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Pattern and process in metabolic ecology : from biotic interactions to cultural diversity gradients

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PATTERN AND PROCESS IN METABOLIC ECOLOGY: FROM BIOTIC INTERACTIONS TO CULTURAL DIVERSITY GRADIENTS

By

William R. Burnside

B.A., Human Biology, Stanford University, 1989
M.S., Natural Resources, University of Michigan, 1995

DISSERTATION

Submitted in Partial Fulfillment of the
Requirements for the Degree of

Doctor of Philosophy
Biology

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Albuquerque, New Mexico

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Dedication

TO MY MOTHER, PAT MORA, MY FATHER, BILL BURNSIDE, AND MY STEPFATHER, VERNON SCARBOROUGH

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I so appreciate the support of my parents, my stepdad, and sisters: Pat Mora, Bill Burnside, Vernon Scarborough, Libby Martinez, and Cissy Burnside. I also greatly appreciate my wonderful friends, including Siv Limary, Erik Erhardt, Kwaku Sraha, Deepta Dasgupta, Leslie Merriman, Chris Bickford, Bill Jarrold, Brad Gornstein, and others. They have all supported me tremendously, and I wouldn't be here without them. I also owe so much to those family members who came before me, especially my grandparents, Estella and Raul Mora, my great uncle, Lalo Delgado, and my great aunt, Ignacia Delgado. Thanks for your help; *muchisimas gracias por su ayuda*.

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PATTERN AND PROCESS IN METABOLIC ECOLOGY: FROM BIOTIC INTERACTIONS TO CULTURAL DIVERSITY GRADIENTS

By

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ABSTRACT

Many ecological patterns and processes are functions of metabolism (Brown 2004), meaning the acquisition, transformation, and allocation of energy, materials, and information within the bodies of individuals and among members of human and other animal societies. Individual metabolic rate should influence behavior by determining the energy available for action as well as the rate at which the body requires fuel. First, I test a key prediction of the metabolic theory of ecology (MTE), that biotic interaction rates are characteristic functions of temperature. Findings support this prediction and suggest that herbivory, predation, parasitism, parasitoidy, and competition increase exponentially with temperature and that this increase echoes that of individual metabolic rates. Second, I extend a metabolic framework to foraging patterns and space use of traditional human societies. Together with colleagues, I build on Hamilton (2007) to offer a model that formally incorporates hypothesized mechanisms affecting population sizes and densities and territory sizes: temperature, productivity, seasonality, and trophic level (degree of carnivory). We test this model on a dataset of 333 traditional foraging societies using multiple linear regression. Interactions between explanatory variables were important, and the influence of temperature, productivity, and seasonality often depended on trophic level. In addition, coastal productivity allowed marine foragers to disassociate themselves from terrestrial energetic constraints and maintain high population densities, small territory sizes, and thus high levels of cultural diversity. A metabolic perspective is useful for interpreting patterns in large scale human ecology and suggesting underlying mechanisms. Third, I argue for a macroecological approach to human ecology and suggest the value of a metabolic perspective using examples from human foraging ecology, life history, space use, population structure, disease ecology, cultural and linguistic diversity patterns, and industrial and urban systems. The ability of a metabolic framework to inform our understanding of behavior, from the interaction rates of small ectotherms to cultural diversity and urban activity patterns in *Homo sapiens*, suggests the power and promise of this approach.

Table of Contents

List of Figures

Chapter 1

Chapter 2

Chapter 3

List of Tables

Chapter 1

Chapter 2

Introduction

Many biological patterns and processes are functions of individual metabolism, meaning the acquisition, transformation, and allocation of energy and materials. By setting the rate resources are delivered to and used by cells, metabolic rate sets the pace of life (Brown et al. 2004). To meet this energetic demand, an organism must acquire a commensurate supply of energy. Thus, the energy organisms have available to fuel behaviors is constrained by metabolism, as is the rate those behaviors must be used to access fuel to keep this “circuit” intact. Despite efforts to test the effect of metabolic rate on linked physiological, life history, and behavioral variables (e.g. Dell et al., 2011), no study has tested the influence of a key metabolic parameter, temperature, on the rates of biotic interactions. Those interactions, including herbivory, predation, parasitism, and competition, are the nuts and bolts of community ecology. The interaction between predator and prey, for example, links individual metabolic need with the exchange of materials and energy through the medium of behavior. Considered together, the myriad interactions in ecological communities drive ecosystem function, from nutrient turnover to ecological succession.

My dissertation explores three aspects of metabolic ecology, working from small-scale interactions of ectotherms to large-scale ecological patterns and processes of humans. In chapter 1, “Rates of biotic interactions scale predictably with temperature,” I collaborate with James H. Brown on a macroecological test of the temperature dependence of biotic interaction rates. In chapter 2, “Energetics, range size, and geographic gradients of human cultural diversity,” I collaborate with Jordan Okie, Erik Erhardt, and Marcus Hamilton model the influence of environmental factors on demographic and spatial characteristics of traditional foraging societies. Finally, in chapter 3, “Human macroecology: linking pattern and process in big-picture human ecology," I collaborate with Oskar Burger, James H. Brown, Marcus Hamilton, Melanie Moses, and Luis Bettencourt explore the power and promise of a macroecological approach to humans.

Together, the first two studies and the final synthesis further illuminate the deep influence of metabolism on ecological pattern and process. They also argue for the continuing value of a "broad view" in our continuing effort to understand that most basic of ecological questions: what are the relationships among organisms and their environment?

Chapter 1: Rates of biotic interactions scale predictably with temperature

William R. Burnside and James H. Brown

Abstract

Biological processes, from DNA substitution to ecosystem succession, are temperature dependent. We extend this influence to rates of key biotic interactions: herbivory, predation, parasitism, parasitoidy, and competition. We compile a database of studies testing the temperature dependence of two-species interactions of live, mobile organisms. Using macroecological techniques, we test the prediction from the metabolic theory of ecology that interaction rates will echo the temperature dependence of metabolic rates generally, about 0.65 eV. Despite variation within and across interaction types, overall findings support this prediction. In addition, studies with greater resolution conformed more closely. These findings add to growing evidence that ecological patterns and processes depend crucially and characteristically on metabolism and have implications for a warming world.

Introduction

Many ecological processes are temperature-dependent. This is apparent in macroecological patterns, where temperature is the single most consistent and pervasive environmental variable associated with variation in species diversity across gradients of latitude and elevation on land and latitude and depth in the oceans (Schemske et al., 2009; Tittensor et al., 2010; Lomolino et al., 2010). Temperature-dependent ecological processes have also been demonstrated experimentally, from classic studies of interspecific competition in flour beetles (Park, 1954) to recent comparisons of decomposition rates across ecosystems (Gholz et al., 2000). The qualitative phenomenology is well-established: rates typically increase with increasing temperature, at least up to some stressfully high temperature, as illustrated in Figure 1a (Huey and Kingsolver, 1989). Much less is known, however, about the quantitiative form and mechanistic underpinnings of the temperature dependence of ecological processes.

Empirical and theoretical studies also suggest that many ecological patterns and processes can be directly and mechanistically linked to metabolism (Peters 1983; Yodzis and Innes, 1992; Brown et al., 2004; Sibly et al., 2012). Biological metabolism is about the uptake, transformation, and allocation of energy and materials by organisms. Ecology is about interactions between organisms and their abiotic and biotic environments, and all such interactions entail the exchange of energy or materials. So much of ecology is functionally linked to metabolism. Indeed, many ecological rates, including rates of resource use, turnover of carbon and other elements, life history processes, secondary succession, and organic matter decomposition, vary systematically with body size and temperature similar to the scaling of metabolic rate (e.g., Peters, 1983; Brown et al., 2004; Sibly et al., 2012, and many references therein).

Recent efforts to build and test a metabolic theory of ecology (MTE) aim to synthesize, conceptualize, and quantify the mechanistic role of metabolism. It has been known for over a century that metabolic rate varies predictably with body size and temperature. This relationship has been quantified in the "central equation" of MTE:

[illegible] (1)

where B is mass-specific metabolic rate, B_0 is a normalization constant that typically varies with taxon, functional group, and environmental setting, M is body mass, E is an "activation energy" determined by the underlying biochemical reactions and physiological processes, k is Boltzmann's constant, and T is absolute temperature in degrees Kelvin (Gillooly et al., 2001; Brown et al., 2004; Brown and Sibly, 2012). The last term of the above equation describes the near-exponential temperature dependence of metabolism in terms of the Arrhenius factor, $e^{-E/kT}$, which expresses the variation in biochemical reaction rates with increased kinetic energy of the molecular reactants (Arrhenius, 1915; Figure 1). The value of *E* is predicted to be close to 0.65 eV for metabolic rates governed primarily by aerobic respiration because this is the activation energy of the mitochondrial respiratory complex (Gillooly et al., 2001).

This paper evaluates whether MTE, as expressed in Eq 1, can be applied and extended to understand the temperature-dependence of rates of biotic interactions in ecology. This extension is based on the premise that the rates of interactions are closely correlated with and mechanistically linked to metabolic rate, which sets the requirements for energy, water, and nutrients and affects the fluxes of these commodities among individuals and species (Brown et al., 2004). Biotic interactions determine how the basic metabolic currencies of energy and materials are exchanged between organisms in networks of competitive, trophic, and mutualistic relationships. So, the metabolic mechanisms of competition, predation, herbivory, parasitism, disease, and mutualism link the physiology and behavior of individual plants, animals, and microbes to the abundance and distribution of populations, the organization and diversity of communities, and the biogeochemical processes of ecosystems. For example, it is straightforward to conjecture that rates of predation and herbivory should directly reflect metabolic rates, because consumers must acquire food at rates sufficient to fuel their metabolisms. It is less obvious that other interactions, such as competition and mutualism, should be directly related to metabolic rate.

A linkage is reasonable, however, because these interactions are often mediated by physiological and behavioral traits that in turn depend on metabolic processes (e.g., see chapters in Sibly et al., 2012) and because they are driven by the need for resources to fuel metabolism.

This paper looks across studies that assess how temperature affects rates of herbivory, predation, parasitism, parasitoidy, and competition between two species, to ask: 1) Do biotic interaction rates increase characteristically with temperature? 2) If so, does this temperature dependence echo that of metabolic rate generally and so follow the predictions of the metabolic theory of ecology. We compiled and analyzed published data from experimental and non-manipulative studies that reported rates of interactions at two or more temperatures. The mathematical form and quantitative magnitude of temperature dependence can be evaluated empirically by plotting the logarithm of rate as a function of $1/kT$ (Figure 1). Eq 1 predicts that in such an Arrhenius plot, the relationship will be linear. Additionally, the slope of the relationship with sign reversed gives an estimate of the "activation energy", E. So, if rates of these biotic interactions vary with temperature similar to metabolic rate, we predict: 1) the data should be well fitted by linear regressions, reflecting the applicability of the Arrhenius expression; and 2) the slopes should cluster around a central value of approximately -0.65, reflecting the ultimate rate-limiting effect of aerobic respiration.

An important caveat is that Eq 1, like all models, is a deliberate oversimplification of a more complex reality. Therefore we do not expect data to conform exactly to the above predictions. Three considerations are especially relevant. First, experimental data always exhibit variation and deviate somewhat from model predictions. Some of the variation reflects imprecision in controlling conditions and errors and possible biases in taking measurements and performing statistical analyses. Other variation reflects the real influence of other important factors not included in the deliberately simplified model. Second, the Arrhenius expression itself, $e^{-E/kT}$, is a simplification. The full relationship between temperature and metabolic rate is hump-shaped: an approximately exponential curve that rises to a peak and then declines precipitously as the temperature changes from optimal to stressful (Knies and Kingsolver, 2010; Hoekman, 2010). The Arrhenius expression appears to be adequate for many ecological applications, however, because most organisms spend most of their time within a limited range of non-stressful temperatures where the approximately exponential temperature-dependence can be quantified by the "activation energy" of the Arrhenius expression (above) or the Q_{10} expression traditionally used in physiology. Nevertheless, some departures from linearity, especially at the highest temperatures, are to be expected (see below). Third, the predicted value of the "activation energy", $E \approx 0.65$ eV, is only an approximation, which oversimplifies the complex biochemistry and kinetics of metabolism and assumes that the overall process of aerobic respiration has approximately this temperature dependence. However, this assumption is supported by the empirical generalization that many biological processes have an E of approximately 0.65 eV, equivalent to a Q_{10} of approximately 2.5 (Gillooly et al., 2001). We expect the slopes of Arrhenius plots to exhibit considerable variation but also a central tendency, with a median and mode of approximately -0.65.

The present study is a meta-analysis in the sense that it is based on compilation and analysis of published data. But we used macroecological methods, rather than traditional strict meta-analytical procedures, to assess the effects of temperature on biotic interaction rates. We assembled a database of published studies that measured interaction rates or time to outcome (e.g., time to extinction of one species), which we then converted to rates, at two or more temperatures. We made Arrhenius plots of the data (i.e., ln (rate) versus $1/kT$) and fitted linear regressions. This allowed standardized comparisons of temperature dependence by comparing slopes within and across categories of biotic interactions.

Methods

Study Criteria and Data Sources. We compiled data from the literature by searching for the keywords "temperature," and "rate," with any of "herbivory," "predation," "parasitism," "parasitic," "parasitoid," "parasitoidy," and "competition" using the *ISI Web of Science* and *Google Scholar* databases. We supplemented these with additional data found during our efforts to survey the relevant literature.

We included only those studies that

1. were published in the peer-reviewed literature
2. involved live organisms (i.e., no dead prey, hosts, etc.)
3. explicitly reported biotic interaction rates or times (e.g., time to competitive exclusion)
4. provided data on at least two non-zero rates or times measured at two or more different controlled or standardized temperatures within the taxa's thermally optimum range
5. measured interactions involving mobile organisms (except, in the case of herbivory, for plants) directly (rather than, for example, simply reporting growth rates)
6. provided reasonable detail on the methods, including measurements of rates or times, so as to ensure suitability for inclusion

7. provided original data on measured rates or times rather than parameters of models fitted to data (e.g. capture rate, C, in Holling's disc equation (Holling, 1959a))
8. where reported, held body size of interactants relatively constant.

We used original rate-temperature data values when reported, and otherwise extracted these values from published graphs (using DataThief III, http://www.datathief.org/). In the rare instances when either explicit values were not reported or points on graphs were difficult to differentiate, we used appropriate model parameters (e.g., attack rate or handling time) calculated by the authors directly from the data. We used the rate (or the inverse of the time) for the entire biotic interaction rather than for subcomponents, such as attack rate and handling time, separately. This approach effectively integrates the subcomponents as they occur naturally and thus considers interactions holistically. When studies repeated experiments and reported values for the replicates, we used the mean value for each temperature. With functional response studies, we used predation rates at intermediate prey densities to avoid satiation of predators and because these usually had the most accurately resolved data.

The biotic interactions we considered are herbivory, predation, parasitism, parasitoidy, and competition. We did not include mutualism because we could too few studies on temperature dependence. Our intent was to quantify and synthesize data on temperature dependence of rates of representative biotic interactions and to evaluate predictions of MTE rather than to perform an exhaustive literature survey. Throughout the study, we continued to find additional papers with suitable data, and we have undoubtedly overlooked some relevant studies, especially on predation. The enormous literature on predation reflects the large number of studies investigating the functional response, or consumption rate of a predator in response to varying prey density, often with only passing reference to the temperature dependence of the interaction per se. Most of the data came from papers on biological control, fisheries management, and parasitology.

Some studies provided useful context but no data that met our criteria. For example, Fogleman and Wallace (1980) investigated the effect of temperature on competitive interactions in three *Drosophila* species, but the data reported, on the percent of males eclosing, did not include the time periods involved and thus precluded calculation of rates. Bystrom & Andersson (2005) and Bystrom et al. (2006) measured the temperature-dependence of “attack rate” of char, but the chironomid prey were frozen and unable to interact, so the study really measured the rate of food consumption more than the rate of predation. Several microbiological studies assessed outcomes of competition in two or more bacteria or protists, but most compared Q_{10}’s of growth in pure cultures at different temperatures rather than measuring the interaction rate (e.g. Ogilvie, Rutter, & Nedwell, 2006).

Database. Our database, compiled using the above criteria, consisted of 84 studies and 32 sub studies for a total of 116 estimates of E. The database includes the authors and year of publication, type of interaction, taxa tested, specific dependent variable measured (e.g. number larvae eaten/hour or time to extinction of one species), and temperatures. For each study, we used the rate or time reported for each different temperature along the rising portion of thermal performance but did not use the value (if any) beyond the optimum (i.e., we used only values on the rising portion of the curve in Figure 1A). For each pair of values for interaction rate and temperature, we calculated the natural log of the rate, converted temperatures to degrees Kelvin, and calculated 1/kT. The complete database is in S1 (supplemental electronic materials); Table 1 shows a subset.

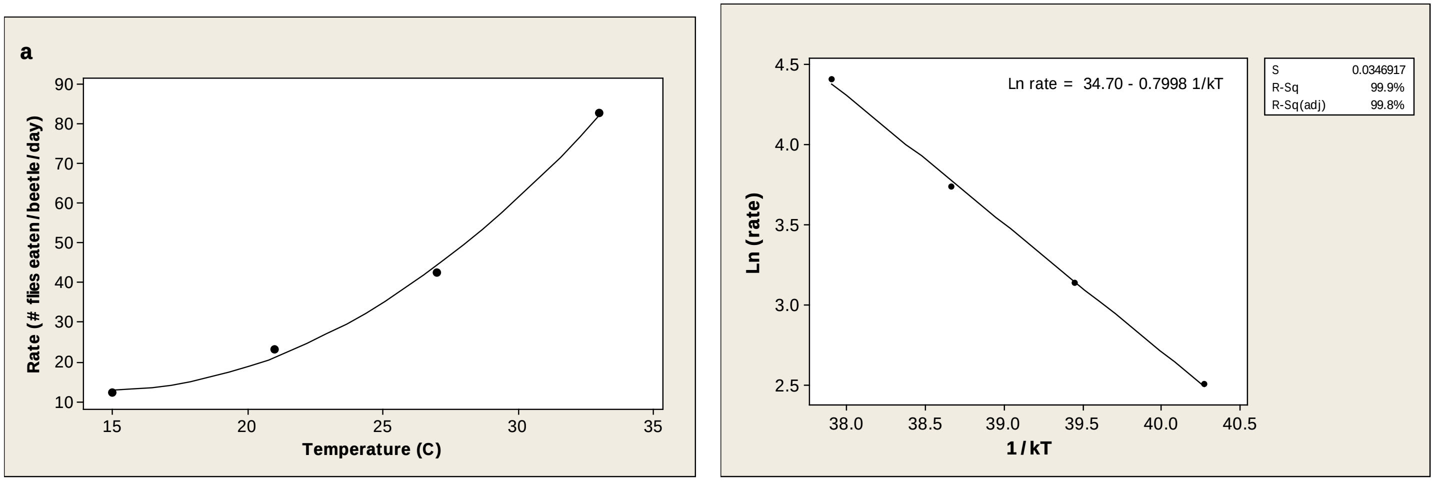

Figure 1. Temperature dependence of the rate of an ecological interaction – here predation of a beetle on fly larvae – plotted in two ways: a. rate as a function of temperature (in ^{o}C) on linear axes, showing a typical near-exponential curve; b. as an Arrhenius plot, with the natural logarithm of rate plotted as a function of inverse temperature, 1/*kT*, where *k* is Boltzmann's constant and *T* is temperature in Kelvin. Replotted in this way, an exponential relationship becomes linearized, an OLS regression line can be fitted, and the slope with sign reversed gives the value of E, a quantitative measure of temperature dependence. Data from Geden & Axtell (1988).

Table 1. A subset of the database of published studies used to assess the temperature dependence of rates of biotic interactions. The full dataset (S1) includes additional detail.

Study	Interaction	Taxa 1	Taxa 2	Rate terms	Rate	Temp (°C)	Ln (rate)	1/kT	Slope (eV)
Aelion & Chisholm 1985	herbivory	zooplankter (Favell	phytoplankter (Hete	cells eaten/indivi	2.320	8.000	0.842	41.275	-0.703
					2.460	11.500	0.900	40.768	
					5.270	16.500	1.662	40.064	
Kishi et al 2005	herbivory	caddisfly larvae (G	periphyton	mm2 periphyton	6.700	3.000	1.902	42.022	-2.997
					33.400	6.000	3.509	41.571	
					97.400	9.000	4.579	41.129	
	predation	trout, Dolly Varden	caddisfly larvae (Gl	% of 120 larvae e	24.200	3.000	3.186	42.022	-0.929
					83.000	12.000	4.419	40.696	
Bailey et al 1989	predation	water scorpion (Re	backswimmer (Anis	mean # prey eate	7.810	15.000	2.055	40.272	-0.601
					14.080	20.000	2.645	39.586	
					17.560	25.000	2.866	38.922	
McCutcheon & Simmons 2001	parasitoidy	wasp (Eretmoceru	whitefly, sweetpotat	mean % 2nd inst	6.780	20.000	1.914	39.586	-1.015
					20.030	25.000	2.997	38.922	
					25.390	30.000	3.234	38.280	
Molineux 1986	parasitoidy	nematode, entomo	blowfly, sheep, 3rd	mean % parasitiz	5.000	8.160	1.609	41.252	-1.941
					20.320	9.860	3.012	41.004	
					24.750	11.760	3.209	40.730	
					54.790	14.650	4.004	40.321	
					90.330	17.700	4.503	39.899	
McCarthy 1999	parasitism	trematode worm la	snail (Lymnaea per	Mean instantane	0.553	10.000	-0.592	40.984	-0.517
					1.005	15.000	0.005	40.272	
					1.365	20.000	0.311	39.586	
					1.623	25.000	0.484	38.922	
Tucker et al 2000	parasitism	copepod, ectopara	salmon, Atlantic, sn	% of copepodid s	6.230	7.050	1.829	41.415	-1.831
					24.810	12.250	3.211	40.660	
Cunjak & Green 1986	competition	rainbow trout (Salr	brook charr (Salveli	days (mean #)	0.100	8.000	-2.303	41.275	-0.592
					0.143	13.000	-1.946	40.554	
					0.250	19.000	-1.386	39.721	
Park 1954	competition	tenebrionid flour b	tenebrionid flour be	days	0.001	24.000	-6.800	39.053	-0.541
				days	0.001	29.000	-6.719	38.406	
				days	0.002	34.000	-6.109	37.781	
Stelzer 2006	competition	rotifer (Synchaeta	rotifer (Brachionus	days to compete	0.063	12.000	-2.773	40.696	-0.874
					0.165	20.000	-1.802	39.586	

Analytical methods. We calculated the temperature dependence of the interaction as the slope of the OLS (ordinary least squares) regression of ln(rate) as a function of 1/kT. OLS is appropriate in this case, because interaction rate and temperature clearly are the dependent and independent variables, respectively, and because temperature was usually closely controlled and hence measured with less error than interaction rate (see White et al., 2012: White, E.P., Xiao, X., Isaac, N.J.B. & Sibly. R.M. 2012. Methodological tools. in Sibly, R.M., Brown J.H., & Kodric-Brown, A. eds. *Metabolic ecology: a scaling approach.* Wiley-Blackwell, Oxford.).

Results

Results of our compilation and analyses of temperature dependence of ecological interaction rates are presented in Figures 2-5, Table 1, and the supplemental materials (Table S1, which contains all the data). Figure 2 shows all of the data, presented as Arrhenius plots with each interaction plotted separately and color-coded by interaction type. The vertical displacement of the fitted regression lines is uninformative because the reported rates depend on the units used to measure them. The slopes, which give the estimated value of the "activation energy", *E*, as our quantification of temperature dependence, are informative. The vast majority of slopes are positive, and many are similar to the predicted value of approximately 0.65 eV.

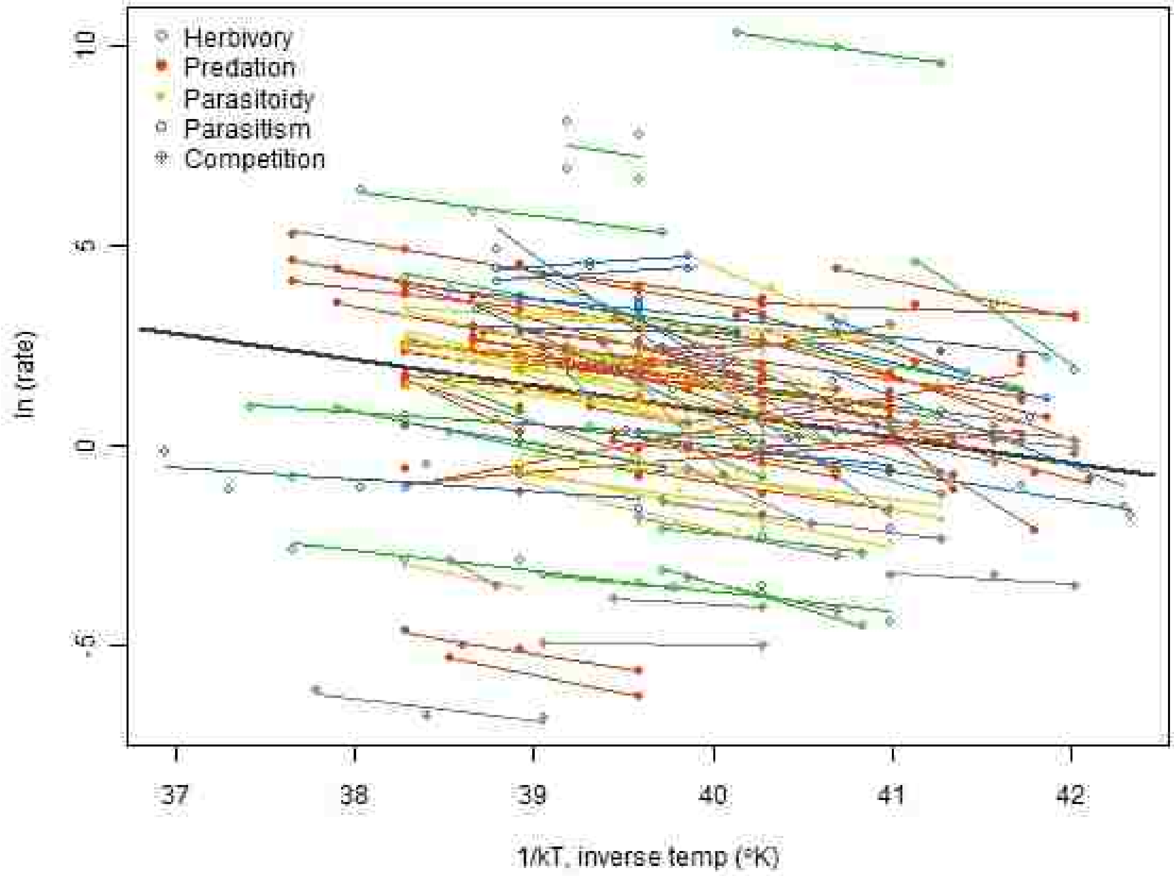

Figure 2. Arrhenius plots of the temperature-rate relationships for all data in the analysis. Each point is the temperature dependence of a single rate from a single study, and lines are OLS regressions fitted to the points for different temperatures in that study. Different kinds of interactions are color-coded, while the thick dark line running through the middle of the graph has the predicted slope of exactly -0.65 and is for reference. The Y-axis is relatively arbitrary, because the reported rates depend on the units of measurement. Note that the slopes vary substantially but that many are roughly coincident and similar to the predicted value.

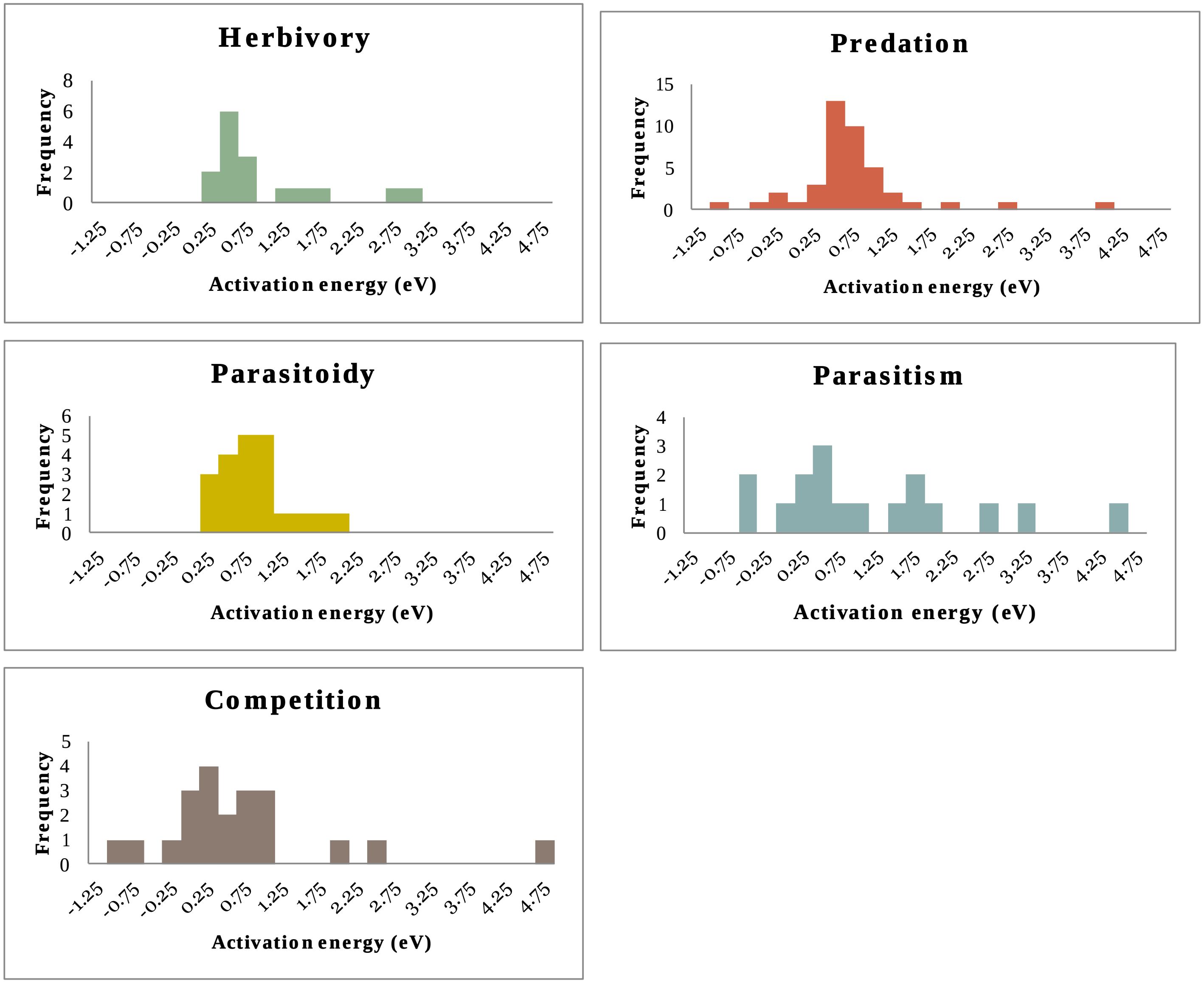

Figure 3. Frequency distribution histograms showing variation in estimated temperature-dependence of the different kinds of biotic interactions. Temperature dependence is quantified as "activation energy", *E*, and estimated by OLS regression in an Arrhenius plot (see Figures 1 and 2). Note that there is considerable variation, but a definite central tendency, in each type of interaction.

The frequency distributions of activation energies for the different types of biotic interactions are shown in Figure 3, and all types together are plotted in Figure 4. These two figures convey three messages: i) there is wide variation in the estimated values of *E* for each kind of interaction; ii) the frequency distributions of *E* for the different interaction types overlap broadly and do not differ conspicuously; and iii) each of the interaction types individually, with the exception of parasitism, and particularly when considered them together showed a pronounced central tendency, clustering fairly closely around the predicted value of 0.65 eV. Statistical analysis of the distributions of *E* among interaction types reveals no significant differences (Table 1: Kruskall-Wallis ANOVA: P = 0.44).

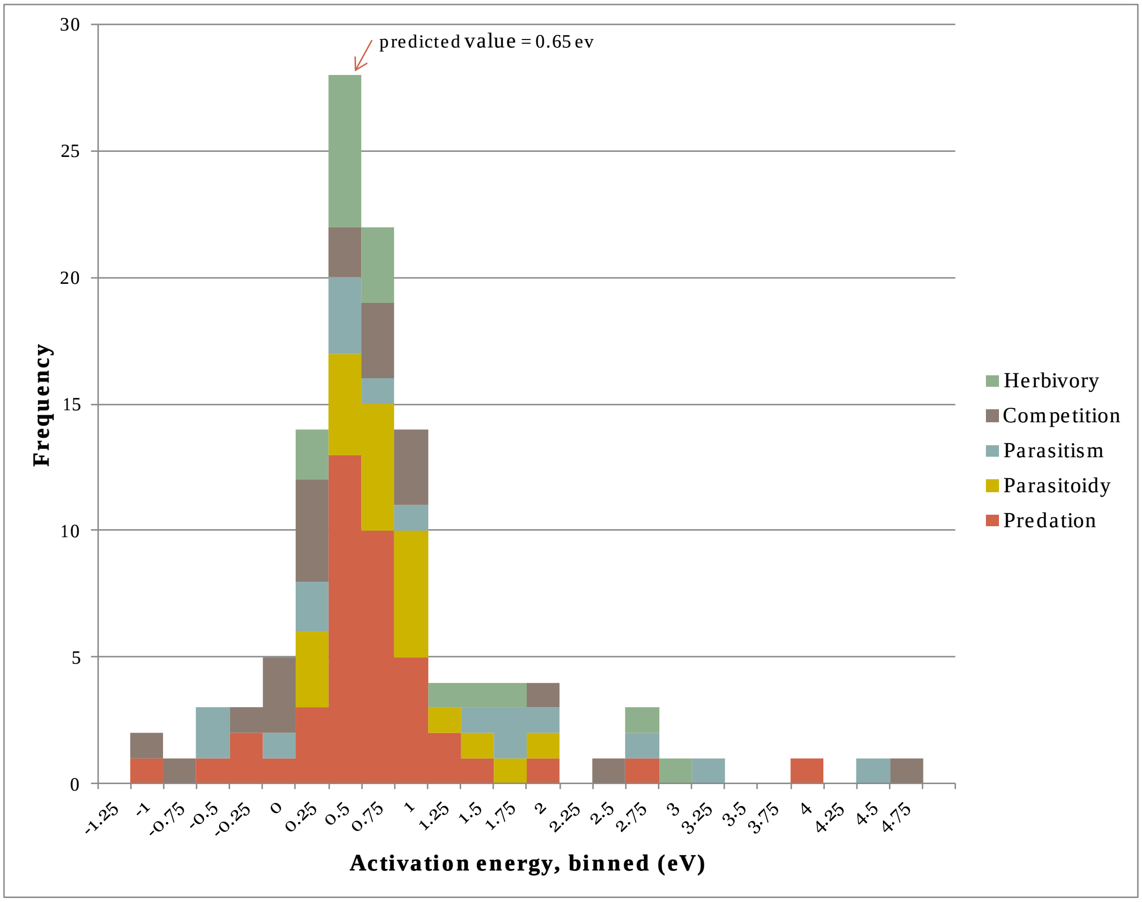

Figure 4. Frequency distribution histogram showing variation in estimated temperature-dependence of all kinds of biotic interactions plotted together but coded by color. Temperature dependence is quantified as "activation energy", *E***,** and estimated by OLS regression in an Arrhenius plot (see Figures 1 and 2). Note that there is considerable variation but a definite central tendency with a distinct mode very close to the predicted value of approximately 0.65 eV.

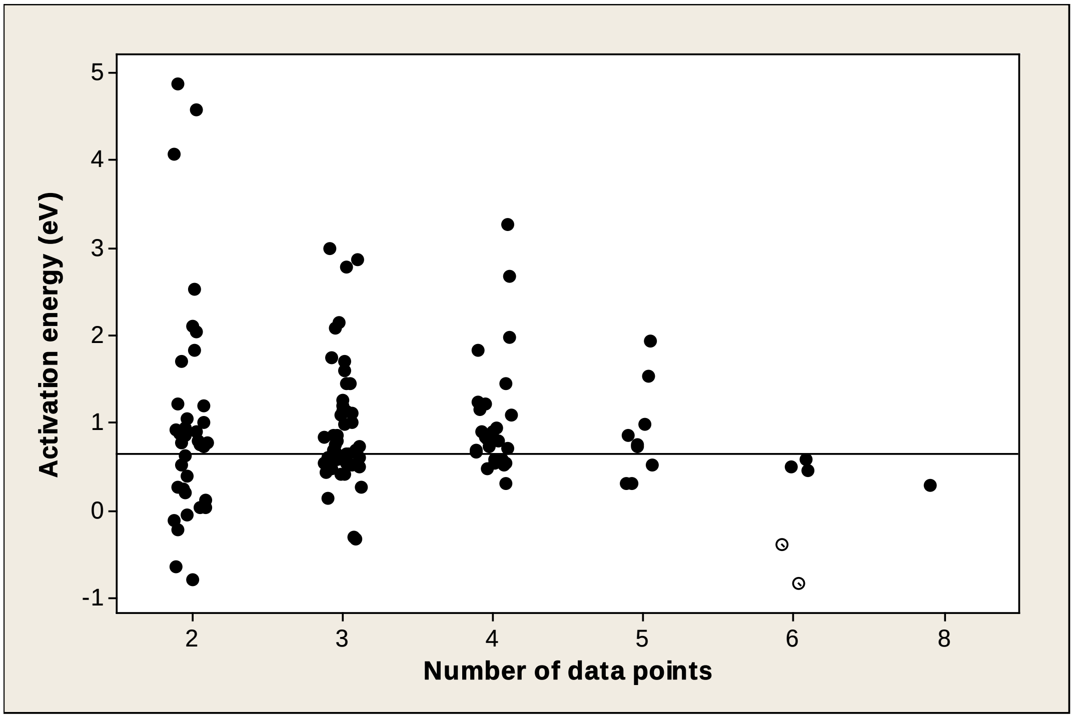

Figure 5. Plot of the estimated magnitude of temperature dependence, measured as the value of E from the slopes of Arrhenius plots, as a function of the number of temperatures at which rates were measured within each study. Note that measurements at more temperatures provided increased resolution, with more clustering around the predicted value of 65 eV (horizontal line). This graph suggests that extreme values of *E* obtained from data collected at only a few (and sometimes a narrow range of) temperatures may reflect measurement error and lack of resolution. Other variation may be informative. The two low values with six data points (unfilled circles) correspond to predation rates of carabid beetles on fruit flies (Kruse et al., 2008). The beetles seemed to take advantage of a mismatch between the temperature dependence of their activity and that of their prey; although the beetles were more active and moved faster at higher temperatures, they caught more flies at lower temperatures because the flies were even more sluggish and escaped by walking rather than flying, presumably because flying requires more energy.

Table 2. Statistics for the temperature-dependence of biotic interactions analyzed in this study. Temperature dependence was measured as the value of *E* from the slope of Arrhenius plot of data for each interaction. There was considerable variation in the values of *E* for each interaction type but no significant difference in the overall distributions among interaction types (non-parametric Kruskall-Wallis ANOVA: P = 0.44).

Interaction	n	Mean	Std dev	Median	K-W z-score
herbivory	15	0.98	0.71	0.70	0.17
predation	42	0.85	0.79	0.75	-0.37
parasitoidy	21	0.97	0.50	0.91	1.13
parasitism	17	1.32	1.34	0.80	0.82
competition	21	0.80	0.54	0.54	-1.57
Overall	**116**	**0.95**	**0.93**	**0.76**	**0.66**

Discussion

Overall the results supported our predictions. Rates of the biotic interactions we assessed centered around the predicted temperature dependence of 0.6 – 0.7 eV. When all interaction types are considered together, the median and mode are strikingly close to the predicted value of 0.65 eV (Figure 3). In addition, the data were generally well fit by linear regressions, reflecting the appropriateness of the Arrhenius expression in describing temperature dependence. As expected, there was substantial variation generally but the temperature dependence was more pronounced in herbivory and predation, two interactions involved directly with procuring metabolic energy.

Like all meta-analyses based on published studies, this one has potential sources of error and bias and room for improvement. First, we controlled for differences among studies as much as possible by using strict criteria for inclusion and consistent methods to quantify rates across studies, but differences in methodologies of the studies may affect our findings in unforeseen ways. In this first effort to compile and analyze data on temperature dependence of interaction rates (but see Dell et al., who analyzed a wider variety of biological rate processes), we tried to include as many relevant data as possible, including studies with only pairs of data points from measurements conducted at only two different temperatures, and did not exclude any potential outliers. Second, we included only data for antagonistic interactions – herbivory, predation, parasitism, parasitoidy, and competition – because we could not find enough appropriate studies of mutualism to include in our comparison. Third, our database is highly biased toward interactions involving mobile animals. We did not try to include studies of mutualisms, competition in plants, or interactions between microbes. We justify these exclusions for two reasons. First, the underlying metabolic processes in these groups – photosynthesis in plants and the variety of energy-transforming biochemical pathways in microbes – might be expected a priori to have different "activation energies" (e.g. Anderson et al., 2008; Okie, 2012), complicating quantitative comparisons. Second, the different traditions of plant ecology and microbiology, as opposed to animal community ecology, have resulted in investigators asking different questions and using different methodologies, again making comparisons across groups problematic and difficult to interpret.

Despite general support for our predictions about the interactions we did consider, the variation in temperature dependencies calls for explanation. Including more studies on some interaction types might have clarified patterns, as they did when we added more and more on predator-prey interactions (Figure 3). Apart from studies on predation, we found a limited pool of research that met our criteria. In addition, some of the variation may be due to difficulties and resulting inaccuracies in measuring interaction rates. We were interested in the overall rate of an interaction rather than individual behavioral or physiological components of an interaction (such as search or handling time or attack rate in studies of predation). There are formidable challenges in accurately measuring the overall rates in some standardized way that can be compared across studies. Among other criteria are issues of how many measurements to take over what range of temperatures. More measurements should allow more-accurate estimation of the temperature-dependence, including a determination of the "ecologically realistic," non-stressful temperature range in which the organisms normally operate. Figure 5 suggests that some of the measurements at only two or three temperatures, depending also on the range of values, give misleading estimates of overall temperature dependence.

Natural biological variation certainly contributed to the spread in observed temperature dependence rates as well, but it does not invalidate the overarching influence of Boltzmann kinetics. Thermal acclimation may have modestly shifted the interaction rates of individual organisms to favor higher performance at higher temperatures, perhaps contributing to the right skew within and across interaction types (see Figures 3 and 4). Likewise, variation in peak thermal performance within or between species could cause a reversal of competitive dominance, whereby the interactant with the lower temperature optimum dominates at low temperatures and vice versa (e.g. Ayala, 1966). Such condition-specific dominance is especially common between species along natural gradients of temperature, such as between fish in mountain streams that become warmer as they descend (e.g. Taniguchi and Nakano, 2000; and see discussion by Dunson & Travis, 1991). Yet as much as thermal performance curves vary within and between populations and species, they vary around the common left-skewed shape of Figure 1a (Izem and Kingsolver 2005). Even if a portion of all curves are beyond the peak and still presumably the subject of selection (Englund et al., 2011), thermodynamic constraints limit how much biochemical adaptation can circumvent the effects of temperature on performance (Angilletta et al., 2010). The ability of a single line of inverse 0.65 slope to describe the majority of the Arrhenius relationships in Figure 3 graphically makes this point.

The effect of temperature on biotic interactions is important for understanding geographic patterns of biodiversity and the evolutionary and ecological processes that generate and maintain them. Species diversity is generally highest in lowland and shallow-water regions in the tropics and declines with increasing latitude, elevation on land, and depth in oceans and lakes. This pattern is very general, holding across diverse taxonomic and functional groups and habitat and ecosystems (Hillebrand et al., 2004; Mittelbach et al., 2007; Schemske et al., 2009; Tittensor et al., 2010). The pattern is generally correlated with environmental temperature, but ecologists and evolutionary biologists debate the underlying reasons, due in large part to apparently confounding effects of productivity, stoichiometry (water and nutrient availability), and phylogenetic and Earth history (Lomolino et al., 2010). Our findings support the hypothesis that faster biotic interactions in the warmer tropical latitudes, lower altitudes, and shallower aquatic depths contribute to diversity gradients by increasing coevolutionary pressures and attendant diversification rates (Freestone et al., 2011; Mittelbach et al., 2007; Benton, 2009; Schemske et al., 2009).

Understanding the effects of temperature on biotic interactions is particularly important in the context of a warming planet (Lavergne et al., 2010). Hotter temperatures are already affecting organisms and ecosystems (Parmesan & Yohe, 2003). Warming may increase the relative importance of “top down effects,” or the strength of herbivory and predation relative to biomass production (Hoekman, 2010) and affect predator-prey and food web dynamics (Vucic-Pestic et al., 2010; Petchey et al., 2010). Hotter may be better for individual organisms (Angilletta et al., 2010), in which metabolic rate, interaction rate, and fitness tend to increase with temperature, but speeding up the pace of ecology may have unforeseen consequences for the planet’s web of life.

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Chapter 2: Energetics, range size, and geographic gradients of human cultural diversity

William R. Burnside, Jordan G. Okie, Erik B. Erhardt, & Marcus J. Hamilton

Abstract

Indigenous human cultures and biological species have similar geographic patterns, being most diverse in the lowland tropics and along some coasts. An increase in the range size of many species with increasing latitude, called Rapoport's rule, might contribute to the latitudinal biodiversity gradient. Key explanatory hypotheses for biodiversity and cultural diversity gradients invoke environmental factors that vary with latitude. We formalized these hypotheses in a model of the effects of temperature, productivity, seasonality, and trophic level, or the relative proportion of meat eaten, on traditional human population sizes and densities and territory sizes. We tested the model on a database of 333 traditional human foraging societies. Population density was more responsive that population size, and the increase the "cultural Rapoport's effect" we found was driven by lower densities of populations of similar size at higher latitudes. The influence of environmental variables was strongly affected by trophic level. Much of this influence was due to marine foragers, whose access to coastal productivity enabled them to maintain high population densities and levels of cultural diversity. This work suggests an underappreciated role for access to productivity in generating and maintaining gradients of cultural diversity and suggests that the energetic carrying capacity of different environments affects humans and other organisms similarly.

Introduction

Human cultures display patterns of diversity strikingly similar to those of biological species (Maffi, 2005). Both terrestrial species and human cultures, including linguistic groups, are concentrated in the humid tropics and subtropics, and this diversity declines with distance from the equator (see Hillebrand, 2004, for species; Collard & Foley 2002; Sutherland, 2003). This correspondence between biodiversity and cultural diversity applies globally as well as within continents. Examples include similarity in the distribution of cultural diversity and vertebrate species richness in sub-Saharan Africa at the 2° scale (Moore et al., 2002), between diversity gradients of North American languages and mammals (Pagel, 2000), and between Passeriform bird diversity and human cultural diversity in Central and South America (Manne, 2003). The correspondence is especially striking in the Americas, where the cultural pattern formed in only the 15,000 years since human occupation (Collard & Foley, 2002). There is no consensus on what drives gradients of biodiversity or cultural diversity, much less what might drive them both (Lomolino et al., 2010; Nettle, 1999; Pagel & Mace, 2004; Fincher & Thornhill, 2008).

However, the striking similarity between gradients among different species and within a single, cosmopolitan species, *Homo sapiens*, suggest that powerful underlying constraints may be acting on attributes common to species and cultures. Environmental factors that might affect both and that vary with latitude include temperature, precipitation, biotic productivity, seasonality, and land area. A key attribute common to terrestrial species and cultures is the range size, meaning the area of land they occupy.

The range is a spatial reflection of the niche: the abiotic and biotic environmental conditions required for survival and reproduction (Lomolino et al., 2010). Range size is determined by the balance between organismal energy demand and environmental energy supply. Organisms with higher metabolic rates require more food and so need larger home ranges. Environments with lower biotic productivity supply less food per unit area, so organisms living there need larger home ranges. Finally, a smaller proportion of environmental energy is available to organisms feeding at higher trophic levels capture so they need larger home ranges (McNab, 1963).

Range sizes of terrestrial species also exhibit a latitudinal gradient that that may contribute to the latitudinal biodiversity gradient (see Stevens 1989; Schipper et al., 2008). Range sizes tend to increase with latitude, a pattern called Rapoport's rule (Rapoport, 1982; Stevens 1989; Lomolino et al., 2010). A variety of taxa, including human pathogens, display this pattern (Guernier & Guegan 2010; Ruggiero & Werenkraut, 2007). The smaller the range size, the more species or cultures can occupy a given area (but see Sizling et al., 2009, for a contrasting view on species). This is most clearly true for groups that occupy non-overlapping ranges, such as most human cultures. Indeed, traditional North American linguistic groups display both a latitudinal diversity gradient and a Rapoport's rule (Mace & Pagel 1995). So factors that tend to increase minimally overlapping range sizes will tend to decrease diversity.

Given this relationship, we tested for a Rapoport's effect in a worldwide sample of traditional foraging societies (Binford 2001) and built a model to evaluate hypotheses about the relative influence of possible underlying mechanisms. Figure 1, below, shows the geographic distribution of the societies in our sample. This dataset integrates a suite of ecological and social variables on 333 societies compiled from published ethnographies.

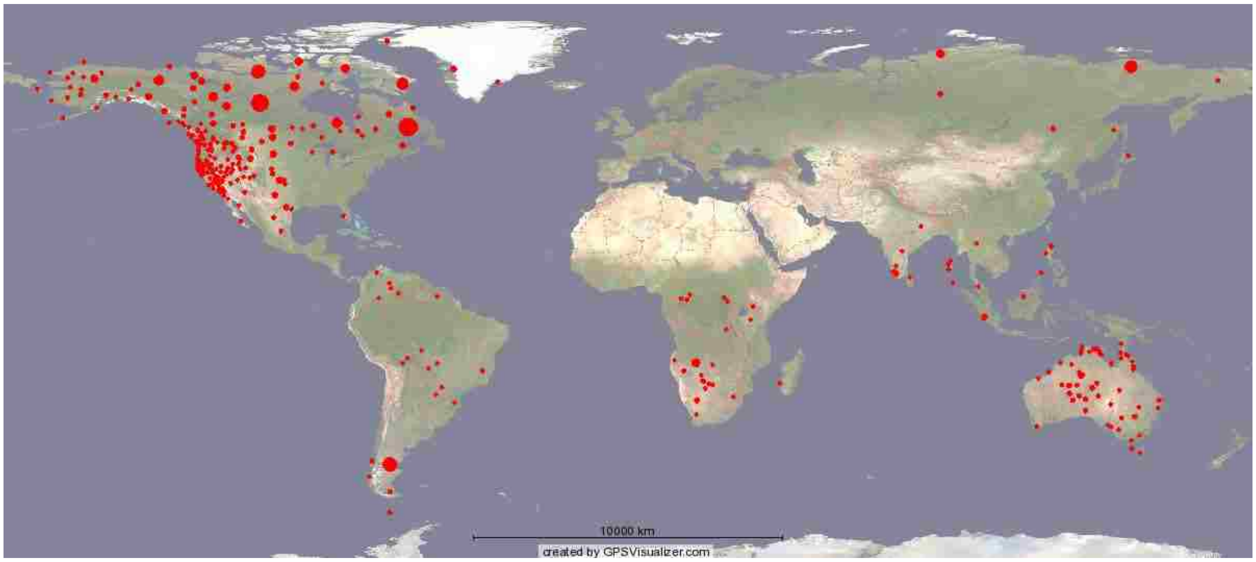

Figure 1. Location and relative size of 333 traditional foraging societies from Binford (2001) used to test hypotheses about the relative influence of energetic variables on range sizes and associated cultural diversity patterns. The relative size of a circle is proportional to the range size of the society living in that location. The overrespresentation of societies in North America and Australia reflects the large number of ethnographic studies, which in turn reflects the larger number of traditional foraging societies surviving in these regions into the 20th Century.

Building on Hamilton et al. 2007, we compiled data and derived a descriptive statistical model to account for the variation in range size. The model incorporated factors that vary with latitude and environmental energy: temperature, productivity, seasonality, and trophic foraging level. We tested the model on a database compiled by Binford (2001), which includes hunter-gatherers and a few mixed horticulturalists. Although the database includes societies worldwide, groups in North America and Australia are overrepresented because these continents had the most foraging societies at the time the ethnographies were produced and the most societies with the full range of variables described.

Methods

The model. The area of a culture is related to two basic variables, the total number of individuals, *N*, and the average population density, or number of individuals per unit area, *D*, such that

$$A = \frac{N}{D} \qquad (1)$$

Population density, D, is limited by the availability of food resources, which are a function of the solar energy entering an ecosystem, the seasonality or variation in energy and water inputs, the trophic position at which energy is acquired, the efficiency of energy transfer between trophic levels, *R*, and the efficiency of human acquisition of energy by foraging and food transport, storage, and preparation. This leads to several predictions. First, groups inhabiting areas with greater ecosystem energy fluxes, as indexed by net primary productivity, should have higher population densities. Second, groups accessing their energy source lower on food chains should acquire a greater proportion of the energy captured by autotrophic plants, allowing them to maintain higher population densities. Assuming that R is approximately similar across trophic levels, population density can be related to plant productivity, P, and the average trophic level of the culture, L, by:

$$D \propto P\langle R \rangle^{L} \qquad (2)$$

In this formulation, pure gatherers feeding only on plants are at trophic level one, pure hunters feeding on herbivores are at trophic level two, and groups with some combination of plant and animal diets are at non-integer trophic positions between one and two.

We incorporate the exponential effect of temperature, T, on production, P, through the Bolztmann function, such that $P \propto e^{-E/kT}$. In this term, k is Boltzmann's constant and E is the activation energy of photosynthetic reactions, which averages around 0.30 eV (see Allen et al., 2005, Anderson et al., 2006, López-Urrutia et al., 2006). Substituting this term into equation (3), we now have an equation relating population density to environmental temperature:

$$D \propto e^{E/kT} \langle R \rangle^{L} \tag{3}$$

Finally, we incorporated the effect of seasonality, which tends to increase with latitude. We developed a new metric of seasonality, S. We found that annual mean monthly temperature range and annual mean monthly precipitation range are inversely correlated (r = -0.578). We used a principal components analyses of the standardized ranges to account for this correlation. The first principal component of this relationship explained 78.7% of the correlation. We used the sign-corrected second principal component, excluding one tropical outlier, as our metric of seasonality. This metric captures the tendency for a given environment to experience relatively high annual variation in temperature, precipitation, or both.

As shown in Figure 2, below, societies with high values for this component, indicated by more-saturated colors, have relatively high combinations of seasonal climatic variability. More-seasonal climates should require foragers to travel and trade more widely to survive the unproductive winters, reducing population density (see Nettle and Nettleton 1999). Thus we predict that seasonality is inversely related to density: $D \propto S^{-1}$.

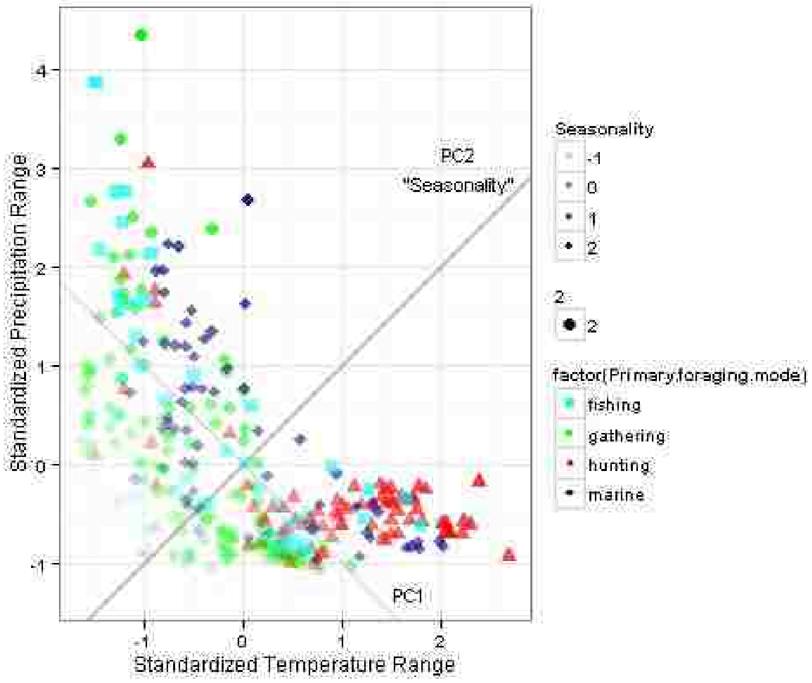

Figure 2. Seasonality (*S*) reflects the relative annual variation in both temperature and precipitation in the environments of societies. We used the second principal component of standardized mean annual temperature and precipitation ranges as this metric to account for their correlation. In this figure, darker colors have greater seasonality.

Adding the seasonality term, S, to equation (3) gives:

$$D \propto e^{E/kT} \langle R \rangle^{L} S^{-1} \qquad (4)$$

Overall population size can also affect the area occupied and, in this way, affect cultural diversity gradients. As seen in equation (1), a larger population size with a given population density will require a larger area in a similar environment. Research suggests that humans may decrease their group size in response to increasing pathogen loads, including both virulent pathogens (Cashdan, 2001) or a wide diversity of parasites and pathogens (Fincher and Thornhill, 2008), as way of minimizing their exposure and pathogen burden, and thereby increasing individual fitness. Disease diversity, like species diversity, is highest in the humid lowland tropics and related exponentially to temperature (Guernier & Guegan, 2004). In addition, development rates (Zuo et al., 2012) and biotic interaction rates (Burnside & Brown, unpublished) tend to follow the Boltzmann temperature relationship for ectothermic organisms, presumably including parasites and pathogens. Therefore, higher temperatures may promote low populations, assortative sociality, and limited dispersal among traditional tropical societies, resulting in large populations splintering into smaller ones (see Fincher & Thornhill, 2008 for discussion). A zeroth-order model for the effect of temperature on population size acting through disease pressure is

$$N^{-1} \propto e^{-E/kT} \tag{5}$$

where E is low and approaches zero in modern societies, where disease burdens are minimal due to medical and public health measures.

However, given that temperature affects productivity and perhaps also trophic level and seasonality, as through a relationship between mean annual temperature and temperature range, we tested for how these energetic variables affect population size, N, population density, D, and the area occupied, A:

$$A^{-1} \propto D \propto N^{-1} \propto e^{-E/kT} \langle R \rangle^{L} S^{-1} \tag{6}$$

Analysis

We assessed graphical patterns to guide our analysis and to partially assess regression model assumptions. We produced scatterplots of temperature, NPP, trophic level, and area occupied as functions of latitude to examine the baseline geographic patterns in the dataset. We color coded societies by primary foraging mode, assigning a society as “gatherers,” “hunters,” or “fishers” based on whether they consumed the largest share of calories from plants, meat, or fish, respectively. We assigned a different color to differentiate coastal fishers from inland fishers. Finally, we produced a color-coded matrix plot of all main dependent variables as functions of all main independent variables.

We tested our model by logarithmically transforming equation 6 and using linear multiple regressions (ANCOVA) to quantify the relative effects of temperature, trophic level, and seasonality on population size, population density, and area (e.g., Brown et al., 2004; Hechinger et al., 2011). After finding limited support for the model (6) with only these main effects, we tested extensions of this model that included net primary productivity as a separate term, P. We hypothesized that marine productivity might produce different patterns for coastal fishing societies, where a substantial fraction of the diet may be composed of marine and intertidal resources. So we assigned an indicator variable, M, to coastal fishing societies in our regression model. This allowed us to assess the strength and form of the relationship between marine foraging and cultural diversity patterns. The revised model, which includes productivity and marine foraging status and is written to allow straightforward interpretation of results when log-transformed for regression (see SI), is:

$$A \propto 10^{\beta_M} e^{-(E/k)T} \langle R \rangle^{L} NPP^{\beta_P} (10^{S})^{\beta_S} \qquad (7)$$

We tested model (7) as written above, and also included interaction terms (e.g. $T \times L$) and quadratic terms (e.g. L^2). Interactions reflect the tendency for one variable, such as temperature or trophic level, to affect how another variable, such as productivity, affects a response variable, such as population density. Quadratic terms, such as L^2 reflect the tendency for some predictor variables to contribute nonlinearly to a model's ability to explain variation in a response. We included both interactions and quadratic terms to capture more of the variability in the data and ensure that our model was adequate and biologically realistic.

We minimized the potential negative impact of a multiple stepwise procedure (see Mantel 1970, Derksen and Keselman 1992) by carefully considering all possible models and selecting among models based on three widely used criteria for model section: the Bayesian information criterion (BIC), the process capability index (Cp), and the adjusted r^2. Together, these criteria provide a wholistic measure of model adequacy, penalizing models options for both unexplained variation in dependent variables as well as for overfitting, or adding extra parameters to explain that variation.

Results

We found support for some of our predictions but overall a more-complex picture than we had hypothesized. As suggested by Figure 3, below, the productivity of terrestrial and coastal environments affected the area societies used, and the filtering of this productivity through trophic level had direct and indirect effects on area and cultural diversity.

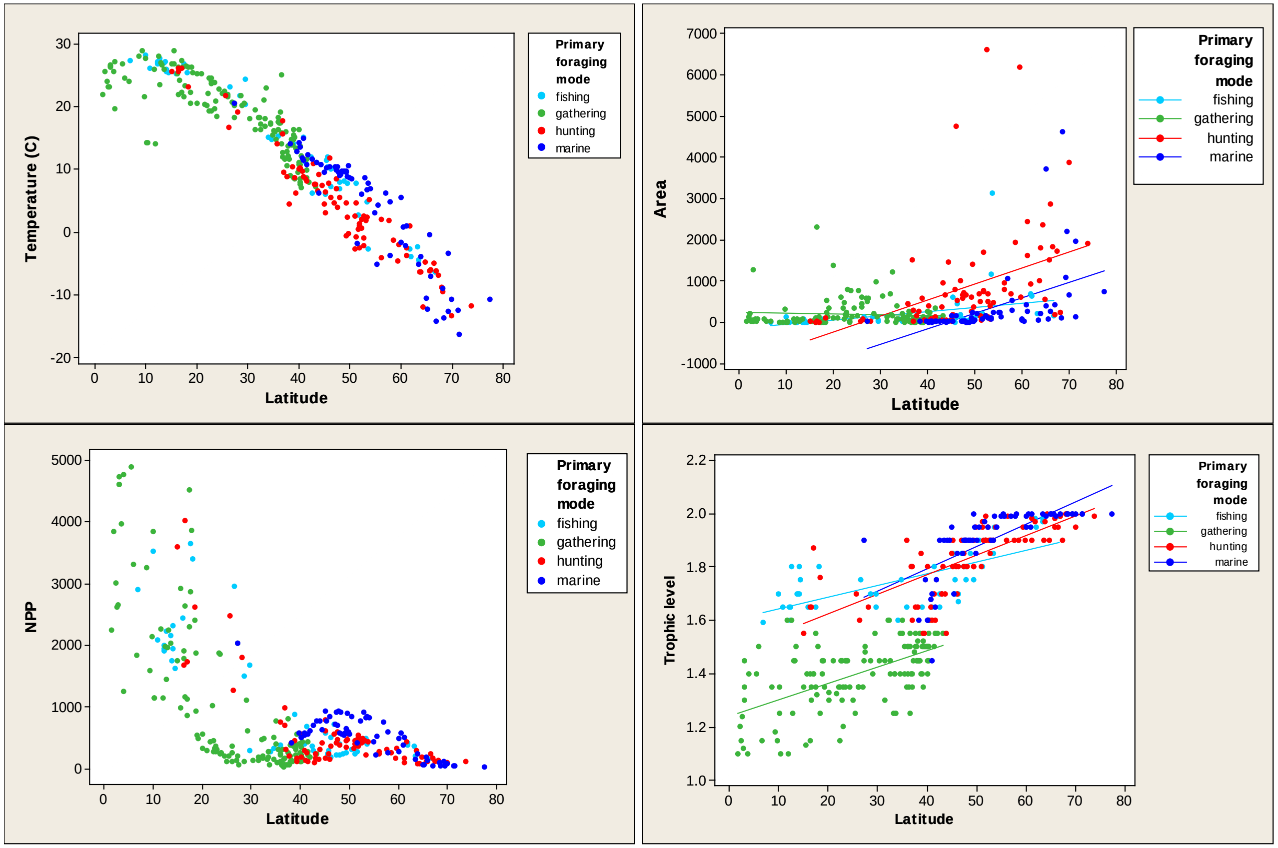

Figure 3. "Gathering" societies tend to obtain relatively more calories from plant gathering in the warm, productive tropics, whereas populations of coastal foragers are subsidized by marine productivity that peaks around 50 degrees latitude. Consequently, the area inhabited increased with latitude and trophic level. The relationships between latitude and NPP and their likely relationship with marine foragers prompted us to further explore their relationships with range sizes and implications for cultural diversity gradients.

The patterns in Figure 3 suggests a latitudinal threshold of about 40 degrees, beyond which productivity decreases sharply and hunting and marine foraging replaced plant gathering as the primary source of calories. We found similar rates of increase of area with latitude among hunters and marine foragers. In addition, the effect of trophic level on range area was similar across foraging types: low for plant gathers and elevated similarly for hunting, fishing, and marine foragers.

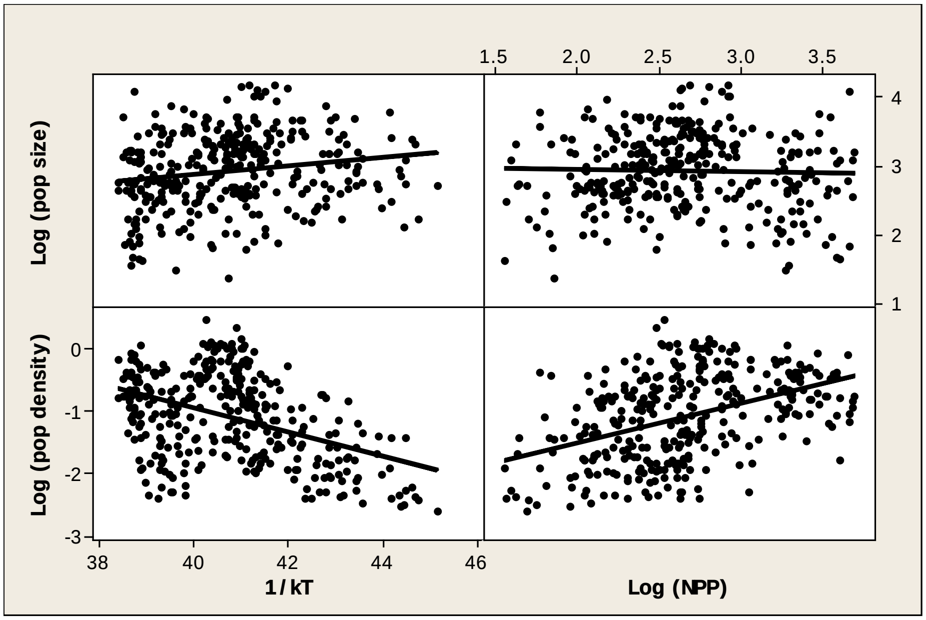

Figure 4. Among these traditional foragers, increased environmental energy supply tends to support more people/area (higher D) rather than smaller overall populations and finer group sub-division (lower N). Higher temperature seems to act primarily by increasing productivity, as seen by the steeper relationships between population size and density and both temperature and productivity.

Our original overall model, (6), described relatively little variation in population size, density, and cultural diversity (S1). However, adding productivity (7) as well as interactions between variables, which capture strong, realistic indirect effects in ecosystems, markedly improved the model fits. Relationships among the main variables in our final models are shown in Figure 5, and the contributions of these main parameters as well as those of indirect interactions and quadratic terms are given in Table 1.

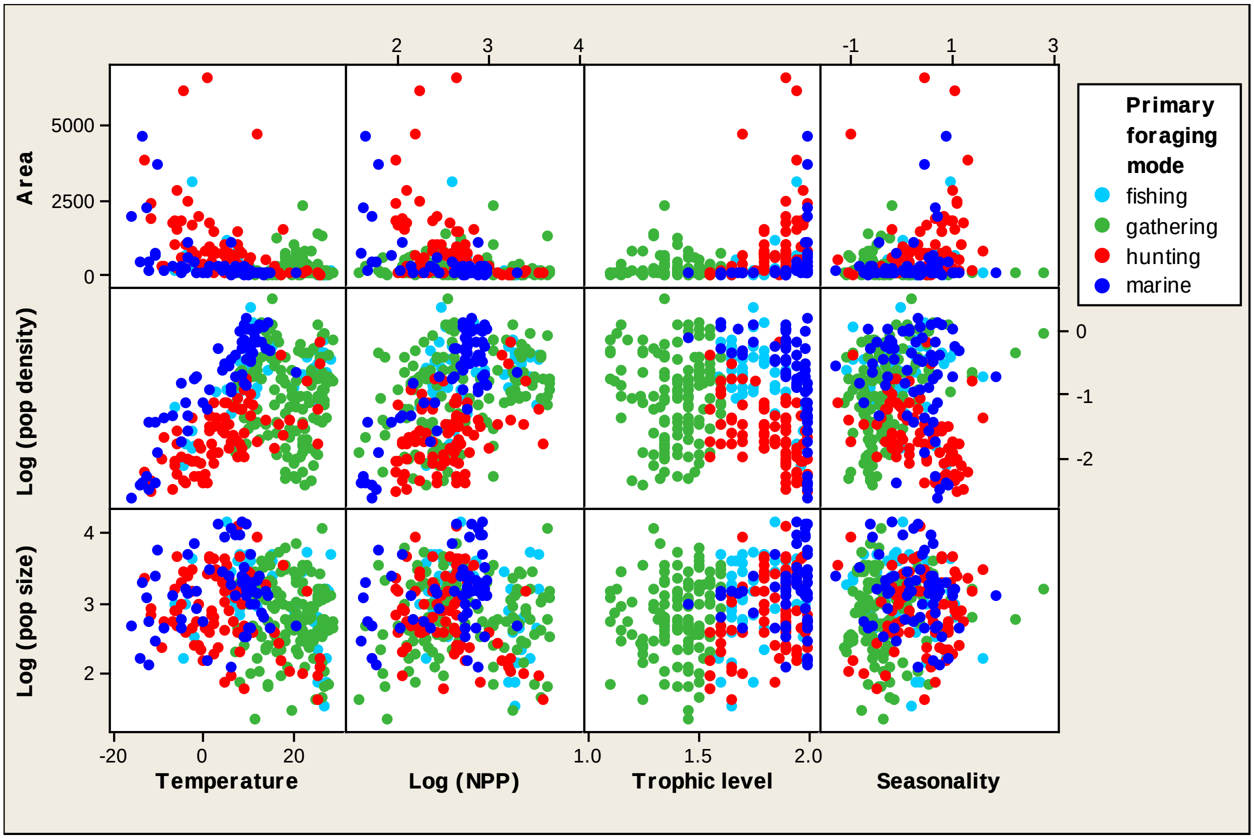

Figure 5. Relationships between the cultural attributes of population size, population density, and cultural diversity and the key environmental variables of temperature, primary productivity, trophic level, and seasonality, color coded by primary foraging mode. These are the main variables used in our final linear models, which also included interaction and quadratic terms. We log-transformed variables to reduce skewness and allow for linear modeling. Relationships of these variables to latitude are shown in Figure 3. Note how the different foraging types segregate out with respect to the environmental variables.

Table 1. Parameter estimates for the best fit models for the linear relationship among energetic variables and each of population size, population density, and attendant cultural diversity.

Population size

Coefficients	Estimate	Std. Error	t value	p-value	
Intercept	2.85	0.0543	52.5	0	***
t	-1640	634	-2.59	0.0101	*
P	0.0269	0.0974	0.276	0.782	
L	1.04	0.284	3.68	0.000272	***
t^2	-6950000	2070000	-3.36	0.000871	***
P^2	-0.38	0.137	-2.77	0.00601	**
L^2	1.54	0.595	2.58	0.0103	*
P:L	-1.36	0.373	-3.65	0.000309	***

t = 1/temperature
P = productivity (NPP)
L = trophic level

Signif. codes: 0 `***' 0.001 `**' 0.01 `*' 0.05 `.' 0.1 ` ' 1

Population density

Coefficients	Estimate	Std. Error	t value	p-value	
Intercept	-0.89	0.054	-16.5	0	***
t	1070	633	1.68	0.0931	.
P	0.266	0.0914	2.91	0.00385	**
L	-0.989	0.285	-3.47	0.000585	***
S	0.278	0.0613	4.54	8.08E-06	***
M	0.722	0.0833	8.67	2.23E-16	***
L^2	2.9	0.805	3.61	0.000357	***
t:L	-15600	1920	-8.1	1.18E-14	***
P:L	-1.31	0.379	-3.47	0.000593	***
L:S	-0.775	0.212	-3.66	0.000292	***

t = 1/temperature
P = productivity (NPP)
L = trophic level
S = seasonality
M = marine foraging

Signif. codes: 0 `***' 0.001 `**' 0.01 `*' 0.05 `.' 0.1 ` ' 1

Area

Coefficients	Estimate	Std. Error	t value	p-value	
Intercept	1.72	0.0632	27.2	0	***
t	-1456	780	-1.87	0.0629	
P	-0.24	0.107	-2.26	0.0247	*
L	1.41	0.264	5.34	1.76E-07	***
S	-0.177	0.0632	-2.81	0.00534	**
M	-0.707	0.0959	-7.37	1.44E-12	***
t:P	1820	554	3.29	0.00113	**
t:L	11500	1553	7.40	1.19E-12	***

t = 1/temperature
P = productivity (NPP)
L = trophic level
S = seasonality
M = marine foraging

Signif. codes: 0 `***' 0.001 `**' 0.01 `*' 0.05 `.' 0.1 ` ' 1

All of the energetic variables tested were important in some way, but how they affected population size, population density, and cultural diversity depended crucially on their interactions. Population sizes decreased modestly with temperature but increased more with productivity and trophic level, especially at higher trophic levels. For density, the effects of temperature, productivity, and seasonality all depended on trophic level. Area occupied decreases slightly with temperature but moreso with productivity, and area increased with trophic level.

Two key findings reflect the crucial role of productivity, including marine supplemental productivity, on population size and density and how energy is transferred between trophic levels. First, trophic level influences how climatic variables affect the population size and density and attendant diversity patterns of traditional foragers. The rate of increase in population size with productivity diminishes with increasing trophic level, perhaps reflecting the decreasing proportion of total energy fixed by primary producers (terrestrial plants, algae) that is consumed by human foragers. Second, much of the effect of trophic level is due to marine foragers, whose primarily animal diet is largely a function of coastal productivity. Marine foragers have population densities that are, on average, more than five times that of non-marine foragers. Since population sizes are generally similar across latitude, the high cultural diversity along productive coasts can be attributed to utilization of marine food sources.

Discussion

Energetic factors that vary with latitude affect the area occupied by traditional foraging societies, and the resulting Rapoport effect contributes to the latitudinal cultural diversity gradient. Findings supported our predictions that population sizes would be smaller in hotter regions and that population densities would be lower in regions with lower productivity and among hunting societies. However, the relationship between energetic variables and the size, density, and area occupied by societies in this sample was more complex than that hypothesized in our original model (6).

The combined and indirect relationships between productivity, trophic level, and marine foraging were especially important. Productivity accounted for significant variation beyond that described by temperature or seasonality alone. The sharp decrease in productivity at around 40 degrees latitude coincided with a switch from plant foraging as the primary mode to hunting or fishing for marine resources. The "cultural Rapoport effect," then, is seen primarily beyond this threshold and is driven both by the decrease in ecosystem productivity as well as by a greater reliance on hunted and fished animals rather than gathered plants. Together, these factors largely explain the increase in range areas above 40 degrees latitude.

Reliance on marine resources insulated coastal fishing societies from the constraints of terrestrial productivity. The productive coastal upwelling zones centered at around 50 degrees latitude in both hemispheres provide an abundant supply of animal biomass. Coastal populations, foraging in marine and intertidal environments, typically had several-fold higher population densities and increased cultural diversity compared to inland populations at comparable mid-latitudes.

Our findings generally support the more-individuals hypothesis, also called the species-energy hypothesis, for geographic patterns of biodiversity, at least as applied to human cultural diversity. According to this hypothesis, productivity contributes to diversity by increasing the number of individuals that can be divided into populations of some minimal size (Wright 1983; Gaston 2000). Support for the species-energy hypothesis as applied to species diversity is mixed (Mittelbach et al., 2001), but the coincidence of human population density and biodiversity (see Luck 2007 for a review) combined with our findings suggests that the energetic carrying capacity of different environments affects humans and other organisms similarly.

Our results suggest that environmental factors related to food supply may be at least as important as disease in determining range sizes and attendant cultural diversity patterns among traditional human foragers. Population density increased significantly with both temperature and productivity and decreased with trophic level, suggesting the importance of energetic constraints related to food. On the other hand, studies have found a positive relationship between cultural diversity and disease burdens and parasite and pathogen diversity, especially at large scales (e.g. Cashdan 2001). A hypothesized mechanism for this correspondence is assortative behaviors and reduced mobility to avoid transmission of infections among neighboring groups, thereby contributing to the evolution and maintenance of cultural divisions (Cashdan, 2001; Fincher and Thornhill, 2008). Since the diversity of parasites and diseases and the rates of transmission of ectothermic pathogens to humans should increase with increasing temperature, two logical corollaries of the disease hypothesis are that population sizes and population densities should decrease with increasing temperature and be especially low in the wet tropics. Larger population sizes increase the potential infective pool, and higher population densities increase contact rates with others who may be infected. Indeed, population densities of primates are negatively correlated with parasite diversity (Nunn et al., 2004). In our analysis, population size declined with both temperature and productivity, but the effects were relatively modest, as seen in Figure 5.

Our results suggest an important role of food supply in determining range size and cultural diversity in hunter-gatherers. Human population size, density and cultural diversity generally increase with increasing primary productivity in latitudinal and climatic gradients. In addition, however, factors that disassociate productivity from terrestrial NPP, such as subsidies of marine food resources, apparently allow for high populations and diverse cultures in temperate regions with low disease burdens (see also Borrero & Barberena 2006; Small & Nicholls 2003; Day et al., 2007). Our results are consistent with classic work by the anthropologist Joseph Birdsell, which clearly showed that small territories and high cultural diversity of aboriginal Australians were highest on the continent's productive coastal margins (Birdsell, 1957). Australian biological species diversity maps onto cultural diversity strikingly well.

This work builds on previous studies (e.g. Binford, 2001; Hamilton et al., 2007) to provide macroecological insight into human energetics and the traditional human niche. Our extension and testing of formal models on a dataset with a relative wealth of socio-environmental variables supported the crucial role of energetics in structuring ecological communities, including ones containing humans. It suggests that the signature of optimal foraging by traditional humans (e.g. Hawkes et al., 1982) can be integrated in macroscopic resource acquisition patterns. Metabolic opportunities and constraints strongly affect the ecology of even the Earth's most dominant forager. In effect, the question of why hunters gather can be rephrased to ask why gatherers hunt and fish, and the answer, in both cases, is not only because they can, but also because their use of animal foods allows them to meet their energetic needs in regions of low terrestrial productivity.

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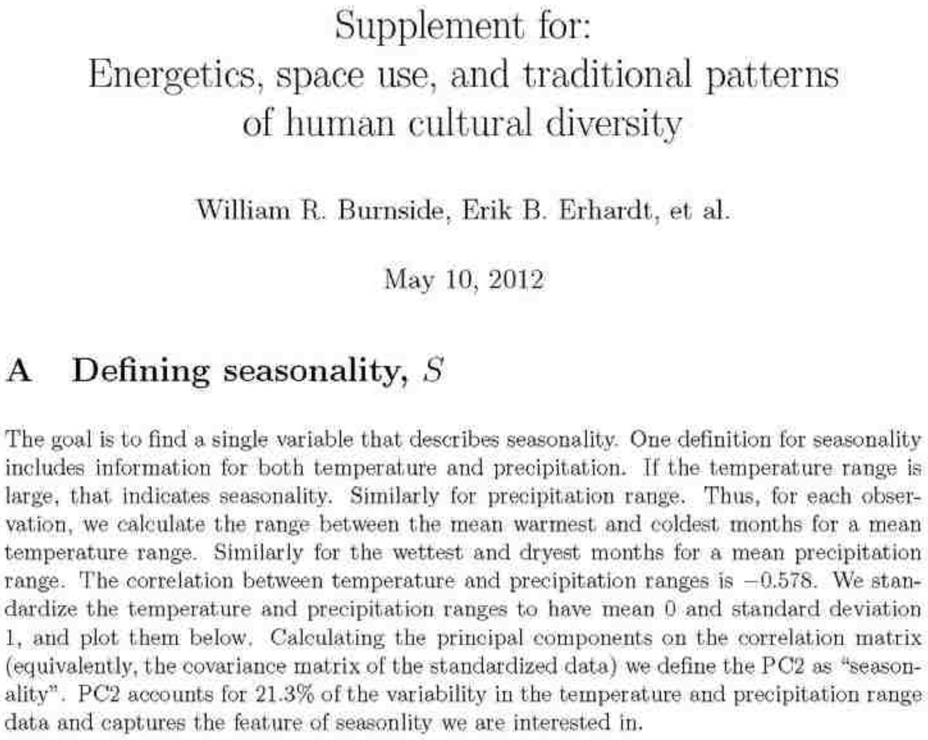
Supplemental Online Materials (See Appendix A)

Appendix A

Supplemental Material: Energetics and human cultural diversity



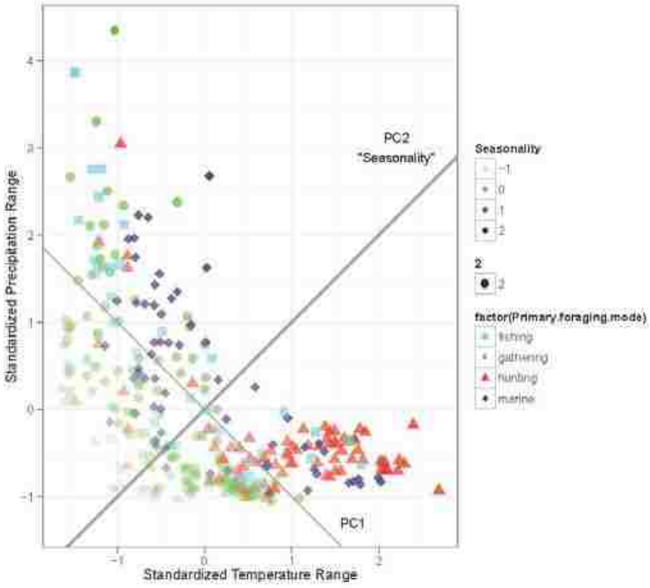
Supplement for: Energetics, space use, and traditional patterns of human cultural diversity

William R. Burnside, Erik B. Erhardt, et al.

May 10, 2012

A Defining seasonality, S

The goal is to find a single variable that describes seasonality. One definition for seasonality includes information for both temperature and precipitation. If the temperature range is large, that indicates seasonality. Similarly for precipitation range. Thus, for each observation, we calculate the range between the mean warmest and coldest months for a mean temperature range. Similarly for the wettest and dryest months for a mean precipitation range. The correlation between temperature and precipitation ranges is -0.578. We standardize the temperature and precipitation ranges to have mean 0 and standard deviation 1, and plot them below. Calculating the principal components on the correlation matrix (equivalently, the covariance matrix of the standardized data) we define the PC2 as "seasonality". PC2 accounts for 21.3% of the variability in the temperature and precipitation range data and captures the feature of seasonlity we are interested in.



```
Eigenanalysis of the Correlation Matrix
Eigenvalue  1.5740  0.4260
Proportion   0.787   0.213
Cumulative   0.787   1.000

Variable                  PC1     PC2
Precip range (MWM-MDM)  -0.707  -0.707
Temp range (MWM-MCM)     0.707  -0.707
```

B Modeling details

Because of the relationships we observe in the data, we posit a model that we believe will explain those relationships and is motivated by ecological theory. The variables considered are defined here:

A Area (data, response)

Z Population Size (data, response)

D Population Density (data, response)

C Cultural diversity $C = A^{-1}$ (data, response)

E E (estimated as $E = -\beta_t k / \log_{10}(e)$)

k k (constant, $k = 8.617343 \times 10^{-5}$)

T Temperature (Celcius) (data, predictor)

t $1/T$ (Kelvin) (data, predictor, centered $t = (1/T - 1/(12 + 273.15))$, -12°C)

R Proportion of energy transferred from one trophic level to a higher trophic level (estimated as $R = 10^{\beta_L}$)

L Trophic Level (data, predictor, centered -1.5)

S Seasonality, defined as the second prinicipal component of the correlation matrix between the temperature range and precipitation range (data, predictor)

M Marine or not indicator (1=marine, 0=not) (data, predictor, 63 are $M = 1$, while 269 are $M = 0$)

NPP Net primary productivity (data, predictor)

P $P = \log_{10}(\mathrm{NPP})$: (data, predictor, centered -2.5 on log scale)

We will model the response variables of A, Z, D, and C, with a focus on A. Below, we use A as an example, but Z, D, and C may be substituted.

Because we will use a linear analysis of covariance model to estimate the model parameters on the $\log_{10}$ scale, we will rewrite the hypothesized "main-effects product model" based on ecological theory in (1) in base 10 in (2). The log-linear form is (3).

$$\begin{aligned} A &\propto 10^{\beta_M} e^{-(E/k)t} R^L \mathrm{NPP}^{\beta_P} (10^S)^{\beta_S} & (1) \\ &= 10^{\beta_0} 10^{\beta_M} 10^{(-\log_{10}(e)E/k)t} 10^{\log_{10}(R)L} 10^{\log_{10}(\mathrm{NPP}^{\beta_P})} 10^{\beta_S S} \\ &= 10^{\beta_0 + \beta_M M} 10^{\beta_t t} 10^{\beta_L L} 10^{\beta_P P} 10^{\beta_S S} \\ &= 10^{\beta_0 + \beta_M M + \beta_t t + \beta_L L + \beta_P P + \beta_S S} & (2) \\ \log_{10}(A) &= \beta_0 + \beta_M M + \beta_t t + \beta_L L + \beta_P P + \beta_S S & (3) \end{aligned}$$

Notes on model parameters:

- β_0 is the estimate for the constant of proportionality for the model, estimating the $\log_{10}(A)$ when all other predictors are equal to zero.
- Because $k = 8.617343 \times 10^{-5}$ is a constant, β_t estimates a scaled version of E via $\beta_t = (-\log_{10}(e)E/k)$ as $E = -\beta_t k/\log_{10}(e)$.
- β_L estimates $\log_{10}(R)$, so $R = 10^{\beta_L}$.
- β_S estimates the power for seasonality, S. Base 10 here is for convenience, but it could be any base without changing the significance of the relationship, but a different base would change the scale of the relationship.
- β_P estimates the power for NPP.
- β_M estimates an effect for whether the society forages primary as Marine, M, compared to nonmarine.

B.1 Assessment of model adequacy

To assess whether (2) is adequate to describe the relationship with the response, we consider a more complete model with interactions and quadratic terms on the product scale, the "quadratic product model", and assess whether these additional terms can be excluded without substantially reducing the amount of variability explained in the response A.

$$\begin{aligned} A \;=\; & 10^{\beta_0+\beta_M M+\beta_t t+\beta_L L+\beta_P P+\beta_S S} \\ & \times 10^{\beta_{tM} tM+\beta_{LM} LM+\beta_{PM} PM+\beta_{SM} SM} \\ & \times 10^{\beta_{tL} tL+\beta_{tP} tP+\beta_{tS} tS+\beta_{PL} PL+\beta_{LS} LS+\beta_{PS} PS} \\ & \times 10^{\beta_{t_2} t^2+\beta_{L_2} L^2+\beta_{P_2} P^2+\beta_{S_2} S^2} \end{aligned} \tag{4}$$

The β parameters will be estimated on the $\log_{10}$ scale using the following "quadratic log-linear model", which includes all parameter main-effects, two-way interations, and quadratic terms.

$$\begin{aligned} \log_{10}(A) \;=\; & \beta_0 + \beta_M M + \beta_t t + \beta_L L + \beta_P P + \beta_S S \\ & + \beta_{tM} tM + \beta_{LM} LM + \beta_{PM} PM + \beta_{SM} SM \\ & + \beta_{tL} tL + \beta_{tP} tP + \beta_{tS} tS + \beta_{PL} PL + \beta_{LS} LS + \beta_{PS} PS \\ & + \beta_{t_2} t^2 + \beta_{L_2} L^2 + \beta_{P_2} P^2 + \beta_{S_2} S^2 \end{aligned} \tag{5}$$

B.1.1 Best subset GLM versus backward selection

There are criticisms of stepwise selection methods, including that redundant (or correlated) predictors can adversely affect model selection and that resulting models have an inflated risk of capturing chance features of the data (Mantel, 1970; Henderson and Velleman, 1981; Judd et al., 2009; Derksen and Keselman, 1992). We minimize the potential negative impact a stepwise procedure can have on a resulting model by carefully considering all possible models ($2^{19} = 524288$ models), and selecting among models based on smallest Bayesian information criterion (BIC), Mallows' C_p close to the number of predictors (Cuthbert and Wood, 1980), and largest Adj-R^2.

B.2 Model results

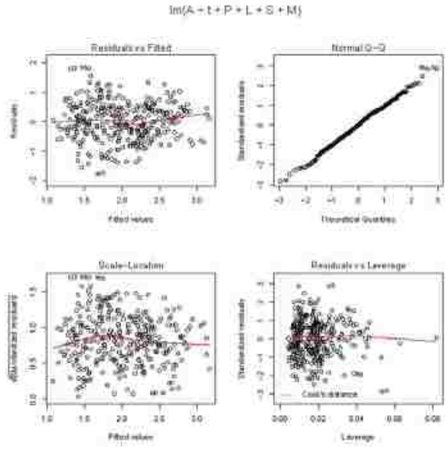
The primary analysis is for Area, A. Additional analyses are provided for Population Size, Z, and Population Density, D. The analysis for Cultural Diversity, C, is equivalent to A when estimated parameters are multiplied by -1.

B.2.1 Area

Main effects

```
Call:
lm(formula = A ~ t + P + L + S + M)

Residuals:
     Min       1Q   Median       3Q      Max
-1.74587 -0.41224  0.00213  0.45032  1.80599

Coefficients:
              Estimate Std. Error t value Pr(>|t|)
(Intercept)    2.03209    0.04866  41.763  < 2e-16 ***
t           2787.19775  569.59560   4.893 1.57e-06 ***
P             -0.17563    0.10751  -1.634   0.1033
L              0.53725    0.25233   2.129   0.0340 *
S             -0.14430    0.06758  -2.135   0.0335 *
MTRUE         -0.60087    0.10225  -5.876 1.04e-08 ***
---
Signif. codes:  0 *** 0.001 ** 0.01 * 0.05 . 0.1   1

Residual standard error: 0.6342 on 324 degrees of freedom
  (2 observations deleted due to missingness)
Multiple R-squared: 0.349,	Adjusted R-squared: 0.339
F-statistic: 34.74 on 5 and 324 DF,  p-value: < 2.2e-16

(Intercept)           t           P           L           S       MTRUE
      2.030    2790.000      -0.176       0.537      -0.144      -0.601
```

Residual plots:



Main effects, best subset selection The first few, sorted by BIC.

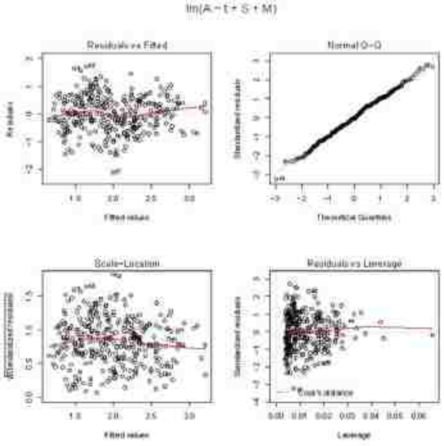
```
  (Intercept) t P L S MTRUE         rsq      rss     adjr2        cp         bic
2           1 1 0 0 0     1 0.326629516 134.7797 0.322511043 11.147197 -113.104392
3           1 1 0 0 1     1 0.337997994 132.5042 0.331905951  7.488924 -112.924238 *
3           1 1 1 0 0     1 0.333316038 133.4413 0.327180909  9.819209 -110.598554
4           1 1 0 1 1     1 0.343664485 131.3700 0.335586509  6.668622 -109.961981
3           1 1 0 1 0     1 0.328259565 134.4534 0.322077904 12.335896 -108.105109
4           1 1 1 0 1     1 0.339917937 132.1199 0.331793850  8.533338 -108.083604
4           1 1 1 1 0     1 0.339867465 132.1300 0.331742757  8.558459 -108.058372
5           1 1 1 1 1     1 0.349026222 130.2968 0.338980330  6.000000 -106.869797
3           1 0 1 1 0     1 0.299909014 140.1279 0.293466459 26.446416  -94.463470
...
```

Model 2 selected since both high BIC and Adj-R^2 and substantially lower C_p.

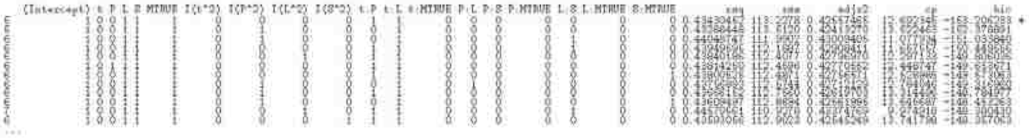
Main effects, reduced

```
Call:
lm(formula = A ~ t + S + M)

Residuals:
     Min       1Q   Median       3Q      Max
-2.07005 -0.40081 -0.02199  0.45781  1.71593

Coefficients:
              Estimate Std. Error t value Pr(>|t|)
(Intercept)    2.07261    0.03923  52.830  < 2e-16 ***
t           3878.29836  311.47740  12.451  < 2e-16 ***
S             -0.14394    0.06164  -2.335   0.0201 *
MTRUE         -0.55338    0.09567  -5.784 1.71e-08 ***
---
Signif. codes:  0 *** 0.001 ** 0.01 * 0.05 . 0.1   1

Residual standard error: 0.637 on 327 degrees of freedom
  (1 observation deleted due to missingness)
Multiple R-squared: 0.3382, Adjusted R-squared: 0.3322
F-statistic: 55.71 on 3 and 327 DF,  p-value: < 2.2e-16

(Intercept)          t          S      MTRUE
      2.070   3880.000     -0.144     -0.553
```

Residual plots:



Quadratic effects, best subset selection The first few, sorted by BIC.



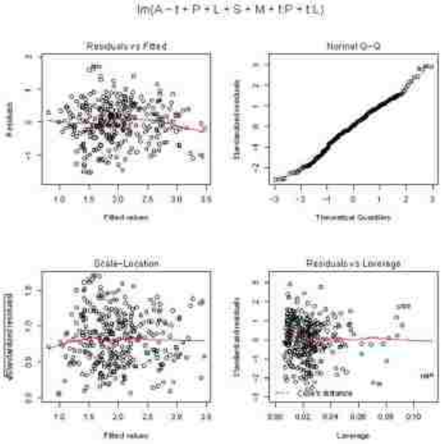
```
  (Intercept) t P L S MTRUE I(t^2) I(P^2) I(L^2) I(S^2) t:P t:L t:MTRUE P:L P:S P:MTRUE L:S L:MTRUE S:MTRUE       rsq      rss     adjr2        cp        bic
```

Model 1 selected since high BIC and Adj-R^2 and low C_p, then added t and P since interactions include these main effects.

Quadratic effects, reduced

```
Call:
lm(formula = A ~ t + P + L + S + M + t:P + t:L)

Residuals:
     Min       1Q   Median       3Q      Max 
-1.51028 -0.34679  0.01794  0.41369  1.68764 

Coefficients:
              Estimate Std. Error t value Pr(>|t|)    
(Intercept)  1.721e+00  6.317e-02  27.245  < 2e-16 ***
t           -1.456e+03  7.804e+02  -1.866  0.06290 .  
P           -2.404e-01  1.065e-01  -2.257  0.02469 *  
L            1.408e+00  2.637e-01   5.340 1.76e-07 ***
S           -1.771e-01  6.315e-02  -2.805  0.00534 ** 
MTRUE       -7.065e-01  9.585e-02  -7.371 1.44e-12 ***
t:P          1.819e+03  5.537e+02   3.286  0.00113 ** 
t:L          1.150e+04  1.553e+03   7.400 1.19e-12 ***
---
Signif. codes:  0 *** 0.001 ** 0.01 * 0.05 . 0.1   1 

Residual standard error: 0.5878 on 322 degrees of freedom
  (2 observations deleted due to missingness)
Multiple R-squared: 0.4442, Adjusted R-squared: 0.4321 
F-statistic: 36.76 on 7 and 322 DF,  p-value: < 2.2e-16 

(Intercept)           t           P           L           S       MTRUE         t:P         t:L 
      1.720   -1460.000      -0.240       1.410      -0.177      -0.706    1820.000   11500.000 
```

Residual plots:



Quadratic effects, reduced interpretation

$$\begin{aligned}
\log_{10}(A) &= \beta_0 + \beta_M M + \beta_t t + \beta_L L + \beta_P P + \beta_S S + \beta_{tL} tL + \beta_{t_2} t^2 \\
A &= 10^{\beta_0 + \beta_M M} 10^{\beta_t t + \beta_L L + \beta_P P + \beta_S S + \beta_{tL} tL + \beta_{t_2} t^2} \\
A &= 52.6 \times 0.197^M \times 10^{-1460t + 1.41L - 0.240P - 0.177S + 11500tL + 1820tP}
\end{aligned}$$

Holding all other variables constant:

- The predicted area is 52.6 at 12°C, trophic level 1.5, $\log_{10}$(NPP) 2.5 for non-marine foragers, and seasonality 0 (average seasonality).
- Marine foragers ($M = 1$) increase the area by 0.197 times (only takes 20% of the area) over other foragers ($M = 0$).
- Because of model interactions, the relationship of area with temperature, NPP, and trophic level is a little complicated.
- For each unit increase in t (decrease in T), area is predicted to decrease, though less of a decrease with either higher NPP or trophic levels.
- For each unit increase in P, area is predicted to decrease, and more so at higher temperatures.
- For each unit increase in L, area is predicted to increase, and more so at lower temperatures.
- For each unit increase in S, area is predicted to decrease.

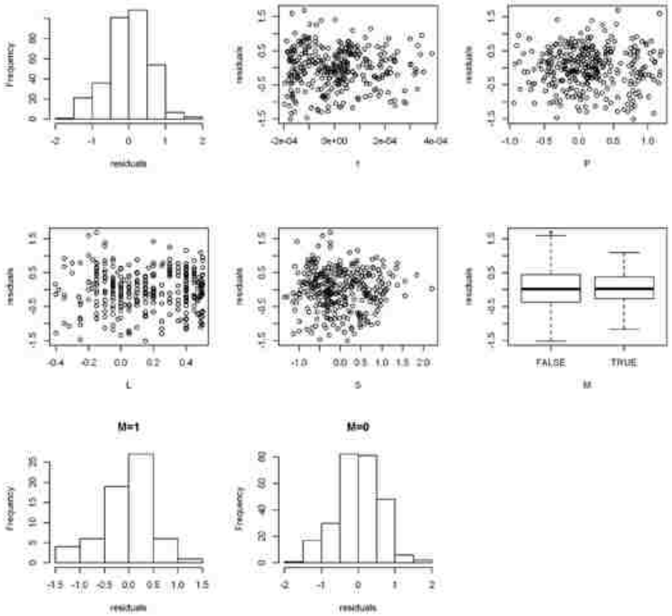
Quadratic effects, reduced further assessment Variance inflation factors (VIF) among main effects are relatively small, all less than 5. Typically, one would worry if any of these values were greater than 10.

```
       t        P        L        S    MTRUE 
4.714823 2.147327 3.247839 1.512825 1.325286 
```

Even among t and the interactions involving t, the VIFs are not overwhelmingly high.

```
        t         P         L         S     MTRUE       t:P       t:L 
10.300554  2.453226  4.127451  1.537178  1.355461  1.628694  4.484849 
```

Additional residual plots do not indicate any cause for concern regarding model fit.

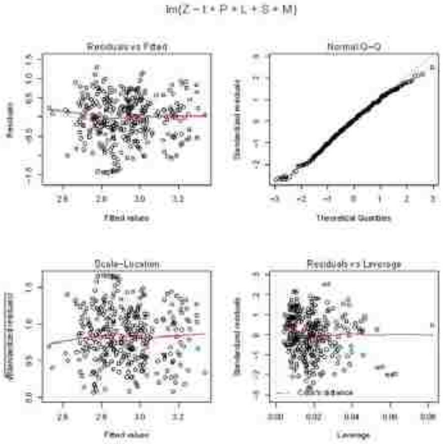


B.2.2 Population Size

Main effects

```
Call:
lm(formula = Z ~ t + P + L + S + M)

Residuals:
    Min      1Q  Median      3Q     Max
-1.4198 -0.3379  0.0222  0.3775  1.2963

Coefficients:
             Estimate Std. Error t value Pr(>|t|)
(Intercept)   2.80272    0.04054  69.129   <2e-16 ***
t            72.42088  474.61122   0.153   0.8788
P             0.04784    0.08958   0.534   0.5937
L             0.56202    0.21025   2.673   0.0079 **
S            -0.09577    0.05631  -1.701   0.0900 .
MTRUE         0.14027    0.08520   1.646   0.1007
---
Signif. codes:  0 *** 0.001 ** 0.01 * 0.05 . 0.1   1

Residual standard error: 0.5284 on 324 degrees of freedom
  (2 observations deleted due to missingness)
Multiple R-squared: 0.08293,  Adjusted R-squared: 0.06878
F-statistic:  5.86 on 5 and 324 DF,  p-value: 3.36e-05

(Intercept)           t           P           L           S       MTRUE
     2.8000     72.4000      0.0478      0.5620     -0.0958      0.1400
```

Residual plots:



Main effects, best subset selection The first few, sorted by BIC.

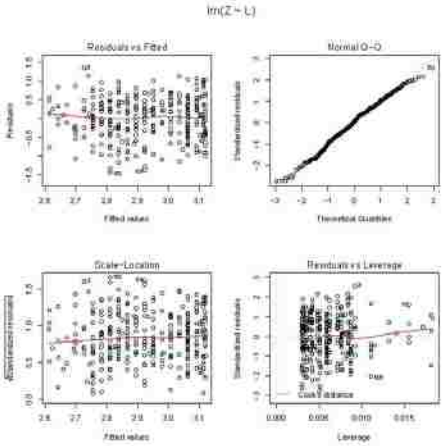
```
  (Intercept) t P L S MTRUE         rsq      rss       adjr2        cp         bic
1           1 0 0 1 0     0 0.064127744 92.31890  0.061274475  4.642820 -10.2729906 •
2           1 0 0 1 0     1 0.073985306 91.34650  0.068321608  3.160152  -7.9682303
2           1 0 0 1 1     0 0.073701264 91.37452  0.068035828  3.260504  -7.8670228
3           1 0 0 1 1     1 0.081835828 90.57209  0.073386464  2.386570  -4.9787217
2           1 1 0 1 0     0 0.064913989 92.24134  0.059194808  6.365041  -4.7512539
2           1 0 1 1 0     0 0.064667392 92.26566  0.058946703  6.452163  -4.6642392
1           1 0 0 0 0     1 0.043738208 94.33022  0.040822775 11.846425  -3.1605901
3           1 0 1 1 1     0 0.075068891 91.23961  0.066557255  4.777323  -2.5555162
3           1 1 0 1 0     1 0.074742917 91.27177  0.066228281  4.892489  -2.4392346
3           1 0 1 1 0     1 0.074353302 91.31020  0.065835081  5.030140  -2.3003047
```

The second model above "backward selects" at the 0.05 significance level down to the first model.

Main effects, reduced

```
Call:
lm(formula = Z ~ L)

Residuals:
     Min       1Q   Median       3Q      Max
-1.44945 -0.33753  0.03073  0.36731  1.34496

Coefficients:
            Estimate Std. Error t value Pr(>|t|)
(Intercept)  2.83926    0.03448  82.344  < 2e-16 ***
L            0.56170    0.11697   4.802 2.39e-06 ***
---
Signif. codes:  0 *** 0.001 ** 0.01 * 0.05 . 0.1   1

Residual standard error: 0.5306 on 329 degrees of freedom
  (1 observation deleted due to missingness)
Multiple R-squared: 0.0655, Adjusted R-squared: 0.06266
F-statistic: 23.06 on 1 and 329 DF,  p-value: 2.39e-06

(Intercept)           L
      2.840       0.562
```

Residual plots:



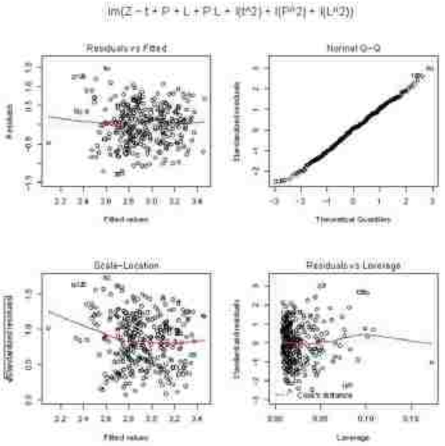
Quadratic effects, best subset selection The first few, sorted by BIC.

Selected model 4 since it had higher Adj-R^2 Model 4 selected since both higher Adj-R^2 and substantially lower C_p, without much lower BIC, then added main effect P since model includes higher-order P terms.

Quadratic effects, reduced

```
Call:
lm(formula = Z ~ t + P + L + P:L + I(t^2) + I(P^2) + I(L^2))

Residuals:
     Min       1Q   Median       3Q      Max 
-1.26505 -0.35411  0.03519  0.36380  1.45512 

Coefficients:
              Estimate Std. Error t value Pr(>|t|)    
(Intercept)  2.850e+00  5.430e-02  52.481  < 2e-16 ***
t           -1.641e+03  6.344e+02  -2.586 0.010142 *  
P            2.692e-02  9.742e-02   0.276 0.782437    
L            1.044e+00  2.836e-01   3.681 0.000272 ***
I(t^2)      -6.945e+06  2.066e+06  -3.361 0.000871 ***
I(P^2)      -3.797e-01  1.373e-01  -2.766 0.006011 ** 
I(L^2)       1.535e+00  5.947e-01   2.581 0.010303 *  
P:L         -1.362e+00  3.734e-01  -3.647 0.000309 ***
---
Signif. codes:  0 *** 0.001 ** 0.01 * 0.05 . 0.1   1 

Residual standard error: 0.5029 on 322 degrees of freedom
  (2 observations deleted due to missingness)
Multiple R-squared: 0.1743, Adjusted R-squared: 0.1564 
F-statistic: 9.712 on 7 and 322 DF,  p-value: 5.614e-11 

(Intercept)           t           P           L      I(t^2)      I(P^2)      I(L^2)         P:L 
   2.85e+00   -1.64e+03    2.69e-02    1.04e+00   -6.94e+06   -3.80e-01    1.53e+00   -1.36e+00 
```

Residual plots:



Quadratic effects, reduced interpretation

$$\begin{aligned}\log_{10}(Z) &= \beta_0 + \beta_t t + \beta_L L + \beta_P P + \beta_{PL} PL + \beta_{t_2} t^2 + \beta_{L_2} L^2 + \beta_{P_2} P^2 \\ Z &= 10^{\beta_0 + \beta_t t + \beta_L L + \beta_P P + \beta_{PL} PL + \beta_{t_2} t^2 + \beta_{L_2} L^2 + \beta_{P_2} P^2} \\ Z &= 708 \times 10^{-1640t - 6940000t^2} 10^{1.04L + 1.53L^2 + 0.0269P - 0.380P^2 - 1.36PL}\end{aligned}$$

The coefficients for t are so large because t is on the scale of 1/Kelvin, so 10–30 degree shifts results in very small changes in t.

Holding all other variables constant:

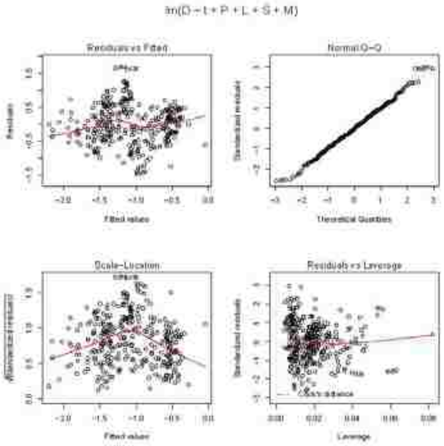
- The predicted population size is 708 at 12°C, trophic level 1.5, and $\log_{10}$(NPP) 2.5. Note that seasonality or marine does not help predict population size.
- For each unit increase in t (decrease in T), population size is predicted to decrease, and more so for lower temperatures.
- For each unit increase in L, population size is predicted to increase, and more so for higher trophic levels, and even more so when P is low.
- For each unit increase in P, population size is predicted to increase, but more for lower NPP and less for higher NPP, and less for higher trophic levels.

B.2.3 Population Density

Main effects

```
Call:
lm(formula = D ~ t + P + L + S + M)

Residuals:
     Min       1Q   Median       3Q      Max
-1.44573 -0.36608 -0.01716  0.37966  1.65162

Coefficients:
              Estimate Std. Error t value Pr(>|t|)
(Intercept) -1.238e+00  4.311e-02 -28.713  < 2e-16 ***
t           -2.731e+03  5.047e+02  -5.410 1.22e-07 ***
P            2.293e-01  9.526e-02   2.407   0.0166 *
L            5.496e-02  2.236e-01   0.246   0.8060
S            5.109e-02  5.988e-02   0.853   0.3942
MTRUE        7.364e-01  9.060e-02   8.127 9.37e-15 ***
---
Signif. codes:  0 *** 0.001 ** 0.01 * 0.05 . 0.1   1

Residual standard error: 0.5619 on 324 degrees of freedom
  (2 observations deleted due to missingness)
Multiple R-squared: 0.3735, Adjusted R-squared: 0.3638
F-statistic: 38.63 on 5 and 324 DF,  p-value: < 2.2e-16

(Intercept)           t           P           L           S       MTRUE
  -1.24e+00   -2.73e+03    2.29e-01    5.50e-02    5.11e-02    7.36e-01
```

Residual plots:



Main effects, best subset selection The first few, sorted by BIC.

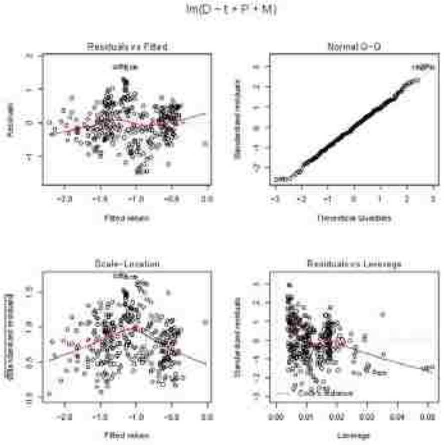
```
  (Intercept) t P L S MTRUE       rsq      rss      adjr2        cp           bic
3           1 1 1 0 0     1 0.37178985 102.5709 0.366008777  2.879923 -130.2142068 •
2           1 1 0 0 0     1 0.35138908 105.9018 0.347422038 11.430218 -125.4670629
4           1 1 1 0 1     1 0.37337449 102.3121 0.365662176  4.060425 -125.2485794
4           1 1 1 1 0     1 0.37208377 102.5229 0.364355569  4.727924 -124.5695453
3           1 1 0 0 1     1 0.35987733 104.5159 0.353986626  9.040506 -124.0151251
3           1 1 0 1 0     1 0.35688164 105.0050 0.350963369 10.589732 -122.4743712
5           1 1 1 1 1     1 0.37349133 102.2931 0.363822089  6.000000 -119.5110250
4           1 1 0 1 1     1 0.36228400 104.1229 0.354435183  9.795893 -119.4590723
3           1 0 1 1 0     1 0.31566198 111.7351 0.309364396 31.906543 -101.9737214
```

Model 1 selected since both high BIC and Adj-R^2 and low C_p.

Main effects, reduced

```
Call:
lm(formula = D ~ t + P + M)

Residuals:
     Min       1Q   Median       3Q      Max
-1.45750 -0.36528  0.00164  0.36293  1.65646

Coefficients:
              Estimate Std. Error t value Pr(>|t|)
(Intercept) -1.237e+00  3.599e-02 -34.366  < 2e-16 ***
t           -2.461e+03  3.155e+02  -7.801 8.32e-14 ***
P            2.700e-01  8.242e-02   3.276  0.00117 **
MTRUE        7.367e-01  8.577e-02   8.589 3.63e-16 ***
---
Signif. codes:  0 *** 0.001 ** 0.01 * 0.05 . 0.1   1

Residual standard error: 0.5602 on 327 degrees of freedom
  (1 observation deleted due to missingness)
Multiple R-squared: 0.3722, Adjusted R-squared: 0.3665
F-statistic: 64.64 on 3 and 327 DF,  p-value: < 2.2e-16

(Intercept)           t           P       MTRUE
     -1.240   -2460.000       0.270       0.737
```

Residual plots:



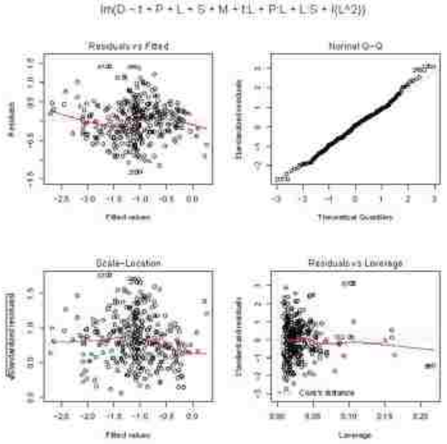
Quadratic effects, best subset selection The first few, sorted by BIC.

Model 1 selected since both high BIC and Adj-R^2 and low C_p. Main effects t and P were added since higher-order terms include them, then backward selection was performed which removed the PS interaction.

Quadratic effects, reduced

```
Call:
lm(formula = D ~ t + P + L + S + M + t:L + P:L + L:S + I(L^2))

Residuals:
     Min       1Q   Median       3Q      Max
-1.29856 -0.30901  0.03771  0.29520  1.40487

Coefficients:
              Estimate Std. Error t value Pr(>|t|)
(Intercept) -8.902e-01  5.402e-02 -16.480  < 2e-16 ***
t            1.067e+03  6.333e+02   1.684 0.093103 .
P            2.660e-01  9.136e-02   2.912 0.003849 **
L           -9.886e-01  2.846e-01  -3.473 0.000585 ***
S            2.783e-01  6.134e-02   4.537 8.08e-06 ***
MTRUE        7.223e-01  8.333e-02   8.668 2.23e-16 ***
I(L^2)       2.904e+00  8.046e-01   3.609 0.000357 ***
t:L         -1.555e+04  1.920e+03  -8.098 1.18e-14 ***
P:L         -1.314e+00  3.788e-01  -3.470 0.000593 ***
L:S         -7.748e-01  2.115e-01  -3.663 0.000292 ***
---
Signif. codes:  0 *** 0.001 ** 0.01 * 0.05 . 0.1   1

Residual standard error: 0.4808 on 320 degrees of freedom
  (2 observations deleted due to missingness)
Multiple R-squared: 0.5469, Adjusted R-squared: 0.5341
F-statistic: 42.91 on 9 and 320 DF,  p-value: < 2.2e-16

(Intercept)           t           P           L           S       MTRUE      I(L^2)
  -8.90e-01    1.07e+03    2.66e-01   -9.89e-01    2.78e-01    7.22e-01    2.90e+00

        t:L         P:L         L:S
  -1.56e+04   -1.31e+00   -7.75e-01
```

Residual plots:



Quadratic effects, reduced interpretation

$$
\begin{aligned}
\log_{10}(D) &= \beta_0 + \beta_M M + \beta_t t + \beta_L L + \beta_P P + \beta_S S \\
&\quad + \beta_{tL} tL + \beta_{PL} PL + \beta_{LS} LS + \beta_{L_2} L^2 \\
D &= 10^{\beta_0 + \beta_M M} 10^{\beta_t t + \beta_L L + \beta_P P + \beta_S S + \beta_{tL} tL + \beta_{PL} PL + \beta_{LS} LS + \beta_{L_2} L^2} \\
D &= 0.129 \times 5.27^M 10^{1070t - 0.989L + 2.90L^2 - 15600tL + 2.24P - 1.31PL - 0.775LS + 0.278S}
\end{aligned}
$$

Holding all other variables constant:

- The predicted population density is 0.129 at 12°C, trophic level 1.5, $\log_{10}$(NPP) 2.5 for non-marine foragers, and seasonality 0 (average seasonality).
- Marine foragers ($M = 1$) increase the population density by 5.27 times over other foragers ($M = 0$).
- (The relationship between density, temperature, and trophic level is complicated because the other effects depend on what the trophic level is.)
- For each unit increase in t (decrease in T), population density is predicted to decrease with higher trophic levels but increase for lower trophic levels.
- For each unit increase in P, population density is predicted to increase, and less for higher trophic levels, and actually decreasing for trophic levels higher than 3.21 (outside the range of observation).
- For each unit increase in S, population density is predicted to increase, and less for higher trophic levels, and actually decreasing for trophic levels higher than 1.86.

- Everything depends on the trophic level. For each unit increase in L, population density is predicted to be (at 12°C, trophic level 1.5, $\log_{10}$(NPP) 2.5, and seasonality 0) a minimum around 1.7, and increase as you increase or decrease away from 1.7. However, recall the relationship other variables have with trophic level.

B.2.4 Cultural diversity

Since $\log_{10}(C) = -\log_{10}(A)$, these results are the same as for A, except that the sign (+ or −) of the parameter estimates are multiplied by -1.

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Chapter 3: Human macroecology: linking pattern and process in big-picture human ecology

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Abstract

Humans have a dual nature. We are subject to the same natural laws and forces as other species yet dominate global ecology and exhibit enormous variation in energy use, cultural diversity, and apparent social organization. We suggest scientists tackle these challenges with a macroecological approach—using comparative statistical techniques to identify deep patterns of variation in large datasets and test for causal mechanisms. We show the power of a metabolic perspective for interpreting these patterns and suggesting possible underlying mechanisms, one that focuses on the exchange of energy and materials within and among human societies and with the biophysical environment. Examples on human foraging ecology, life history, space use, population structure, disease ecology, cultural and linguistic diversity patterns, and industrial and urban systems showcase the power and promise of this approach.

Key words: macroecology, human, scale, metabolism, society, energy, diversity, network, industrial, hunter-gatherer.

Introduction

Human ecology has an interesting duality. On the one hand, *Homo sapiens* is just another species, subject to the same physical, chemical, and biological laws as any animal, plant, or microbe. On the other hand, *Homo sapiens* is unique, the most powerful species ever to inhabit the Earth. Indeed, in just a few thousand years, this highly social mammal has spread out of Africa to colonize the globe and use technologies of hunting, fishing, agriculture, and industry to transform the ecosystems and biodiversity of the planet.

One might think that ecologists would study human ecology. Many ecologists do study impacts of humans on the environment, focusing on climate change, biodiversity loss, land use practices, pollution, and the destruction and fragmentation of habitats. Few ecologists, however, study the influence of the environment on humans, including the effects of biotic, abiotic, and social conditions on population growth, demography, health, resource use, and economy of our own species. Indeed, that focus is largely the preserve of the social sciences, especially anthropology, sociology, economics, geography, and public health.

Our premise is that human ecology is also a natural science, so it can be pursued using the same conceptual framework, analytical rigour, methodological approaches, and technological tools that ecologists apply to non-human systems. One challenge is that human ecology exhibits enormous variation over both time and space and across the spectrum of socio-economic development, from hunter-gatherers and pastoralists to horticulturalists, agriculturalists, and members of developed industrial societies. One answer to this challenge is to document patterns across scales and to evaluate underlying mechanistic hypotheses. In essence, we suggest adopting a macroecological approach—taking a large-scale, comparative, statistical perspective to identify important patterns of variation and test for causal mechanisms (e.g. Brown, 1995; Gaston & Blackburn, 2000). We define human macroecology as the study of human-environment interactions across spatial and temporal scales, linking small-scale interactions with large-scale, emergent patterns and their underlying processes.

In the following sections, we present selected examples to highlight some of the unique perspectives, new questions, and recent empirical and theoretical advances in human macroecology. We characterize dimensions and consequences of the human niche: interactions with the environment that affect the abundance, distribution, diversity, and social, economic, and technological development of human populations. We adopt a metabolic perspective that focuses on the exchange of energy and materials between humans and their environments and the flows, pools, and transformations of these resources into, out of, within, and among societies. We cover a wide spectrum, from how minimally acculturated hunter-gathers form social groups to forage for food, exchange information, and use space, to how modern technological societies use extra-metabolic energy, especially fossil fuels, and resource supply networks to support dense populations in large cities.

Foraging: Acquiring Energy

Like other animals, humans require energy and nutrients from food to support their metabolism. Patterns and processes of food acquisition in minimally acculturated humans highlight fundamental features of the human niche. Hunting and gathering was the socio-economic framework for the vast majority of human history. The study of traditional non-industrial societies offers valuable insights into human evolution and ecology, and large-scale, cross-cultural studies of variation among hunter-gatherer cultures have a venerable history in anthropology (e.g. Steward, 1938; Murdoch, 1967; Tindale, 1974; Kelly, 1995;

Binford, 2001). Despite extremely diverse diets and foraging behaviours, traditional humans search for food in broadly consistent ways. Like other social animals, such as crows, wolves, lions, and dolphins, humans usually forage in groups (Winterhalder & Smith, 2000). Foraging groups in productive environments travel shorter distances and have smaller home ranges and higher population densities than societies in less-productive cold or arid environments (Figure 1) (Kelly, 1995; Binford, 2001).

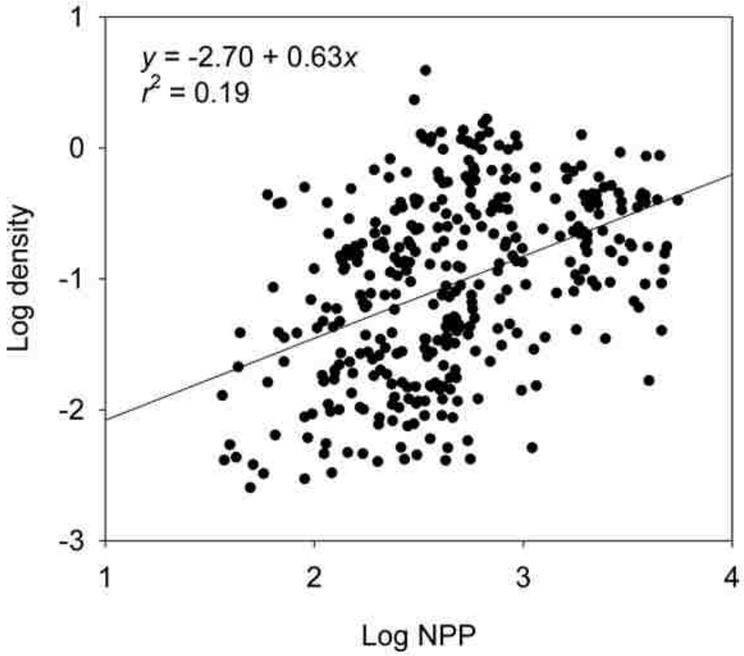

Figure 1. Population density of traditional foraging societies versus net primary productivity (NPP) of the local environment. The relationship is significant ($P < 0.005$), although there is much unexplained variation, likely due to variables such as the proportion of plant and animal foods in the diet and the relative use of terrestrial, fresh-water, and marine resources. Data are from Binford (2001).

Hunter-gatherers are also subject to constraints of trophic position and attendant energy supply. Groups that rely more on hunting animal prey and less on gathering plant foods tend to have lower population densities, occupy larger areas, and move more frequently and over greater distances (Kelly, 1995). Not surprisingly, population densities tend to be high in productive areas, such as river valleys and flood plains, and low in unproductive high-latitude, high-elevation, and desert areas. Population densities also tend to be high along productive coasts and large rivers where humans exploit nutrient-rich aquatic resources, such as fish and shellfish (Kelly, 1995; Binford, 2001). These macroscopic foraging patterns are consistent with humans being optimal foragers who exploit diverse and patchy resources in proportion to their energetic profitability (Sutherland, 1996).

Despite these similarities to other animals, human foragers are distinctive in three ways. First, humans have an exceptionally wide diet breadth. For example, in addition to using many plants Ache hunter-gatherers in the Amazon Basin of Paraguay harvest at least 263 species of game, including birds, mammals, reptiles, and fish (Kaplan et al., 2000). Second, despite their dietary diversity humans preferentially forage for food resources that are highly profitable but rare and hard to acquire, such as large game. Ache hunters and Aleut whalers typically go for days with little or no success. The potential disadvantages of specializing on large, rare prey are offset by hunting in cooperative groups and sharing the returns, thereby reducing risk and *per capita* variance in success (Winterhalder, 1996). Across a worldwide ethnographic sample, large, unpredictable food items are more likely to be shared than small, predictable ones (Gurven, 2004). Although some other primates also share food, the ubiquity of food sharing among distantly related individuals is uniquely human (Kaplan et al., 2000). So humans tend to be optimal social foragers, concentrating on food resources that provide maximal returns per unit effort and using cooperative foraging and food sharing to increase the rate and decrease the variance in energy intake. By efficiently targeting large game, prehistoric humans contributed to size-selective extinctions of megafauna on multiple continents (Lyons, Smith & Brown, 2004) while contemporary humans have hunted whales to near extinction and skewed body-size distributions of commercial fish stocks (Jennings & Reynolds, 2007). Third, humans occupy a high-skill foraging niche, using methods that may take years to master and harvesting a range of foods that require sophisticated understanding of local natural history, harvesting technologies, and intensive processing techniques (Kaplan & Robson, 2002). Developing these foraging skills requires long-term learning in social groups.

These attributes of the human foraging niche have several implications for human evolutionary ecology. Wide diet breadth, cooperative hunting, food sharing, and food processing allowed groups to maintain relatively dense and stable populations. The need to learn the natural history of plants and animals used for food, fiber, and medicine and the technologies used to harvest and prepare them selected for a general intelligence that emphasized memory and spatial relations as well as communication, cooperation, and planning (Kaplan & Robson, 2002). The benefits of distributing shared food resources favoured the formation of social networks and selected for behaviours based on reciprocity and kinship. As prehistoric populations acquired these uniquely human traits, they spread rapidly out of their ancestral home in tropical Africa, exploiting new food resources and colonizing new environments.

Life History: Allocating Energy

The energy acquired by foraging humans is processed through metabolism and allocated to fuel growth, reproduction, and maintenance. The balancing of income and expenditure determines the energy budget. The income comes from foraging, and the expenditure determines the life history. A life history is the pattern, over an organism’s life, for timing key events and allocating resources to maintenance, growth, and reproduction. It is an evolved answer to questions such as how fast to grow, when to reproduce, how long to live, how many offspring to have, and how much resources to invest in each one (Charnov, 1991; Roff, 2002). Life histories have evolved by natural selection to maximize fitness, constrained by trade-offs imposed by the finite energy budget. So, for example, energy invested in maintenance cannot be allocated to growing or producing offspring, and energy invested in reproduction can be used to produce either a few large offspring or many small offspring. Comparing human life-history traits to those of other species illuminates how humans simultaneously obey the same laws as other organisms and where humans use technology, sociality, and culture to lift some constraints in novel ways.

Humans fit the general pattern of having a relatively slow life history as a relatively large animal. Within major animal groups, such as mammals, larger species tend to "live slower lives" (Purvis et al., 2003). Growth rates, lifespans, and other life-history variables increase more slowly than body size due to size-related constraints on metabolism, which fuels the life history. Metabolic rates rise sublinearly with body size because the larger vascular systems of larger animals take longer to service their body's cells, which can metabolize sugars only as fast as they receive them (West, Brown & Enquist, 1997). Since the life history is allocated from the metabolic energy budget, humans and other large animals have slow life histories (e.g. Peters, 1983). However, individual taxa often deviate from the general relationship, as shown in Figure 2, due to selection for specific traits.

Compared to other mammals, the human life history is exceptionally slow, characterized by slow growth, a long time to maturity and lifespan, and a low rate of reproduction. For example, human growth rate is more similar to that of a large reptile than to that of a typical mammal (Figure 2; Walker et al., 2006). The human life history reflects an evolutionary trend in primates towards slower growth rates and correspondingly lower mortality rates and longer lifespans with increasing body size (Charnov & Berrigan, 1993). Indeed, even in poor environments human hunter-gatherers have higher survival at all ages than chimpanzees, our closest relative (Hill et al., 2001). Humans are also unique in having a lifespan substantially longer than the reproductive period, so that post-reproductive females comprise a substantial fraction of hunter-gather as well as modern industrial populations (Hawkes & Paine, 2006). This life history is consistent with suggestions that selection on primates and especially on humans has placed a premium on large brain size and accompanying learning and cognitive capacities, with consequent slow growth rates, long development times, and low mortality (Charnov & Berrigan, 1993; Walker et al., 2006).

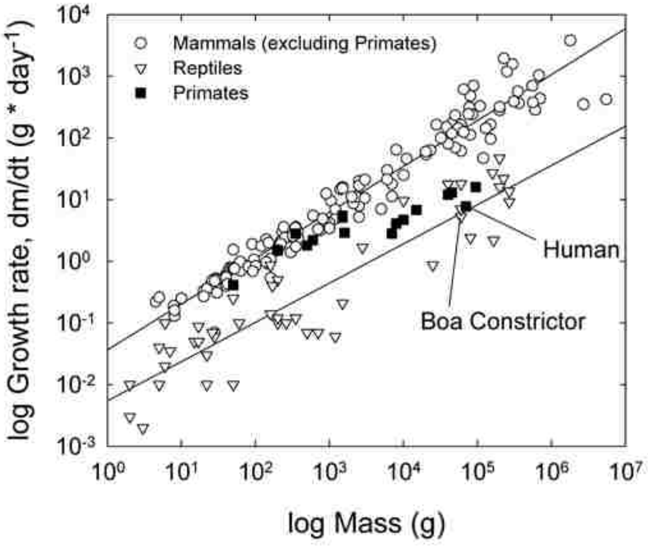

Figure 2. Growth rate as a function of body mass for species of mammals and reptiles plotted on logarithmic axes [from Case (1978) and Walker et al. (2006)]. The regression lines for mammals and reptiles give the scaling of growth rate with body size: log(dm/dt) = log(a) + δ log(m), where m is the mass in g, dm/dt is the change in mass per unit time, log(a) is the y-axis intercept, and δ is the slope of the line, or scaling exponent. The near-parallel lines indicate that growth rates of reptiles are generally slower than those of mammals but scale similarly with size. Small-bodied primates have growth rates similar to those of other mammals, but larger primates have diverged toward progressively lower growth rates. Growth rates of humans are even lower than those of other primates and similar to those of

reptiles of comparable size. Other human life-history traits, such as a long time to reproduction and a long lifespan, also reflect our exceptionally slow life histories.

The unique pattern of survival well beyond the reproductive period is linked to our slow life history through sociality (Kaplan et al., 2000). Among hunter-gatherers, the metabolic demand of multiple dependents exceeds the foraging capacity of a single individual. Cooperative foraging and food sharing supply the essential ‘extra-maternal’ resources (Kaplan et al., 2000; Hrdy, 2006). Adult males hunt in social groups, harvest more resources than they can consume, and bring food back, which is distributed to other group members — females, young, and old — through a complex exchange network. Females typically gather plant foods, and non-reproductive females, including grandmothers and older children, contribute to foraging, food processing, and child care. These contributions of males and non-reproductive females enhance the reproductive success of breeding females, increasing fecundity by shortening the time to weaning and increasing the survivorship of offspring (Marlowe, 2001). Foraging productivity of non-breeding individuals, sharing of food, and social care of young are the crux of the uniquely human life history, with a long period of juvenile dependence, high offspring survival rate, and multiple dependent offspring (Kaplan et al., 2000; Gurven & Walker, 2006; Hrdy, 2006).

Social Networks: Distributing Energy and Using Space

A key to understanding the unique features of human life history is to elucidate how social networks affect the rates and directions of resource flows among individuals and especially to offspring. Where do humans acquire these resources, how do they distribute them, and how do patterns of distribution affect and reflect human ecology?

Humans harvest energetic and material resources that sustain them from the ecosystems in which they are embedded. The social organizations of nonindustrial societies are shaped by several forces. In part, they reflect the intrinsic Darwinian imperative to allocate resources to different components of the life history and to individuals of different ages and degrees of relatedness so as to maximize reproductive success. In part, they reflect extrinsic environmental constraints on resource availability.

Resource constraints are especially evident for hunter-gatherers, who obtain nearly all of their energy and materials for fuel, clothing, food, shelter, and non-lithic tools from plants and animals. Hunter-gatherer cultures must contend with temporal and spatial variation in the abundance and distribution of these biological resources. Macroecological perspectives have been applied to explore variation in the abundance, distribution, and diversity of hunter-gatherer cultures based on theoretical concepts of networks, allometric scaling, and metabolic ecology (Hamilton et al., 2007*a*, *b*, 2009). Indeed, remarkable symmetries in space use and social organization across hunter-gatherer societies worldwide suggest that different foraging cultures have experienced and adapted to resource constraints in fundamentally similar ways.

A fundamental concept in mammalian ecology is the home range, the area of space an individual uses on a regular basis to acquire the resources for growth, maintenance, and reproduction. The home range, H, can be defined as $H \equiv B / R$, where B is the rate of resource use of an individual and R is the rate of resource supply per unit area. The rate of resource use can be equated to the metabolic rate of a free-living animal in the field, so larger animals have higher field metabolic rates and, predictably, larger home ranges (McNab, 1963). Given the home range of an individual, H, and assuming this individual's space use is typical for its population, then the total territory area, A, required by a population of N

individuals to meet their metabolic requirements is $A = HN^{\beta}$. The exponent β quantifies how the home range area scales with population size: when $\beta = 1$ the group territory area is simply the sum of individual space requirements; when $\beta > 1$ individual space requirements increase with population size; and when $\beta < 1$ individual space requirements decrease with population size (Hamilton et al., 2007*a*). We can also derive other metrics of population size and space use and examine their dependencies on the scaling exponent, β. For example, population density is the number of individuals per unit area, or $\frac{N}{A} = H^{-1}N^{1-\beta}$. Thus, population density is simply the inverse of home range when $\beta = 1$ but increases with population size when $\beta < 1$ and decreases when $\beta > 1$. Similarly, for a steady state (non-growing) population we can express the equilibrium abundance as $N = K = \left(\frac{A}{H}\right)^{\frac{1}{\beta}}$ and thereby define the carrying capacity, *K*, as the filling of an area, *A,* with a social group of *N* individuals given their home range requirements, *H,* and their spatial organization, β.

Applying this framework to humans and using a global sample of 339 hunter-gatherer societies shows how the scaling exponent, β, is directly related to the carrying capacity (Hamilton et al., 2009). The space required by an individual is not constant but instead decreases with increasing population size. As shown in Figure 3, $\beta < 1$ and close to 3/4, suggesting an economy of scale (Hamilton et al., 2007*a*). Viewed from a slightly different perspective, the area of space used by an individual decreases with increasing population size at a rate of $A / N \propto N^{-1/4}$. However, because individual resource requirements are essentially constant –field metabolic rates do not change– the rate of resource use per unit area, *R*, increases with population size, as $R \propto N^{1/4}$. Therefore, larger foraging societies are able to extract more resources per unit area of their territory, which implies that either exclusive home ranges are smaller or that overlap among shared home ranges increases. As a consequence of these economies of scale, carrying capacities of the largest human populations in this sample, social groups of a few thousand individuals, are about five times higher than expected if individual space requirements were fixed so that group territory size just scaled up linearly with population size. Effectively, large hunter-gather societies tend to use their environments more efficiently than small ones, extracting more resources per unit area.

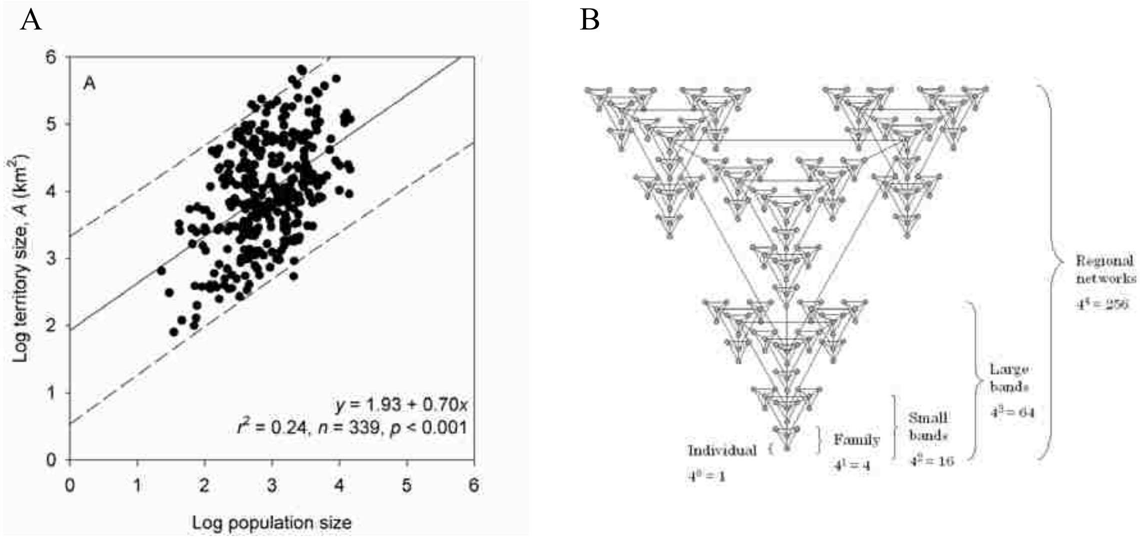

Figure 3. (A) The total area, A, used by a hunter-gatherer population versus population size, N. Although there is considerable unexplained variation (r2 = 0.24), the sublinear scaling ($A \sim N^{0.7}$) is indicated by the fact that the fitted slopes of the overall relationship (solid line; $\beta = 0.70$) and the upper and lower bounds (dashed lines) are all significantly less than 1 (after Hamilton et al., 2007a). (B) A diagram depicting the self-similar topology of a hunter-gatherer social network, showing the typical factor of four separating the nested hierarchy of group sizes (after Hamilton et al., 2007*b*). We suggest that this topology maximizes the flux of resources through traditional human social networks, reducing the average area required per individual as population size increases.

From sedentary coastal fishing societies to nomadic desert bands, hunter-gatherer cultures worldwide also show remarkable similarities in social organization despite large differences in food base and habitat (Hamilton et al., 2007*b*). Societies are organized into a nested hierarchy of modular group sizes, from individual nuclear family units, to seasonal residential groups, up to self-recognized regional populations of about 1000 individuals. Moreover, the nesting of subgroups within higher order groups is statistically self-similar: group size increases by a factor of approximately four with each increasing level of the hierarchy. We hypothesize that this pattern reflects a scaling up from the nuclear family as the fundamental unit of social organization, and in a non-growing population the average family size is four, two parents and two offspring (Figure 3B). The hierarchical organization of these social networks is remarkably similar to those of other social mammal species: gelada baboons (*Theropithecus gelada*), hamadryas baboons (*Papio hamadryas*), African elephants (*Loxodonta africana*), and orcas (*Orcinus orca*) all have scaling ratios between three and four (Hill, Bentley & Dunbar, 2008).

Such symmetries across cultures that vary widely in their environmental circumstances suggest universal processes underlying how politically egalitarian hunter-gatherer cultures self-organize (Hamilton et al., 2007*b*). We posit that the consistently fractal-like structure of traditional human societies serves to maximize the flux of energy, materials, and information through social networks. Similar physical constraints and optimization principles underlie the fractal-like networks of animal societies, plant architectures, stream networks, and mammalian vascular systems (Brown et al., 2002; Hill et al., 2008).

Human Disease: Encountering, Distributing, and Promoting Infection

As societies grow, their ramifying social networks distribute more than energy, materials, and information. Parasites and pathogens move among people, and increased contact among individuals in denser populations with larger social networks spread these scourges further and faster.

“Disease ecology” is a vibrant and important field with a large and rapidly growing literature (e.g. Jones et al., 2008; Smith et al., 2007; Guernier, Hochberg & Guégan, 2004). Many studies examine spatial and temporal dynamics of specific diseases and macroparasites in an ecological context (e.g. Grenfell & Bolker, 1998). Others are primarily theoretical and adapt mathematical models from epidemiology and ecology to address the origin, spread, and dynamics of diseases (e.g. Anderson & May, 1991). Here we take a macroecological approach to human disease and highlight where such a perspective might be especially informative. We focus on the ecology of humans as hosts, the ecology of human parasites and pathogens, and the implications of global change.

As hosts, humans display three important macroscopic patterns: (i) as humans spread geographically, they take along some parasites and pathogens; (ii) as humans colonize new areas, they encounter new organisms, including new pathogens, new parasites, and new alternative hosts for existing pathogens and parasites; and (iii) as agriculture and industrialization have increased human population density and frequency of contact they have drastically affected the ecology of disease. Within the last 50,000 years, anatomically modern humans have migrated out of Africa and spread across Eurasia, Australia, and the Americas. As humans colonized temperate latitudes, they left behind many tropical diseases but brought along others, such as cholera (Lafferty, 2009). More recently, migrating Eurasian populations spread their diseases to previously unexposed populations, causing devastating epidemics. As population density increased with increasing agriculture and urbanization, the number and frequency of diseases increased as new emerging pathogens switched from wild and domesticated animals to humans and as vectors such as mosquitoes and fleas transmitted pathogens between denser and more- frequently infected hosts (Wolfe, Dunavan & Diamond, 2007; Barrett et al., 1998).

Relatively recent changes in human macroecology affect our role as hosts. As long-distance travel and trade networks have expanded, parasites and pathogens have crossed previously impermeable biogeographic barriers. Rising population densities have fostered the geographic spread of ‘crowd-epidemic diseases’ such as influenza and SARS (Wolfe et al., 2007). In just the last thirty years, increased contact with wild, commensal, and domesticated animals due to ecological and social changes has increased the temporal frequency and spatial scale of outbreaks of ‘zoonotic diseases’ (Wilcox & Gubler, 2005). Although advances in nutrition, public health, and medicine have generally extended average lifespans, the coevolutionary race between contemporary humans and our enemies continues unabated and is a major public health concern (Barrett et al., 1998; McMichael, 2004).

Human parasites and pathogens also display macroecological patterns, which offer novel insights into disease ecology. First, there is a latitudinal gradient in the diversity of human disease organisms, similar to the diversity gradients in animals, plants, and microbes. As shown in Figure 4, there are more diseases in the tropics than at higher latitudes (Guernier et al., 2004). Interestingly, in other primates only vector-borne parasites, and not viral diseases and helminth parasites, are most diverse in the tropics (Nunn et al., 2005). Additionally, as illustrated in Figure 4B, assemblages of pathogens form nested subsets, so that humans living at progressively higher latitudes tend to be infected with only a subset of the parasites and diseases in the tropics (Guernier et al., 2004).

A second pattern is that epidemics display 'hierarchies of infection' across gradients of population density, with infections occurring more frequently and outbreaks lasting longer in large cities (Grenfell & Bolker, 1998). Models that represent human population structure as nested hierarchies of subpopulations (see above and Figure 3B) and that incorporate realistic movements of individuals, including both small-scale movements, such as to and from work, and large-scale movements, such as international travel, capture the spatial patterns and temporal dynamics of real epidemics (e.g. Watts et al., 2005; Viboud et al., 2006).

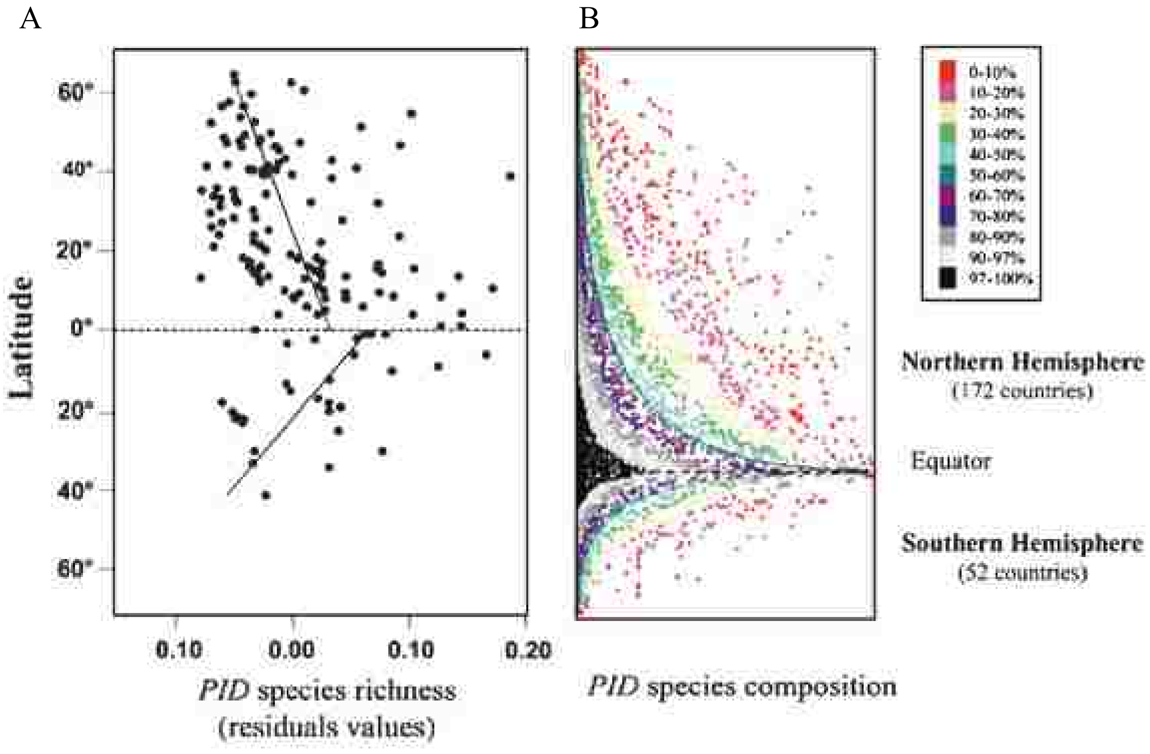

Figure 4. Human parasites and pathogens display macroecological patterns. (A) Species richness of human parasitic and infectious diseases (PIDs) is higher at tropical latitudes and higher in the northern hemisphere, with its greater land area, than in the southern hemisphere. **(B)** In both hemispheres, the relatively few disease organisms present at higher latitudes are

subsets and hence a smaller percentage of the larger number found at lower latitudes (after Guernier et al., 2004).

A third pattern is that geographic and temporal patterns of disease depend on host specificity. Many human-only diseases are globally distributed, because humans take these organisms with them as they travel around the world. By contrast, most zoonotic pathogens are regionally or even locally restricted because they depend on specific, geographically restricted reservoir hosts (Smith et al., 2007). New emerging infectious diseases are mostly zoonotic, and most of these do not become epidemic (Jones et al., 2008).

All three of these macroecological patterns of human disease—latitudinal gradients, nested hierarchies, and their joint dependence on host specificity—reflect basic ecological processes. The latitudinal gradient of pathogen diversity is strongly correlated with climatic variables, including both temperature and precipitation (Guernier et al., 2004). Warm, moist conditions are conducive to the survival and spread of diverse species of pathogens, parasites, vectors, and reservoir hosts, including birds and other mammals (see Dunn et al., 2010). Higher temperatures closer to the tropics probably speed up rates of parasite and pathogen transmission, infection, and evolution by increasing the movement and frequency of encounters, decreasing generation times, increasing mutation rates, and intensifying selection and coevolutionary arms races with hosts and competitors (see Rohde, 1992; Allen, Brown & Gillooly, 2002; Jablonski, Roy & Valentine, 2006). The nested patterns of decreasing pathogen diversity with increasing distance away from the equator likely reflect the filtering effects of increasingly stressful climates and decreasing biotic interactions on parasite, pathogen, vector, and reservoir host diversity. The differences in the geographic distributions and epidemic dynamics between human-only and zoonotic diseases (Figure 5) undoubtedly reflect differences in the abundance and distribution of *Homo sapiens* compared to the animal species that are sources of and reservoirs for diseases. Although *H. sapiens* has a population of about 7 billion and a truly cosmopolitan distribution, most of the animals that harbour zoonotics are rare or geographically restricted.

A macroecological perspective can also contribute to understanding effects of global change on human disease. By focusing on large-scale empirical patterns of abundance and distribution and seeking mechanistic theoretical explanations, macroecology complements ‘the frequently local focus of global change biology’ (Kerr, Kharouba & Currie, 2007, p. 1581). For example, a macroecological approach and metabolic perspective helps to account for observed impacts of climate change on emerging patterns of disease. WHO estimates that 6-7% of the incidence of malaria in some regions is due to recent climate change (McMichael, 2004). Other human parasites, pathogens, and vectors will undoubtedly shift their ranges with rising temperatures and changing precipitation patterns. One feature of human-caused change is biotic homogenization due to human-aided spread of invasive species (Kerr et al., 2007). We can expect that diseases, too, will become more homogenized and cosmopolitan as parasites, pathogens, and vectors expand their ranges. Macroecological perspectives that address such problems of variation and scale by drawing on comparisons across multiple pathogens and over geographic space and long periods of time should help us tackle these and other pressing questions of human disease ecology (Pascual & Bouma, 2009). For example, Guernier & Guégan (2009) found that most human parasites and pathogens conform to ‘Rapoport’s rule’, a tendency for the geographic range sizes of species living further from the equator to be larger than the ranges of species in the tropics. If temperate parasites and pathogens have larger ranges in part because they are adapted to wider climatic ranges and so can live in more places, the expansion of tropical climates with global warming may select for smaller ranges and thus higher disease diversity further from the equator.

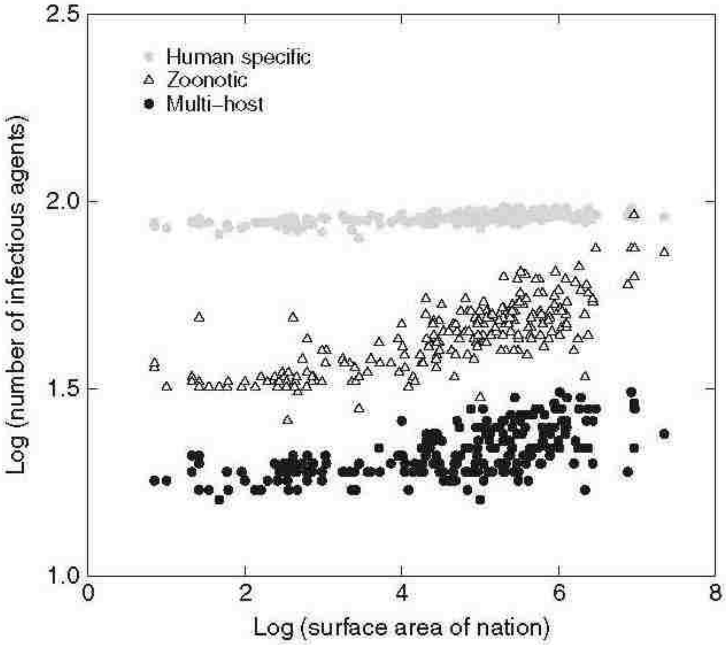

Figure 5. A plot, on logarithmic axes, of number of infectious agents as a function of country area for three host categories: human-only, zoonotic (resident in native animals with occasional outbreaks in humans), and multi-host (life history includes a stage that infects a non-human host). The invariant human-specific pattern implies that diseases with direct human-to-human transmission are cosmopolitan, whereas the positive species-area relationships in the other categories show that agents that depend on non-human hosts are more restricted geographically (after Smith et al., 2007).

Cultural and Linguistic Diversity: Echoing Biodiversity

One of the most striking features of human ecology is the similarity among the geographic patterns of diversity of indigenous human cultures and the diversity patterns of plant, animal, and microbe species. Recent studies have documented a latitudinal gradient in the diversity of aboriginal cultures and languages (e.g. Mace & Pagel, 1995; Nettle, 1998; Cashdan, 2001; Collard & Foley, 2002; Moore et al., 2002; see also Maffi, 2005). The geographic pattern mirrors species diversity of animals, plants, parasites, and pathogens, being highest in topographically diverse regions in the tropics, such as New Guinea, southern Asia, equatorial Africa, and Mesoamerica, and lowest in polar and desert regions (Figure 6). In addition to these global and continental-scale patterns, there is substantial variation at regional to local scales. This reflects the influence of cultural history, sociopolitical factors, and local environments on cultural diversification, similar to the influences of phylogenetic history and taxon-specific niche relationships on biological diversification.

Three features of the macroscopic patterns are particularly interesting. First, human cultures generally occupy non-overlapping ranges (Nettle, 1998), so the pattern is expressed in terms of density of cultures or sizes of tribal territories rather than as number of locally coexisting taxa, as for animal and plant species. Second, the patterns have been established rapidly – since modern humans expanded out of Africa about 50,000 years ago, and since they colonized the New World about 15,000 years ago (Collard & Foley, 2002). Indeed, the time since settlement "has surprisingly little effect on language diversity" (Sutherland, 2003). Patterns of cultural and linguistic diversity are also strikingly similar to patterns of human-dispersed exotic plant and animal diversity, many of which were established within just the last few centuries (Sax, 2001). Third, as would be expected from the similar geographic patterns, cultural diversity and species diversity are correlated with similar environmental variables: both are high in regions with high temperature, rainfall, topographic relief, and habitat diversity [e.g. for cultural diversity see Nettle (1998) and Cashdan (2001); for species diversity see Hawkins et al. (2003).

Are the similar patterns of cultural diversity and biodiversity generated by similar mechanistic processes? Two points seem particularly relevant. First, both cultural diversification and biological diversification are the result of a balance between coalescent processes that tend to keep a population together and disruptive processes that tend to break apart and isolate populations. Second, the same environmental variables operating in similar ways are likely to determine the balance between cohesive and divisive forces for both cultures and species. The rapid establishment and repeated, independent formation of similar latitudinal diversity gradients of human cultures and biological species on multiple continents suggest that the primary causes are ecological.

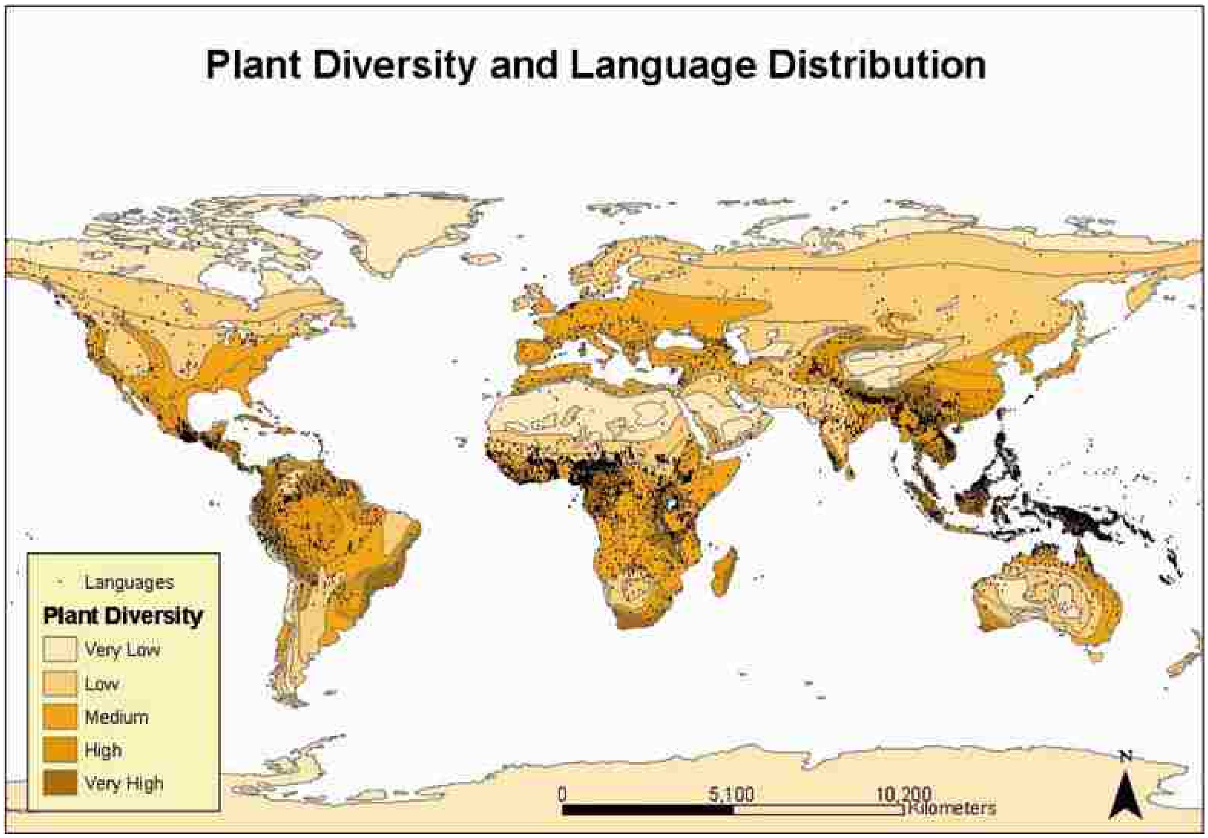

Figure 6. Human linguistic diversity compared with the diversity of vascular plant species at a global scale. Darker shades correspond to higher levels of plant species richness; each dot indicates the centre of a living language. Both human languages and plant species are most diverse in mountainous areas of the tropics [after Stepp et al. (2004), based on data from Barthlott, Lauer & Placke (1996), and Grimes (2000)].

Three classes of ecological mechanisms may strongly affect these gradients: (1) environmental heterogeneity, due to temporal variation in weather and climate and spatial variation in topography, geology, and soil; (2) biotic productivity, due to spatial variation in rates of energy, water, and nutrient supply, and (3) Red Queen kinetics, due to spatial variation in temperature, which affects rates of metabolism, ecological interactions, evolution, and coevolution with other organisms. Red Queen kinetics refers to species interactions and attendant evolutionary arms races, which tend to increase with temperature through its effect on metabolism and in which species must evolve to persist, much like Alice in *Through the Looking Glass* must run just to stay in place in the Red Queen's race (Brown et al., 2004).

Empirical evidence and theory suggest that all three mechanisms, which are not mutually exclusive, may contribute to the similar patterns among cultures and species. Both cultural and biological diversity are highest in regions of high environmental heterogeneity, especially in mountainous regions of the tropics and semitropics (Cashdan, 2001; Stepp, Castaneda & Cervone, 2005). At least two processes may contribute to this pattern. First, the occurrence of dramatically different environments in close proximity promotes differentiation based on specialization. For both cultures and species, spatial heterogeneity in abiotic conditions, habitat types, and ecological communities leads to the origin and cohesion of specialized local populations better able to tolerate the physiological stress, use the resources, and avoid the predators, parasites, and diseases in the distinctive local environments. Second, topographic relief and complex landscapes tend to create isolated and patchy environments, which have divisive effects, creating barriers, reducing migration, and promoting development of specialized populations.

Both cultural and biological diversity also tend to be high in regions of high net primary productivity, so where rates of supply of resources are high and relatively constant (Nettle, 1998; Hawkins et al., 2003; Field et al., 2008). All things being equal, more-productive environments can support more individuals per unit area. Assuming some minimum viable population size required to avoid extinction due to demographic and environmental stochasticity, more individuals can aggregate into more populations with smaller ranges, promoting greater biological and cultural diversity (Moore et al., 2002). For humans, more-productive areas also tend to have longer growing seasons, reducing variation in food supplies across the seasons and facilitating the formation of small, sedentary, specialized cultural and linguistic groups (Nettle, 1998; Smith, 2001). Intriguingly, human languages display a Rapoport's rule of increasing 'range size' with increasing distance from the equator (Mace & Pagel, 1995), much like human parasites and pathogens.

Finally, cultural diversity tends to increase exponentially with environmental temperature, just like species diversity (Figure 7). This pattern is consistent with the fact that metabolic rates increase exponentially with temperature. In warmer climates, higher metabolic rates in plants and ectothermic animals, including parasites, pathogens, and invertebrate vectors, increase rates of ecological interactions and evolutionary processes, and these in turn generate and maintain higher diversity (Rohde, 1992; Brown et al., 2004; Allen et al., 2002). Indeed, phylogenetic evidence suggests higher rates of diversification among tropical clades and palaeontological findings support the existence of higher rates of origination among tropical taxa (Mittelbach et al., 2007). Higher plant, animal, and microbial species richness and diversification rates may affect cultural and linguistic diversity in several ways. Traditional human societies have specialized vocabularies for local plants, animals, parasites, and diseases; specialized technologies and customs for food capture and processing; and specialized plant and fungal pharmacopeias. (Berlin, 1992). In addition, temperature-dependent Red Queen processes are consistent with the high incidences of parasites and diseases in tropical human, animal, and plant populations (see above and Grenfell & Dobson, 1995; Guernier et al., 2004). Limiting movements and interactions with neighbouring groups should reduce the risk of catching and spreading diseases, promoting cultural and linguistic diversification (Fincher & Thornhill, 2008). Supporting this possibility, there is a positive correlation between pathogen prevalence and the degree of collectivistic and ethnocentric values (Fincher et al., 2008) as well as a positive correlation between infectious disease diversity and the incidence of intrastate armed conflict and civil war (Letendre, Fincher & Thornhill, 2010). Broadly put, the Red Queen argument suggests that as biodiversity increases with rising temperature, there is a corresponding increase in interactions between humans and other organisms, which contributes to the diversification of cultures and languages.

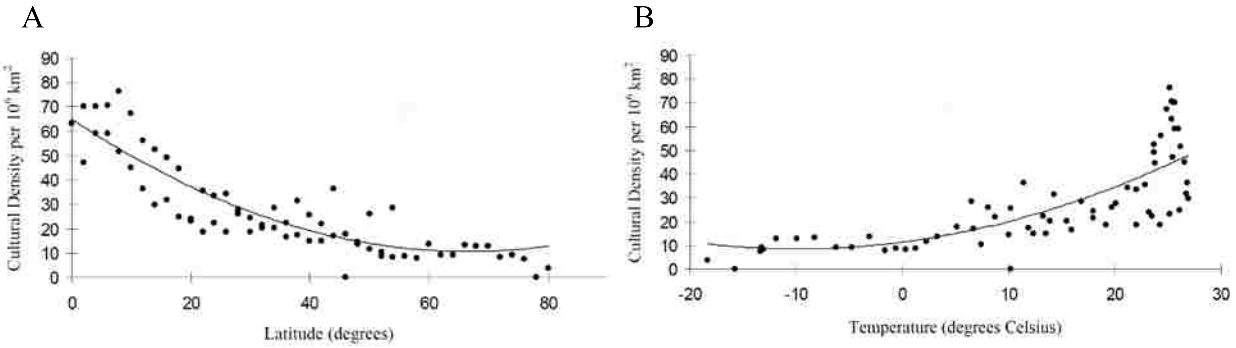

Figure 7. Latitudinal (A) and temperature (B) gradients of human cultural diversity. There is an exponential relationship between the density of cultures and environmental temperature. The exponential form of this relationship appears to be a diagnostic signal of the exponential effect of temperature on metabolic rate and consequently on "Red Queen" processes of ecological interactions and coevolutionary rates (after Collard & Foley, 2002, with one outlier removed representing tropical islands).

Industrial Metabolism: Using Energy in Modern Times

Humans evolved as hunter-gatherers, and we have seen how this ancestral context shaped macroecological patterns of cultural diversity, infectious disease, population structure, space use, life history, and foraging ecology. In just the last 10,000 years, however, the agricultural, industrial, and high-tech revolutions have introduced new socioeconomic constraints and altered old ones. These revolutions were possible because humans learned to harness non-metabolic energy, first wood and dung and now primarily fossil fuels. Human biological metabolism is about 120 W, comparable to that of other mammals of our size. But contemporary humans use much more energy, from about 300 W in hunter-gatherer societies to 11,000 W in the most developed nations (Moses & Brown, 2003; World Resources Institute, 2009). Among hunter-gatherers, this energy comes from burning biofuels such as wood and dung. Agricultural societies burn biofuels and use animal labour. The enormous non-biological metabolism of contemporary industrial societies is fueled by oil, coal, and natural gas and by nuclear, solar and hydroelectric power. The average U.S. citizen uses about 100 times more energy than his or her biological metabolism.

Does the extra-metabolic energy use affect life history? Among animals, including aboriginal humans, metabolic rate constrains the life history because all biological activity is fueled by metabolism (Brown et al., 2004). In modern societies, however, female fecundity and reproductive rates are not constrained by biological metabolism but instead vary with total energy use (Moses & Brown, 2003). Human reproductive rates are negatively correlated with *per capita* energy use across modern nations (Figure 8). Fossil fuels, by supplying extra-metabolic energy, extend the negative relationship between reproductive rate and mass-specific metabolic rate seen in other mammals, including other primates. Put quantitatively, metabolic rate, *B*, scales with body mass, *M*, as $B \propto M^{3/4}$, and fertility rate, *F*, as $F \propto M^{-1/4}$. Rearranging terms gives fertility scaling with *per capita* energy use as $F \propto B^{-1/3}$, the scaling relation seen for mammals in Figure 8.

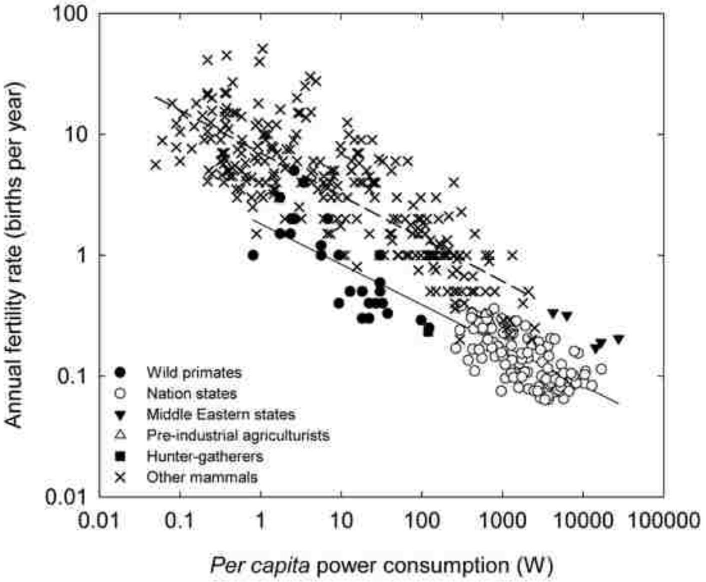

Figure 8. Fertility rate, measured as number of offspring per year versus energy use (W) in mammals. This plot, on logarithmic axes, includes data for non-primate mammals (crosses) and primates (black circles) as a function of metabolic rate as well as for modern humans as a function of energy consumed from all sources. The human data span the entire spectrum of development, from hunter-gatherers (squares) to members of the most energy-intensive nation-states (black triangles). The slope of the parallel lines, -1/3, corresponds to the theoretically predicted relationship. Note that the human pattern across nations continues the scaling relationship seen in primates (solid line) (after Moses & Brown, 2003; data from World Resources Institute, 2009).

Humans and other primates have slower life histories and lower fecundities than other mammals. The relationship between fertility rate and rate of *per capita* energy use across modern nations appears simply to extend the relationship between reproductive rate and metabolic rate in primates. As explained in Section III, metabolic rate fuels allocation to life history, leading to a predictable scaling with body size: larger organisms have slower life histories. The use of extra-metabolic energy by modern societies effectively increases *per* *capita* metabolic rate, and the non-linear scaling relationship of fecundity with energy use, $F \propto B^{-1/3}$, has led to reduced fecundity. Indeed, the total energy use from fossil fuels and other sources for a female in the U.S. today is equivalent to the metabolic rate predicted for a hypothetical 30,000 kg primate, and the average U.S. female's lifetime fertility rate is similar to what would be predicted for a primate this size. The qualitative relationship between fecundity and economic development is well known to social scientists as part of the 'demographic transition'. The metabolic perspective of macroecology provides a quantitative explanation for the drop in fertility with economic development based on life-history theory.

Given that members of wealthier and more energy-intensive societies can presumably support more children, why does human fertility drop with societal energy use? As explained above, metabolism constrains the life history by determining the energy available for offspring to grow to maturity. How much energy is required to raise a fit, competitive child in a modern industrial society? It takes far more than the 120 W of biological metabolism because of the extra-metabolic energy used to grow and transport food in distant locations; to build, heat, and cool the home; to drive to school and music lessons; to provide health care and formal education; and to supply ever more electronics and other consumer goods. In the U.S. middle class, this amounts to about $220,000 and the equivalent number of barrels of oil to raise a child to age 17 (Lino, 2010). The more energy required to raise a child, the fewer children women tend to have.

Given the analogy of industrial metabolism with biological metabolism, consider how a contemporary society is like a whole organism. Both require energy and resources, which are delivered through networks. Biological metabolism is fueled by energy-rich sugars and micronutrients delivered by vascular networks. Modern 'industrial metabolism' is fueled by energy-rich oil, coal, and natural gas and by nuclear, solar and hydroelectric power. Fuels and electricity are delivered by physical networks of pipe lines, power grids, roads, and railroads and by shipping and air traffic lanes. Recent work linking vascular networks and body size may underlie these similarities.

A theory for why metabolic rate scales sublinearly with body mass (M), as approximately $M^{3/4}$ rather than linearly as M^1, is based on the observation that larger bodies have larger networks that can deliver resources at a faster rate but not in direct proportion to their larger size. As more branches are added to a network, the network transports materials over greater distances, taking more time and requiring progressively more infrastructure. Therefore, the rate of supply of resources to cells does not keep pace, so the mass-specific metabolic rate must decrease with increasing body size (West et al., 1997; Banavar et al., 2010). This theory illustrates two key features of biological energetics: (i) diminishing returns, so that a large organism uses proportionately less energy than a small one; and (ii) economies of scale, so that a large organism requires a lower rate of energy supply per unit mass than a small organism.

We hypothesize that industrial networks are similar to biological networks in two respects. First, modern industrial networks exhibit diminishing returns in that the investment in infrastructure must increase faster than the energetic return on those investments. Second, *per capita* industrial metabolism both drives and constrains many activities in modern human societies, including the activities of the individual people that consume resources from these networks (Moses, 2009).

Diminishing returns are evident in the scaling of U.S. urban road networks (Samaniego & Moses, 2008). The *per capita* distance driven in U.S. metropolitan statistical areas (MSAs) increases with city size, but it increases less than expected for two reasons. First, population density tends to increase with metro area. Packing more people into a smaller area is an economy of scale that does not occur in organisms, where cell density does not change with body size. Second, unlike a vascular network where all blood flows out from a heart, much urban transport is decentralized—commuting to a local grocery store or gasoline station does not require driving through the city centre. To varying degrees, 'city morphology is reflected in a hierarchy of different subcenters or clusters across many scales, from the entire city to neighborhoods, organized around key economic functions' (Batty, 2008, p. 770).

Another economy of scale is evident in the relationship between *per capita* energy use and *per capita* gross domestic product (GDP) across nations. GDP is the total value of all goods and services exchanged in one year, in this case expressed in terms of $US *per capita*. As shown in Figure 9, this relationship is sublinear with an exponent close to 3/4, uncannily similar to the scaling of metabolic rate. As national economies grow and consume more energy, less energy is required to generate each additional dollar of economic activity.

The relationship between individual energy use and societal economic growth exemplifies the difficulty of distinguishing economies of scale from decreasing returns. Consider the effect of switching the axes of Figure 9. The figure makes the point that proportionately less energy is needed to fuel rising economic growth, but if the axes were reversed it would make the point that proportionately more money must be spent to produce each additional unit of energy. Clearly there are feedbacks between energy consumption and economic activity—over time, proportionately more money must be spent to extract resources (diminishing returns), but extracting resources generates proportionately more economic activity (increasing returns).

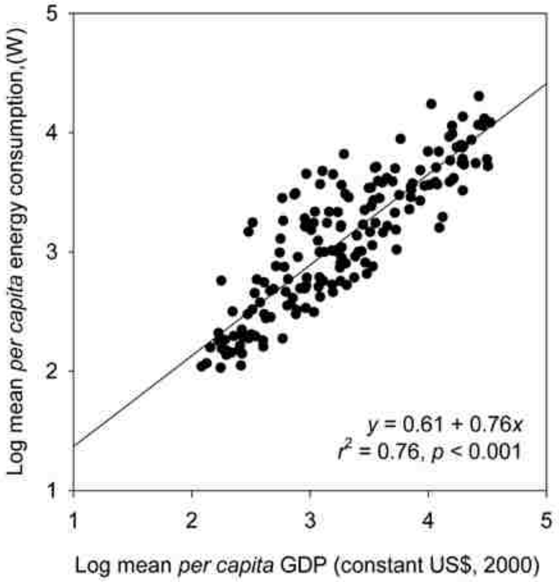

Figure 9. A plot, on logarithmic axes, of *per capita* energy consumption as a function of *per capita* gross domestic product (GDP). The energy used to support an average individual's economy scales sublinearly with GDP, with an exponent of 0.76 using ordinary least squares (OLS) regression (95% CI 0.69 – 0.82) (data from World Resources Institute, 2009, for the years 1980 to 2003). Total *per capita* energy consumption is calculated as the biological metabolism of individuals plus the energy derived from all other sources, including fossil fuels and renewables. Both sources of energy consumption were standardized by converting into W.

The trend of decreasing individual energy use with economic growth recalls similar patterns we have seen, including the economy of scale seen in the metabolism of organisms, where less energy is used per cell as body size increases. Tellingly, the scaling of energy use and economic activity in contemporary industrialized societies also recalls the economy of scale in space use with increasing population size in hunter-gatherer societies. The industrial networks that distribute energy, materials, and information are effectively modern extensions of traditional social networks, enabling people to extract and transport astronomically more resources and live at much higher population densities but at the cost of a slower life history and lower reproductive rate.

Urban Systems: Concentrating People, Energy, and Innovation

Throughout most of human history, societies were small and social relationships were based largely on kinship networks. With the transition to modern industrial societies, new networks for distributing energy, materials, and information accentuated some existing patterns while altering the socioeconomic basis of human existence. The human population, resource use, and technological and economic development have exploded on a staggering scale. What put humans on this path of ever-increasing exponential population and economic growth?

During the Paleolithic, rising population densities and attendant economic stresses promoted and accelerated cultural and technological evolution (Stiner et al., 1999; Kuhn & Stiner, 1998). Similar dynamics are now at play at an unprecedented pace. Driving this pattern is the close connection between larger human populations, concentration of people in cities, and an increasing pace of innovation, which gives access to more natural resources and fuels the positive feedbacks (Bettencourt et al., 2007*a*; Bettencourt, Lobo & West, 2009).

Cities highlight three conflicting trends driving human demands on ecological systems (Bettencourt et al., 2007*a*). First, cities concentrate people in smaller land areas, allowing economies of scale in infrastructure and social services. For example, the use of gas and electricity scales sublinearly with population size. As these efficiencies of scale are exploited, urban populations have a smaller ecological footprint *per capita*, in terms of space and resource use within a city, than the same population at a lower density. Second, urbanization spurs increased innovation, wealth creation, and attendant resource consumption

(Romer, 1986; Krugman, 1991). As shown in Figure 10, average income rises superlinearly, so that a doubling of urban population size raises the average income of residents by 10-20 % (Bettencourt et al., 2007*a*; Bettencourt, Lobo & Strumsky, 2007*b*). The number of people in ‘supercreative’ jobs also grows superlinearly, as artists, entrepreneurs, companies, and universities spur innovation. Given the economic calculus of urban life, it is not surprising that cities emerged in similar form time and again in human history (Krugman, 1991). Third and on the flip side, social ills such as incidences of violent crime and infectious disease also increase superlinearly with population density.

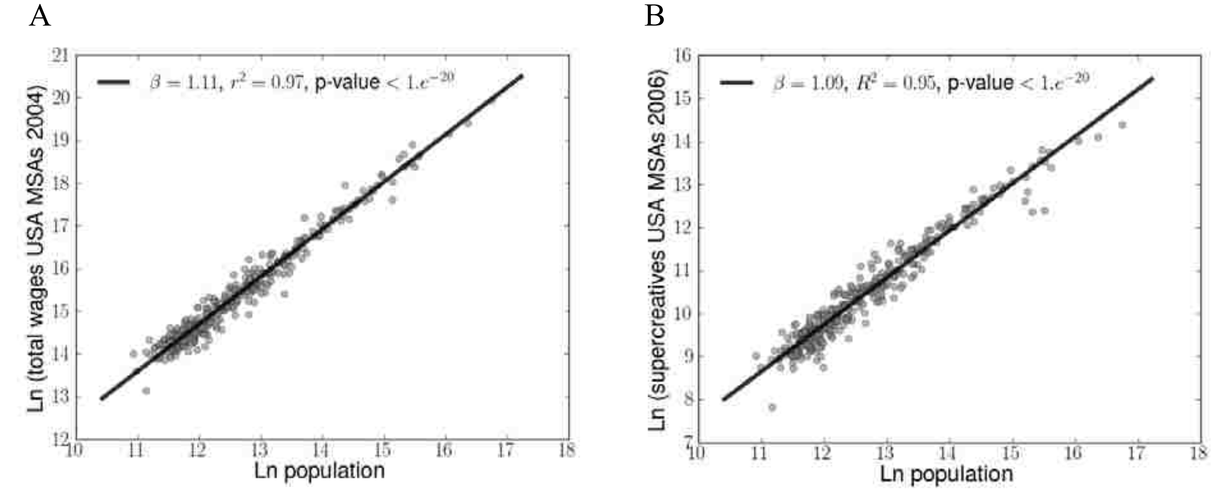

Figure 10. Examples of superlinear scaling relationships in urban systems. (A) Relationship between wages and population size in U.S. metropolitan statistical areas (MSAs), regions formally designated as cities by the U.S. government. (B) The number of people employed in ‘supercreative’ jobs, such as artists, architects, scientists, and engineers, *versus* population size within MSAs. Data are plotted on logarithmic axes and exponents, β, and r^2 values from best-fit scaling relationships are shown (after Bettencourt et al., 2007*a*).

These social changes accompany the demographic transition characteristic of economic development, the decrease in birth and death rates that follows rising wealth and cost of living. This change in life history is seen most notably in cities (Mace, 2008). Thus, urbanization affects the balance between the biological and human facets of our dual nature, enhancing sociocultural prerogatives while affecting basic metabolic and life-history parameters.

Two remarkable and universal features of human societies follow from these macroecological relationships. First, because socioeconomic quantities are rates (e.g. wages earned/person/year), their relative increase accelerates the pace of society (Bettencourt et al., 2007*a*). As a city grows, wealth creation, innovation, and other rhythms of social behaviour rise ever faster. Even the average pace that people walk increases with urban population. In essence, cities act as social accelerators. Second, because the relationships are self-similar, there are no characteristic scales at which they change qualitatively. Instead, the phenomena are power-law functions of city population size, rising superlinearly as long as urban populations grow.

There are no theoretical limits to such increasing returns with urban population size (Romer, 1986; Bettencourt et al., 2007*a*). Ecologists are familiar with growth curves that follow logistic shapes, reaching an asymptote at some environmental carrying capacity that constrains future population growth. However, human societies, and cities in particular, have repeatedly evaded resource constraints through continual innovation (Mumford, 1961). So long as the increasing returns feed back to sustain larger urban populations, then population growth will accelerate indefinitely as population size increases.

In reality, external perturbations or internal disruptions tend periodically to slow growth, resulting in punctuated, ever-shorter cycles (see Turchin, 2003). If a population grows faster than it can innovate or adapt to environmental change, then it can quickly collapse. Indeed, historians and archaeologists have documented multiple catastrophic declines and disappearances of cities and even entire societies (e.g. Mumford, 1961; Tainter, 1988; Diamond, 2005). So there are exceptions to the pattern of accelerating growth, often due to limitations of food and water supply or to outbreaks of violence and disease. Study of these cases will suggest when and why the pace of innovation was unable to keep up with the pace of growth and demand. Ultimately, it is important to reconcile this theoretical point with another, seemingly contradictory one: that it is impossible to sustain exponential growth trajectories indefinitely in a world of finite resources.

Given the Earth's finite resources and the tendency for feedbacks to increase the frequency of cyclical crises, population growth fueled by increasing returns is never stable. If the dominant mechanisms of human innovation and resource appropriation are the result of increasing returns to scale, then growth depends on continual and ever-faster adaptation. Given this caveat, what is the role of urbanization in the ecology of contemporary societies? Can the continued growth of cities contribute to rising living standards while decreasing the burden of human demands on the biosphere?

An optimistic scenario for the future of humanity offsets the seemingly unavoidable forces of urbanization with the attendant drop in fertility. Some of the most developed nations in Europe and Asia have stabilized population growth. However, they continue to urbanize, realizing increasing returns in wealth creation and innovation while exploiting economies in infrastructure and social services. Added to these advantages are opportunities to return formerly occupied land to natural habitat and to develop new technologies that may shrink *per capita* ecological footprints. A pessimistic scenario would take note that economic and population growth has been fueled by increased rates of *per capita* energy use (see above and Figure 9). So far, this energy has come predominantly from fossil fuels, which are finite and being depleted rapidly. Unless the pace of innovation can supply energy at rates required to meet the demand for continued growth, current trajectories are unsustainable.

Conclusions

1. The dual nature of *H. sapiens* is probably why most ecologists have shied away from studying our own species. Human ecology is subject to the same laws of nature that govern all living things. Human ecology is also affected by the uniquely human attributes that are the subjects of anthropology, sociology, economics, geography, and public health. Most scientists like to remain within the comfortable confines of their own discipline. Delving into human ecology means crossing the boundaries between the natural sciences and the social sciences.
2. We have tried to show how studying relationships between humans and their environments through the lens of macroecology can lead to new insights and ways of thinking. Macroecological studies use large databases and statistical methods to integrate and synthesize across large scales of space and time. Applied to humans this means studying humans as they spread out of Africa to colonize the entire world, and as they transitioned from traditional hunter-gathers harvesting local resources to maintain subsistence economies to modern industrial-technological societies harvesting fossil fuels and other resources on a global scale in an effort to sustain exponentially growing populations, cities, and economies.
3. We define human macroecology as the study of human-environment interactions across spatial and temporal scales, linking small-scale interactions with large-scale, emergent patterns and their underlying processes.

4. Macroecology has much to say about what it means to be human and about the present status and future prospects for humanity. Many of the ways that humans appear unique, as in our energetic, life-history, and cultural diversity patterns, are more matters of degree than kind and are often reflected in extensions of macroecological patterns common to other species. Others, such as the range of economies themselves, are uniquely human. Placing the scale and variation of human ecology in a grounded, mechanistic framework, one that can look across the range of human ecologies, is what differentiates this approach and what enables it to consider our dual nature in a powerfully unified manner.

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Conclusion

Metabolic constraints and opportunities influence ecological patterns at multiple scales, from interactions between insects to space use in humans. My dissertation explored the influence of metabolism on three topics. In chapter 1, “Rates of biotic interactions scale predictably with temperature,” I showed that rates of two-species biotic interactions increased characteristically with temperature and that this temperature-dependence mirrored that of metabolic rate generally. In chapter 2, “Energetics, range size, and geographic gradients of human cultural diversity,” I used multiple linear regression models to test the relative influence of environmental factors on the population size, population density, and territory size of traditional foraging societies. Colleagues and I found that primary productivity acted through trophic level to condition the demographics and space use of societies and that the indirect interactions between variables were important. In chapter 3, “Human macroecology: linking pattern and process in big-picture human ecology,” colleagues and I synthesized examples from foraging ecology to urban activity rates to highlight the insight of a macroecological approach to studying human-environment interactions.

These two studies and final synthetic piece have important implications for understanding and action in several areas of ecology. The first chapter supports the kinetics/biotic interactions hypothesis for biotic diversity gradients, the idea that faster ecological and evolutionary rates in warmer environments speed evolution and diversification at low latitudes, altitudes, and depths. The second chapter also supports the importance of temperature and rates but finds more influence for higher productivity, a function of temperature, in supporting more individuals that can populate more cultures and species. The final chapter extends the metabolic perspective and macroecological approach from the first two chapters, and especially the second, to humans more broadly. Ecologists tend to avoid humans as subjects of direct study because we are so seemingly idiosyncratic in our abilities to manipulate environments and avoid constraints and because they assume this is the purview of anthropology and other social scientists. The social scientists, in turn, rarely take a rigorous ecological view of humans and even more rarely use macroecological approaches to understand *Homo sapiens*. Human macroecology provides methodologies for integrating data and understanding to provide a wholistic, complementary view of the inherently ecological nature of the human enterprise.