ***
per_water           0.147936   0.027216    0.027247   5.430 1.00e-07 ***
Precip             -0.125453   0.032002    0.032039   3.916 9.02e-05 ***
Precip_seasonality  0.275747   0.032523    0.032560   8.469  < 2e-16 ***
WinAvg             -0.094329   0.028703    0.028735   3.283 0.001028 **
NPP                -0.061803   0.028636    0.028666   2.156 0.031087 *
per_ag              0.047274   0.027577    0.027609   1.712 0.086840 .
Mean_temp          -0.052475   0.062667    0.062739   0.836 0.402929
per_dist            0.033392   0.027102    0.027133   1.231 0.218448
per_intro           0.030172   0.026794    0.026824   1.125 0.260681
Temp_seasonality    0.027271   0.032888    0.032926   0.828 0.407521
Mean_diurnal_range  0.007741   0.034843    0.034883   0.222 0.824390
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Relative variable importance: 
                     per_urban per_water Precip_seasonality elevation
Precip WinAvg NPP  per_ag Mean_temp per_dist per_intro Temp_seasonality
Mean_diurnal_range
Importance:          1.00      1.00      1.00               0.98      0.98
0.87   0.16 0.06   0.04      0.03     0.03      0.02              0.02
N containing models:   11        11        11                 10        10
9      2    1      1         1        1         1                 1
```

July 2008

```
Model-averaged coefficients:
(full average)
                     Estimate Std. Error Adjusted SE z value Pr(>|z|)
(Intercept)         1.455e-02  4.576e-02   4.585e-02   0.317 0.750991
elevation           1.708e-01  4.980e-02   4.987e-02   3.426 0.000613 ***
NPP                -1.529e-01  3.695e-02   3.702e-02   4.131 3.61e-05 ***
per_ag              1.506e-01  3.724e-02   3.731e-02   4.036 5.43e-05 ***
per_urban           1.531e-01  3.456e-02   3.463e-02   4.421 9.80e-06 ***
WinAvg             -1.547e-01  3.857e-02   3.864e-02   4.003 6.25e-05 ***
per_water           2.370e-02  4.157e-02   4.159e-02   0.570 0.568740
Precip_seasonality  1.844e-02  3.969e-02   3.971e-02   0.464 0.642380
per_dist            4.689e-03  1.867e-02   1.868e-02   0.251 0.801793
Mean_temp           9.619e-05  2.868e-02   2.871e-02   0.003 0.997327
Precip             -2.797e-03  1.511e-02   1.512e-02   0.185 0.853306
per_intro           5.221e-04  6.010e-03   6.017e-03   0.087 0.930848
Mean_diurnal_range  1.929e-05  5.770e-03   5.781e-03   0.003 0.997337
Temp_seasonality    4.437e-05  4.862e-03   4.872e-03   0.009 0.992734

(conditional average)
                    Estimate Std. Error Adjusted SE z value Pr(>|z|)
(Intercept)         0.014549   0.045760    0.045847   0.317 0.750991
elevation           0.173455   0.045448    0.045523   3.810 0.000139 ***
NPP                -0.152940   0.036948    0.037019   4.131 3.61e-05 ***
per_ag              0.150595   0.037240    0.037311   4.036 5.43e-05 ***
per_urban           0.153070   0.034559    0.034625   4.421 9.80e-06 ***
WinAvg             -0.154698   0.038572    0.038643   4.003 6.25e-05 ***
per_water           0.081671   0.034938    0.035004   2.333 0.019640 *
Precip_seasonality  0.084700   0.040307    0.040383   2.097 0.035957 *
per_dist            0.057310   0.035271    0.035339   1.622 0.104857
Mean_temp           0.001348   0.107387    0.107482   0.013 0.989990
Precip             -0.050997   0.041315    0.041393   1.232 0.217934
per_intro           0.030188   0.034541    0.034607   0.872 0.383039
Mean_diurnal_range  0.001226   0.045976    0.046064   0.027 0.978769
Temp_seasonality    0.003160   0.040914    0.040993   0.077 0.938559
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Relative variable importance:
                     NPP  per_ag per_urban WinAvg elevation per_water
Precip_seasonality per_dist Mean_temp Precip per_intro Mean_diurnal_range
Temp_seasonality
Importance:          1.00 1.00   1.00      1.00   0.98      0.29      0.22
0.08     0.07      0.05   0.02      0.02                0.01
N containing models:   17   17     17        17     16         5         5
3        4         3      1         1                  1
```

July 2009

```
Model-averaged coefficients:
(full average)
                     Estimate Std. Error Adjusted SE z value Pr(>|z|)
(Intercept)         7.823e-03  4.050e-02   4.055e-02   0.193 0.847027
elevation           1.572e-01  4.848e-02   4.851e-02   3.241 0.001191 **
per_urban           1.441e-01  2.859e-02   2.862e-02   5.034    5e-07 ***
per_water           1.080e-01  3.031e-02   3.034e-02   3.560 0.000371 ***
Precip_seasonality  1.217e-01  4.779e-02   4.782e-02   2.545 0.010932 *
Temp_seasonality    5.262e-02  5.534e-02   5.536e-02   0.951 0.341841
WinAvg             -9.467e-02  4.285e-02   4.288e-02   2.208 0.027247 *
per_ag              4.463e-03  1.705e-02   1.706e-02   0.262 0.793626
NPP                -3.762e-03  1.566e-02   1.567e-02   0.240 0.810248
Mean_temp           2.966e-03  2.721e-02   2.722e-02   0.109 0.913220
Precip             -8.350e-04  7.729e-03   7.734e-03   0.108 0.914023
Mean_diurnal_range -6.401e-05  8.493e-03   8.500e-03   0.008 0.993991
per_dist           -4.950e-04  5.337e-03   5.340e-03   0.093 0.926156

(conditional average)
                    Estimate Std. Error Adjusted SE z value Pr(>|z|)
(Intercept)         0.007823   0.040501    0.040550   0.193 0.847027
elevation           0.162080   0.040461    0.040503   4.002 6.29e-05 ***
per_urban           0.144094   0.028590    0.028624   5.034 5.00e-07 ***
per_water           0.109032   0.028556    0.028590   3.814 0.000137 ***
Precip_seasonality  0.129281   0.038029    0.038069   3.396 0.000684 ***
Temp_seasonality    0.097260   0.036324    0.036364   2.675 0.007482 **
WinAvg             -0.104514   0.031593    0.031628   3.305 0.000951 ***
per_ag              0.053208   0.029564    0.029599   1.798 0.072233 .
NPP                -0.051456   0.030023    0.030057   1.712 0.086911 .
Mean_temp           0.042948   0.094876    0.094922   0.452 0.650943
Precip             -0.031323   0.035860    0.035901   0.872 0.382945
Mean_diurnal_range -0.002327   0.051158    0.051198   0.045 0.963746
per_dist           -0.023979   0.028575    0.028610   0.838 0.401968
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Relative variable importance:
                     per_urban per_water elevation Precip_seasonality
WinAvg Temp_seasonality per_ag NPP  Mean_temp Mean_diurnal_range Precip
per_dist
Importance:          1.00      0.99      0.97      0.94               0.91
0.54             0.08   0.07 0.07      0.03               0.03   0.02
N containing models:   21        20        20        20                 17
11                3      3    3         2                  2      2
```

July 2010

```
Model-averaged coefficients:
(full average)
                    Estimate Std. Error Adjusted SE z value Pr(>|z|)
(Intercept)         3.172e-02  5.376e-02   5.385e-02   0.589  0.55588
per_ag              1.422e-01  3.445e-02   3.451e-02   4.122 3.76e-05 ***
per_urban           1.147e-01  3.717e-02   3.721e-02   3.081  0.00206 **
Precip_seasonality  1.091e-01  6.650e-02   6.653e-02   1.641  0.10089
elevation           6.641e-02  7.228e-02   7.230e-02   0.919  0.35835
WinAvg             -2.004e-02  3.939e-02   3.940e-02   0.509  0.61096
NPP                -3.085e-02  4.642e-02   4.643e-02   0.664  0.50638
Temp_seasonality    1.552e-02  3.835e-02   3.837e-02   0.404  0.68587
Mean_temp           1.210e-02  3.843e-02   3.844e-02   0.315  0.75290
Precip             -4.189e-03  1.922e-02   1.922e-02   0.218  0.82752
per_water           4.796e-03  1.871e-02   1.872e-02   0.256  0.79779
per_dist           -5.738e-04  6.150e-03   6.154e-03   0.093  0.92572
Mean_diurnal_range  3.623e-04  6.515e-03   6.521e-03   0.056  0.95570
per_intro          -3.249e-05  2.001e-03   2.004e-03   0.016  0.98706

(conditional average)
                    Estimate Std. Error Adjusted SE z value Pr(>|z|)
(Intercept)         0.031717   0.053763    0.053851   0.589 0.555879
per_ag              0.142219   0.034453    0.034506   4.122 3.76e-05 ***
per_urban           0.117390   0.033080    0.033133   3.543 0.000396 ***
Precip_seasonality  0.134482   0.045183    0.045237   2.973 0.002950 **
elevation           0.125346   0.049736    0.049792   2.517 0.011822 *
WinAvg             -0.081515   0.036043    0.036098   2.258 0.023934 *
NPP                -0.086039   0.035501    0.035555   2.420 0.015526 *
Temp_seasonality    0.088535   0.043914    0.043971   2.013 0.044063 *
Mean_temp           0.087990   0.063713    0.063766   1.380 0.167621
Precip             -0.067555   0.040920    0.040981   1.648 0.099258 .
per_water           0.059586   0.032950    0.033003   1.805 0.071003 .
per_dist           -0.037253   0.033002    0.033056   1.127 0.259767
Mean_diurnal_range  0.022712   0.046403    0.046460   0.489 0.624948
per_intro          -0.009536   0.032931    0.032985   0.289 0.772501
---
Signif.  codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Relative variable importance:
                     per_ag per_urban Precip_seasonality elevation NPP
WinAvg Temp_seasonality Mean_temp per_water Precip Mean_diurnal_range
per_dist per_intro
Importance:             1   0.98      0.81               0.53      0.36
0.25   0.18             0.14      0.08      0.06   0.02              0.02
<0.01
N containing models:    67     64        48                34        29
22     19               17         9         7      4                 3
1
```

July 2011

```
Model-averaged coefficients:
(full average)
                     Estimate Std. Error Adjusted SE z value Pr(>|z|)
(Intercept)        -2.678e-02  4.935e-02   4.943e-02   0.542 0.587904
elevation           1.175e-01  8.207e-02   8.210e-02   1.431 0.152399
per_ag              6.471e-02  5.275e-02   5.278e-02   1.226 0.220124
per_dist           -1.224e-01  3.343e-02   3.348e-02   3.655 0.000257 ***
per_urban           1.374e-01  3.240e-02   3.244e-02   4.234 2.29e-05 ***
Precip_seasonality  1.084e-01  5.791e-02   5.794e-02   1.872 0.061256 .
WinAvg             -1.172e-01  5.177e-02   5.181e-02   2.262 0.023683 *
Mean_diurnal_range  6.683e-02  7.119e-02   7.121e-02   0.939 0.347980
Mean_temp          -1.469e-02  5.561e-02   5.563e-02   0.264 0.791699
per_water           1.169e-02  2.888e-02   2.889e-02   0.405 0.685729
NPP                -5.040e-03  2.022e-02   2.023e-02   0.249 0.803236
Temp_seasonality   -1.504e-03  1.223e-02   1.223e-02   0.123 0.902124
Precip             -2.279e-04  4.471e-03   4.476e-03   0.051 0.959386
per_intro           6.656e-05  2.319e-03   2.322e-03   0.029 0.977135

(conditional average)
                   Estimate Std. Error Adjusted SE z value Pr(>|z|)
(Intercept)        -0.02678    0.04935     0.04943   0.542 0.587904
elevation           0.14670    0.06423     0.06428   2.282 0.022470 *
per_ag              0.09622    0.03326     0.03331   2.889 0.003870 **
per_dist           -0.12295    0.03245     0.03249   3.784 0.000154 ***
per_urban           0.13739    0.03240     0.03244   4.234 2.29e-05 ***
Precip_seasonality  0.12665    0.04013     0.04018   3.152 0.001622 **
WinAvg             -0.12769    0.03977     0.03982   3.207 0.001342 **
Mean_diurnal_range  0.12470    0.04732     0.04738   2.632 0.008486 **
Mean_temp          -0.10188    0.11207     0.11215   0.908 0.363665
per_water           0.06754    0.03237     0.03241   2.084 0.037187 *
NPP                -0.06348    0.03796     0.03800   1.670 0.094869 .
Temp_seasonality   -0.05435    0.05028     0.05034   1.080 0.280231
Precip             -0.02313    0.03872     0.03877   0.597 0.550736
per_intro           0.01535    0.03172     0.03177   0.483 0.628911
---
Signif.  codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Relative variable importance:
                     per_urban per_dist WinAvg Precip_seasonality
elevation per_ag Mean_diurnal_range per_water Mean_temp NPP
Temp_seasonality Precip per_intro
Importance:              1         1     0.92   0.86                0.8
0.67   0.54               0.17      0.14      0.08  0.03             0.01
<0.01
N containing models:    55        54       48     45                 41
32     31                 16        13        11     4                2
1
```

July 2012

```
Model-averaged coefficients:
(full average)
                    Estimate Std. Error Adjusted SE z value Pr(>|z|)
(Intercept)        -5.537e-03  3.593e-02   3.598e-02   0.154   0.8777
elevation           1.035e-01  1.036e-01   1.037e-01   0.998   0.3181
per_urban           1.661e-01  2.828e-02   2.832e-02   5.867   <2e-16 ***
per_water           4.979e-02  4.605e-02   4.607e-02   1.081   0.2798
Precip_seasonality  1.215e-01  5.636e-02   5.638e-02   2.155   0.0312 *
WinAvg             -1.532e-01  3.381e-02   3.385e-02   4.526    6e-06 ***
NPP                -4.325e-02  4.682e-02   4.684e-02   0.923   0.3558
Temp_seasonality    5.268e-02  6.038e-02   6.039e-02   0.872   0.3830
Mean_temp           1.048e-01  1.075e-01   1.075e-01   0.975   0.3296
Mean_diurnal_range  1.654e-02  4.075e-02   4.076e-02   0.406   0.6849
per_dist           -2.068e-02  3.499e-02   3.500e-02   0.591   0.5547
Precip             -2.430e-04  3.979e-03   3.982e-03   0.061   0.9513
per_ag              6.993e-05  2.038e-03   2.039e-03   0.034   0.9726
per_intro           5.223e-05  1.729e-03   1.731e-03   0.030   0.9759

(conditional average)
                    Estimate Std. Error Adjusted SE z value Pr(>|z|)
(Intercept)        -0.005537   0.035931    0.035975   0.154 0.877676
elevation           0.191957   0.054248    0.054288   3.536 0.000406 ***
per_urban           0.166141   0.028285    0.028319   5.867  < 2e-16 ***
per_water           0.082335   0.028765    0.028799   2.859 0.004251 **
Precip_seasonality  0.135134   0.041116    0.041155   3.284 0.001025 **
WinAvg             -0.153202   0.033814    0.033848   4.526    6e-06 ***
NPP                -0.082747   0.030441    0.030476   2.715 0.006624 **
Temp_seasonality    0.106386   0.040598    0.040638   2.618 0.008847 **
Mean_temp           0.197061   0.059652    0.059690   3.301 0.000962 ***
Mean_diurnal_range  0.094645   0.045922    0.045965   2.059 0.039487 *
per_dist           -0.068198   0.028246    0.028280   2.412 0.015887 *
Precip             -0.032461   0.032704    0.032744   0.991 0.321509
per_ag              0.026085   0.029504    0.029540   0.883 0.377207
per_intro           0.022154   0.027912    0.027947   0.793 0.427929
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Relative variable importance:
                    per_urban WinAvg Precip_seasonality per_water
elevation Mean_temp NPP   Temp_seasonality per_dist Mean_diurnal_range
Precip per_ag per_intro
Importance:             1        1    0.9                0.6      0.54
0.53      0.52   0.5             0.3     0.17               0.01  <0.01
<0.01
N containing models:    86        86     71                 49        45
56        47    41              36       26                  3      1
1
```

July 2013

```
Model-averaged coefficients:
(full average)
                     Estimate Std. Error Adjusted SE z value Pr(>|z|)
(Intercept)         0.0083652  0.0329539   0.0329769   0.254 0.799751
elevation           0.2145878  0.0590351   0.0590514   3.634 0.000279 ***
per_ag              0.1310987  0.0212944   0.0213090   6.152  < 2e-16 ***
per_intro           0.0405995  0.0338078   0.0338135   1.201 0.229872
per_urban           0.2623586  0.0205813   0.0205954  12.739  < 2e-16 ***
per_water           0.1020364  0.0208029   0.0208173   4.902    1e-06 ***
Precip             -0.0575007  0.0382900   0.0382979   1.501 0.133250
Precip_seasonality  0.1636700  0.0266146   0.0266320   6.146  < 2e-16 ***
Temp_seasonality    0.1772216  0.0278046   0.0278228   6.370  < 2e-16 ***
WinAvg             -0.1194399  0.0235540   0.0235694   5.068    4e-07 ***
Mean_temp          -0.0356714  0.0602983   0.0603082   0.591 0.554196
per_dist           -0.0113044  0.0232110   0.0232140   0.487 0.626283
NPP                -0.0075165  0.0193669   0.0193695   0.388 0.697973
Mean_diurnal_range  0.0006676  0.0067096   0.0067119   0.099 0.920763

(conditional average)
                    Estimate Std. Error Adjusted SE z value Pr(>|z|)
(Intercept)         0.008365   0.032954    0.032977   0.254 0.799751
elevation           0.214588   0.059035    0.059051   3.634 0.000279 ***
per_ag              0.131099   0.021294    0.021309   6.152  < 2e-16 ***
per_intro           0.062023   0.020429    0.020443   3.034 0.002414 **
per_urban           0.262359   0.020581    0.020595  12.739  < 2e-16 ***
per_water           0.102036   0.020803    0.020817   4.902    1e-06 ***
Precip             -0.075401   0.023935    0.023951   3.148 0.001643 **
Precip_seasonality  0.163670   0.026615    0.026632   6.146  < 2e-16 ***
Temp_seasonality    0.177222   0.027805    0.027823   6.370  < 2e-16 ***
WinAvg             -0.119440   0.023554    0.023569   5.068    4e-07 ***
Mean_temp          -0.113396   0.052387    0.052424   2.163 0.030536 *
per_dist           -0.050094   0.021078    0.021093   2.375 0.017552 *
NPP                -0.047505   0.021700    0.021715   2.188 0.028693 *
Mean_diurnal_range  0.036042   0.033990    0.034014   1.060 0.289316
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Relative variable importance:
                     elevation per_ag per_urban per_water
Precip_seasonality Temp_seasonality WinAvg Precip per_intro Mean_temp
per_dist NPP  Mean_diurnal_range
Importance:          1.00      1.00   1.00      1.00      1.00
1.00             1.00   0.76   0.65      0.31      0.23      0.16 0.02
N containing models:   28        28     28        28        28
28               28     16     15        11        11       10    2
```

July 2014

```
Model-averaged coefficients:
(full average)
                     Estimate Std. Error Adjusted SE z value Pr(>|z|)
(Intercept)         0.0388012  0.0465350   0.0465906   0.833   0.4050
elevation           0.2838702  0.0926562   0.0927024   3.062   0.0022 **
Mean_temp          -0.1465151  0.0993165   0.0993577   1.475   0.1403
per_urban           0.1331070  0.0275647   0.0275971   4.823  1.4e-06 ***
per_water           0.0981374  0.0312482   0.0312773   3.138   0.0017 **
Precip_seasonality  0.1893930  0.0386307   0.0386671   4.898  1.0e-06 ***
per_ag              0.0470723  0.0463443   0.0463565   1.015   0.3099
Temp_seasonality    0.0262641  0.0454306   0.0454396   0.578   0.5633
Mean_diurnal_range  0.0161614  0.0379864   0.0379940   0.425   0.6706
Precip             -0.0112891  0.0286554   0.0286622   0.394   0.6937
NPP                -0.0070693  0.0223963   0.0224014   0.316   0.7523
WinAvg             -0.0037847  0.0168977   0.0169020   0.224   0.8228
per_dist           -0.0008219  0.0069018   0.0069046   0.119   0.9052
per_intro           0.0001281  0.0026753   0.0026772   0.048   0.9618

(conditional average)
                   Estimate Std. Error Adjusted SE z value Pr(>|z|)
(Intercept)         0.03880    0.04653     0.04659   0.833 0.404951
elevation           0.28387    0.09266     0.09270   3.062 0.002197 **
Mean_temp          -0.18970    0.06767     0.06774   2.800 0.005106 **
per_urban           0.13311    0.02756     0.02760   4.823  1.4e-06 ***
per_water           0.10028    0.02797     0.02801   3.581 0.000343 ***
Precip_seasonality  0.18939    0.03863     0.03867   4.898  1.0e-06 ***
per_ag              0.08210    0.02950     0.02953   2.780 0.005437 **
Temp_seasonality    0.08930    0.03726     0.03730   2.394 0.016655 *
Mean_diurnal_range  0.08694    0.04011     0.04015   2.165 0.030381 *
Precip             -0.06872    0.03243     0.03247   2.116 0.034319 *
NPP                -0.06241    0.03122     0.03125   1.997 0.045831 *
WinAvg             -0.05860    0.03477     0.03480   1.684 0.092150 .
per_dist           -0.03917    0.02771     0.02775   1.412 0.158012
per_intro           0.02199    0.02735     0.02739   0.803 0.421983
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Relative variable importance:
                     elevation per_urban Precip_seasonality per_water
Mean_temp per_ag Temp_seasonality Mean_diurnal_range Precip NPP  WinAvg
per_dist per_intro
Importance:          1.00      1.00      1.00               0.98      0.77
0.57   0.29             0.19               0.16   0.11 0.06   0.02
0.01
N containing models:   42        42        42                 40        27
24     14                12                11       8    7      2         1
```

APPENDIX D: ADDITIONAL MODEL SUMMARIES FOR CHAPTER 4

Table D1 The most plausible model for each year in January based on mean environmental data.

Year	Model (Coefficient)	Pseudo-Adj. R^2
2008	Elevation (-0.367) + Precip. (-0.294) + Precip. Seasonality (-0.242) + Temp. seasonality (-0.661) + Mean temp. (-0.294) + (1|Ecoregion)	0.208
2009	Elevation (-0.298) + Precip. (-0.326) + Precip. seasonality (-0.214) + Temp. seasonality (-0.457) + Mean diurnal range (-0.193) + Mean temp. (-0.130) + (1|Ecoregion)	0.173
2010	Precip. (-0.284) + Temp. seasonality (-0.516) + Precip. seasonality (-0.284) + Elevation (-0.288) + (1|Ecoregion)	0.1182
2011	Precip. (-0.180) + Temp. seasonality (-0.279) + (1|Ecoregion)	0.0813
2012	Temp. seasonality (-0.220) + (1|Ecoregion)	0.0417
2013	N/A	N/A
2014	Temp. seasonality (-0.167) + Elevation (-0.107) + NPP (-0.127) + (1|Ecoregion)	0.0678

Table D2 The most plausible model for each year in July based on mean environmental data.

Year	**Model**	**Adj. R^2**
2008	Temp. seasonality (-0.269) + (1|Ecoregion)	0.1011
2009	Elevation (-0.240) + Mean temp. (-0.283) + Temp. seasonality (-0.223) + (1|Ecoregion)	0.0489
2010	Mean temp. (-0.407) + Temp. seasonality (-0.536) + Precip. (-0.135) + (1|Ecoregion)	0.1636
2011	Mean temp. (-0.233) + Temp. seasonality (-0.377) + (1|Ecoregion)	0.1045
2012	Mean diurnal range (-0.292) + Mean temp. (-0.247) + Temp. seasonality (-0.378) + Precip. (-0.141) + (1|Ecoregion)	0.1464
2013	Mean diurnal range (-0.184) + Mean temp. (-0.342) + Precip. (-0.180) + Temp. seasonality (-0.450) + Elevation (-0.167) + (1|Ecoregion)	0.1654
2014	Mean temp. (-0.283) + Temp. seasonality (-0.250) + (1|Ecoregion)	0.0796

Table D3 The most plausible model for each year in January based on standard deviations of environmental data.

Year	Model	Adj. R^2
2008	Mean diurnal range (0.196) + Percent agriculture (-0.139) + NPP (0.118) + Wind avg. (0.119) + (1|Ecoregion)	0.1348
2009	NPP (0.159) + Percent urban (-0.156) + Wind avg. (0.169) + Elevation (-0.155) + Percent water (-0.093) + (1|Ecoregion)	0.1539
2010	Percent urban (-0.129) + NPP (0.126) + Precip. Seasonality (-0.114) + (1|Ecoregion)	0.0798
2011	Mean diurnal range (0.230) + Percent agriculture (-0.133) + Percent urban (-0.125) + NPP (0.125) + Elevation (-0.150) + (1|Ecoregion)	0.1468
2012	Mean diurnal range (0.137) + (1|Ecoregion)	0.0137
2013	N/A	N/A
2014	N/A	N/A

Table D4 The most plausible model for each year in July based on standard deviations of environmental data.

Year	**Model**	**Adj. R^2**
2008	Percent agriculture (-0.183) + NPP (0.140) + (1|Ecoregion)	0.1021
2009	N/A	N/A
2010	NPP (0.184) + Precip. (0.152) + Precip. seasonality (0.195) + Percent disturbed (0.109) + (1|Ecoregion)	0.1632
2011	Wind avg. (0.157) + Precip. seasonality (0.135) + Percent agriculture (-0.099) + (1|Ecoregion)	0.1095
2012	NPP (0.163) + Percent urban (-0.135) + Precip. (0.150) + (1|Ecoregion)	0.1277
2013	NPP (0.170) + Precip. (0.219) + Precip. seasonality (0.112) + Percent urban (-0.078) + (1|Ecoregion)	0.1616
2014	Precip. (0.194) + Precip. seasonality (0.102) + (1|Ecoregion)	0.0890

Table D5 The most plausible models predicting conventional Jaccard's dissimilarity for mean environmental variables in January.

Year	Model	Adj. R^2
2008	Elevation (0.284) + NPP (-0.190) + Precip. (0.221) + Precip. seasonality (0.272) + Temp. seasonality (0.253) + (1|Ecoregion)	0.207
2009	Mean diurnal range (0.260) + Mean temp. (-0.385) + Precip. seasonality (0.223) + NPP (-0.194) + Percent Agriculture (-0.112) + (1|Ecoregion)	0.266
2010	Mean diurnal range (0.210) + Mean temp. (-0.236)	0.094
2011	Elevation (0.331) + (1|Ecoregion)	0.113
2012	Elevation (0.399) + Precip. (0.202) + Precip. seasonality (0.224) + Temp. seasonality (0.179) + (1|Ecoregion)	0.168
2013	Elevation (0.197) + Mean diurnal range (0.187) + Mean temp. (-0.291) + NPP (-0.237) + Precip, (0.180) + Wind Average (0.162) + (1|Ecoregion)	0.270
2014	Elevation (0.337) + Precip. seasonality (0.211) + Temp. seasonality (0.217) + (1|Ecoregion)	0.213

Table D6 The most plausible models predicting conventional Jaccard's dissimilarity for mean environmental variables in July.

Year	**Model**	**Adj. R^2**
2008	Elevation (0.250) + Temp. seasonality (0.309) + Precip. seasonality (0.149) + (1|Ecoregion)	0.129
2009	Elevation (0.298) + Precip. seasonality (0.258) + (1|Ecoregion)	0.219
2010	Elevation (0.318) + Precip. seasonality (0.172) + Temp. seasonality (0.198) + (1|Ecoregion)	0.182
2011	Elevation (0.201) + Precip. seasonality (0.358) + Temp. seasonality (0.223) + (1|Ecoregion)	0.221
2012	Elevation (0.302) + Precip. seasonality (0.210) + (1|Ecoregion)	0.238
2013	Elevation (0.249) + NPP (-0.144) + Precip. seasonality (0.199) + Mean diurnal range (0.111) + (1|Ecoregion)	0.289
2014	Elevation (0.232) + Precip. seasonality (-0.132) + NPP (0.202) + (1|Ecoregion)	0.243

Table D7 The most plausible models predicting conventional Jaccard's dissimilarity for standard deviations of environmental variables in January.

Year	**Model**	**Adj. R^2**
2008	NPP (-0.184) + Percent urban (0.137) + Precip. seasonality (0.131) + Elevation (0.142) + Percent water (0.099) + (1|Ecoregion)	0.142
2009	NPP (-0.137) + Percent urban (0.142) + Percent water (0.129) + Average wind (-0.167) + Elevation (0.188) + (1|Ecoregion)	0.169
2010	NPP (-0.179) + Percent urban (0.179) + Precip. seasonality (0.156) + (1|Ecoregion)	0.102
2011	NPP (-0.162) + Percent urban (0.135) + Precip. seasonality (0.220) + (1|Ecoregion)	0.109
2012	NPP (-0.134) + Precip. seasonality (0.168) + Percent urban (0.103) + (1|Ecoregion)	0.084
2013	Elevation (0.182) + NPP (-0.176) + Precip. seasonality (0.237) + Percent urban (0.091) + (1|Ecoregion)	0.162
2014	Percent urban (0.197) + Percent water (0.148) + Precip. seasonality (0.276) + Elevation (0.130) + Precip, (-0.123) + Average wind (-0.082) + (1|Ecoregion)	0.205

Table D8 The most plausible models predicting conventional Jaccard's dissimilarity for standard deviations of environmental variables in July.

Year	**Model**	**Adj. R^2**
2008	NPP (-0.153) + Percent agriculture (0.151) + Percent urban (0.153) + Average wind (-0.155) + Elevation (0.171) + (1|Ecoregion)	0.161
2009	Percent urban (0.144) + Percent water (0.108) + Elevation (0.157) + Precip. seasonality (0.122) + Average wind (-0.095) + (1|Ecoregion)	0.146
2010	Percent agriculture (0.142) + Percent urban (0.115) + (1|Ecoregion)	0.092
2011	Percent urban (0.137) + Percent disturbed (0.112) + Average wind (-0.117) + Precip. seasonality (0.108) + (1|Ecoregion)	0.114
2012	Percent urban (0.166) + Average wind (-0.153) + Precip. seasonality (0.122) + (1|Ecoregion)	0.143
2013	Elevation (0.215) + Percent agriculture (0.131) + Percent urban (0.262) + Percent water (0.102) + Precip. seasonality (0.262) + Temp. seasonality (0.177) + Average wind (-0.119) + (1|Ecoregion)	0.262
2014	Elevation (0.284) + Percentage urban (0.133) + Precip. seasonality (0.189) + Percent water (0.098) + (1|Ecoregion)	0.176

APPENDIX E: ELEVATION CORRELATIONS FOR JACCARD’S β

January 2008

```
Linear mixed-effects model fit by REML
 Data: scaled.data.assembled 
       AIC      BIC    logLik
  2982.454 3002.337 -1487.227

Random effects:
 Formula: ~1 | ecoregion
        (Intercept) Residual
StdDev:   0.2852411 0.945883

Fixed effects: Jaccard ~ elevation 
                 Value  Std.Error  DF  t-value p-value
(Intercept) 0.02864378 0.04602713 988 0.622324  0.5339
elevation   0.18809697 0.03017250 988 6.234053  0.0000
 Correlation: 
          (Intr)
elevation -0.013

Standardized Within-Group Residuals:
       Min         Q1        Med         Q3        Max 
-4.1847759 -0.6918221  0.1206368  0.7695785  1.9698938 

Number of Observations: 1067
Number of Groups: 78 
```

January 2009

```
Linear mixed-effects model fit by REML
 Data: scaled.data.assembled
       AIC      BIC    logLik
  2233.037 2251.755 -1112.518

Random effects:
 Formula: ~1 | ecoregion
        (Intercept)  Residual
StdDev:   0.2232506 0.9517508

Fixed effects: Jaccard ~ elevation
                 Value  Std.Error  DF  t-value p-value
(Intercept) 0.00439021 0.04496611 720 0.097634  0.9223
elevation   0.21782953 0.03474833 720 6.268777  0.0000
 Correlation:
          (Intr)
elevation -0.029

Standardized Within-Group Residuals:
        Min          Q1         Med          Q3         Max
-2.74895369 -0.70819186  0.05649337  0.76294397  2.01519800

Number of Observations: 798
Number of Groups: 77
```

January 2010

```
Linear mixed-effects model fit by REML
 Data: scaled.data.assembled
       AIC      BIC    logLik
  2216.144 2234.771 -1104.072

Random effects:
 Formula: ~1 | ecoregion
        (Intercept)  Residual
StdDev:   0.2355912 0.9711877

Fixed effects: Jaccard ~ elevation
                 Value  Std.Error  DF   t-value p-value
(Intercept) 0.00321817 0.04691606 703 0.0685942  0.9453
elevation   0.09444850 0.03578806 703 2.6391061  0.0085
 Correlation:
          (Intr)
elevation -0.03

Standardized Within-Group Residuals:
       Min         Q1        Med         Q3        Max
-3.2373765 -0.6703014  0.1548106  0.7299168  1.9267413

Number of Observations: 780
Number of Groups: 76
```

January 2011

```
Linear mixed-effects model fit by REML
 Data: scaled.data.assembled
       AIC      BIC    logLik
  2172.268 2190.853 -1082.134

Random effects:
 Formula: ~1 | ecoregion
        (Intercept)  Residual
StdDev:   0.2070525 0.9611685

Fixed effects: Jaccard ~ elevation
                Value  Std.Error  DF  t-value p-value
(Intercept) 0.0090265 0.04445512 695 0.203047  0.8392
elevation   0.1849002 0.03551623 695 5.206075  0.0000
 Correlation:
          (Intr)
elevation -0.026

Standardized Within-Group Residuals:
        Min          Q1         Med          Q3         Max
-2.79468049 -0.73783129 -0.04026237  0.76467032  2.21523835

Number of Observations: 772
Number of Groups: 76
```

January 2012

```
Linear mixed-effects model fit by REML
 Data: scaled.data.assembled
       AIC      BIC    logLik
  3018.057 3037.966 -1505.028

Random effects:
 Formula: ~1 | ecoregion
        (Intercept)  Residual
StdDev:  0.07392811 0.9761241

Fixed effects: Jaccard ~ elevation
                  Value  Std.Error  DF   t-value p-value
(Intercept) -0.00044961 0.03145622 992 -0.014293  0.9886
elevation    0.20435741 0.02996822 992  6.819137  0.0000
 Correlation:
          (Intr)
elevation -0.004

Standardized Within-Group Residuals:
        Min          Q1         Med          Q3         Max
-2.95401672 -0.70368873  0.06186604  0.70098300  2.21861362

Number of Observations: 1074
Number of Groups: 81
```

January 2013

```
Linear mixed-effects model fit by REML
 Data: scaled.data.assembled
       AIC      BIC  logLik
  3093.001 3113.053 -1542.5

Random effects:
 Formula: ~1 | ecoregion
        (Intercept)  Residual
StdDev:   0.1900099 0.9498829

Fixed effects: Jaccard ~ elevation
                  Value  Std.Error   DF   t-value p-value
(Intercept) -0.00045823 0.03760622 1031 -0.012185  0.9903
elevation    0.24545302 0.02911611 1031  8.430145  0.0000
 Correlation:
          (Intr)
elevation -0.015

Standardized Within-Group Residuals:
        Min          Q1         Med          Q3         Max
-3.09145864 -0.68078595  0.09117917  0.73059405  2.16037452

Number of Observations: 1113
Number of Groups: 81
```

January 2014

```
Linear mixed-effects model fit by REML
 Data: scaled.data.assembled
       AIC      BIC    logLik
  3196.746 3216.901 -1594.373

Random effects:
 Formula: ~1 | ecoregion
        (Intercept)  Residual
StdDev:   0.2466666 0.9532426

Fixed effects: Jaccard ~ elevation
                 Value  Std.Error   DF  t-value p-value
(Intercept) 0.00750816 0.04174449 1060 0.179860  0.8573
elevation   0.17756056 0.02947641 1060 6.023819  0.0000
 Correlation:
          (Intr)
elevation -0.025

Standardized Within-Group Residuals:
       Min         Q1        Med         Q3        Max
-2.6146873 -0.7880475  0.0816628  0.7437263  2.2982471

Number of Observations: 1142
Number of Groups: 81
```

July 2008

```
Linear mixed-effects model fit by REML
 Data: scaled.data.assembled
     AIC      BIC  logLik
  2023.6 2041.889 -1007.8

Random effects:
 Formula: ~1 | ecoregion
        (Intercept)  Residual
StdDev:   0.3136927 0.9491857

Fixed effects: Jaccard ~ elevation
                 Value  Std.Error  DF   t-value p-value
(Intercept) 0.02407009 0.05403003 638 0.4454946  0.6561
elevation   0.08771807 0.03745493 638 2.3419634  0.0195
 Correlation:
          (Intr)
elevation -0.04

Standardized Within-Group Residuals:
       Min         Q1        Med         Q3        Max
-3.2686334 -0.6082533  0.1810674  0.7496724  2.0751811

Number of Observations: 717
Number of Groups: 78
```

July 2009

```
Linear mixed-effects model fit by REML
 Data: scaled.data.assembled
       AIC      BIC    logLik
  3012.961 3032.915 -1502.481

Random effects:
 Formula: ~1 | ecoregion
        (Intercept)  Residual
StdDev:   0.2748202 0.9373947

Fixed effects: Jaccard ~ elevation
                 Value  Std.Error   DF  t-value p-value
(Intercept) 0.00555455 0.04479397 1003 0.124002  0.9013
elevation   0.21699796 0.02986834 1003 7.265149  0.0000
 Correlation:
          (Intr)
elevation -0.003

Standardized Within-Group Residuals:
        Min          Q1         Med          Q3         Max
-2.88051307 -0.62658413  0.09705005  0.76485621  2.06101257

Number of Observations: 1086
Number of Groups: 82
```

July 2010

```
Linear mixed-effects model fit by REML
 Data: scaled.data.assembled
       AIC      BIC    logLik
  2283.486 2302.323 -1137.743

Random effects:
 Formula: ~1 | ecoregion
        (Intercept)  Residual
StdDev:   0.3490527 0.9247429

Fixed effects: Jaccard ~ elevation
                 Value  Std.Error  DF  t-value p-value
(Intercept) 0.02073045 0.05432852 741 0.381576  0.7029
elevation   0.13739326 0.03463598 741 3.966778  0.0001
 Correlation:
          (Intr)
elevation -0.033

Standardized Within-Group Residuals:
       Min         Q1        Med         Q3        Max
-2.9879034 -0.6762198  0.1290193  0.6977088  2.1285102

Number of Observations: 822
Number of Groups: 80
```

July 2011

```
Linear mixed-effects model fit by REML
 Data: scaled.data.assembled
       AIC      BIC    logLik
  2450.439 2469.527 -1221.219

Random effects:
 Formula: ~1 | ecoregion
        (Intercept)  Residual
StdDev:   0.3187336 0.9411489

Fixed effects: Jaccard ~ elevation
                 Value  Std.Error  DF   t-value p-value
(Intercept) -0.0270000 0.05146912 798 -0.524586     0.6
elevation    0.1608568 0.03334308 798  4.824292     0.0
 Correlation:
          (Intr)
elevation -0.009

Standardized Within-Group Residuals:
        Min          Q1         Med          Q3         Max
-2.76096642 -0.60623837  0.06559594  0.63659027  2.22166890

Number of Observations: 875
Number of Groups: 76
```

July 2012

```
Linear mixed-effects model fit by REML
 Data: scaled.data.assembled
       AIC      BIC    logLik
  2959.212 2979.125 -1475.606

Random effects:
 Formula: ~1 | ecoregion
        (Intercept)  Residual
StdDev:   0.2165621 0.9338549

Fixed effects: Jaccard ~ elevation
                  Value  Std.Error  DF   t-value p-value
(Intercept) -0.00742379 0.03990278 993 -0.186047  0.8524
elevation    0.28267972 0.02958610 993  9.554477  0.0000
 Correlation:
          (Intr)
elevation -0.011

Standardized Within-Group Residuals:
        Min          Q1         Med          Q3         Max
-2.97286586 -0.65020082  0.07199828  0.72616733  2.32890434

Number of Observations: 1075
Number of Groups: 81
```

July 2013

```
Linear mixed-effects model fit by REML
 Data: scaled.data.assembled
       AIC      BIC    logLik
  5026.112 5048.143 -2509.056

Random effects:
 Formula: ~1 | ecoregion
        (Intercept)  Residual
StdDev:   0.2409791 0.9378492

Fixed effects: Jaccard ~ elevation
                 Value  Std.Error   DF   t-value p-value
(Intercept) 0.00377376 0.03664123 1741  0.102992   0.918
elevation   0.26057736 0.02261044 1741 11.524650   0.000
 Correlation:
          (Intr)
elevation -0.011

Standardized Within-Group Residuals:
        Min          Q1         Med          Q3         Max
-4.46083936 -0.72026295  0.07385916  0.75137677  2.43994870

Number of Observations: 1824
Number of Groups: 82
```

July 2014

```
Linear mixed-effects model fit by REML
 Data: scaled.data.assembled
       AIC      BIC    logLik
  3011.225 3031.234 -1501.613

Random effects:
 Formula: ~1 | ecoregion
        (Intercept)  Residual
StdDev:   0.3313909 0.9118963

Fixed effects: Jaccard ~ elevation
                 Value  Std.Error   DF  t-value p-value
(Intercept) 0.03897083 0.04919527 1019 0.792166  0.4284
elevation   0.24017164 0.02868197 1019 8.373610  0.0000
 Correlation:
          (Intr)
elevation -0.014

Standardized Within-Group Residuals:
        Min          Q1         Med          Q3         Max
-2.60969623 -0.73478850  0.02076841  0.71360697  2.79030110

Number of Observations: 1101
Number of Groups: 81
```