
Electronic Theses and Dissertations, 2004-2019

2015

Does the Journey Matter More Than the Destination? The Contribution of Geospatial and Local Conditions to Invasive *Pomacea Maculata* Distribution Across Ranchland Wetlands

Steffan Pierre
University of Central Florida



Part of the [Biology Commons](#)

Find similar works at: <https://stars.library.ucf.edu/etd>

University of Central Florida Libraries <http://library.ucf.edu>

This Masters Thesis (Open Access) is brought to you for free and open access by STARS. It has been accepted for inclusion in Electronic Theses and Dissertations, 2004-2019 by an authorized administrator of STARS. For more information, please contact STARS@ucf.edu.

STARS Citation

Pierre, Steffan, "Does the Journey Matter More Than the Destination? The Contribution of Geospatial and Local Conditions to Invasive *Pomacea Maculata* Distribution Across Ranchland Wetlands" (2015). *Electronic Theses and Dissertations, 2004-2019*. 5153.

<https://stars.library.ucf.edu/etd/5153>

DOES THE JOURNEY MATTER MORE THAN THE DESTINATION?
THE CONTRIBUTION OF GEOSPATIAL CHARACTERISTICS AND LOCAL CONDITIONS
TO INVASIVE *POMACEA MACULATA* DISTRIBUTION
ACROSS RANGLAND WETLANDS

by

STEFFAN M. PIERRE

B.S. Colgate University, 2010

A thesis submitted in partial fulfillment of the requirements
for the degree of Master of Science
in the Department of Biology
in the College of Sciences
at the University of Central Florida
Orlando, Florida

Fall Term
2015

Major Professor:

Pedro F. Quintana-Ascencio

© Steffan M. Pierre, 2015

ABSTRACT

Geospatial characteristics such as isolation and avenues of connectivity influence an invader's pattern of dispersal and distribution. However many examinations of invasion success ignore the contribution of dispersal to patterns of invasion and focus only on the local environmental/habitat factors. This study examines the interaction of geospatial characteristics, that may influence dispersal, and local environmental factors, that may govern successful occupation, on the likelihood of invasion (invasability) of wetlands within an agriculturally modified landscape. I examined the current invasion of seasonal wetlands in south-central Florida ranchland by non-native apple snails (*Pomacea maculata* (Ampullariidae)) as a model system for understanding this interaction. I surveyed spatial occurrence of *P. maculata* in 171 wetlands in 2014 and found they occurred in 43% of wetlands surveyed. I evaluated how occurrence was related to geospatial variables (proximity to propagule sources, shoreline complexity, interwetland distance, elevation, area and ditch presence) and wetland characteristics (pH, water hardness, conductivity and soil type) for 95 wetlands. Presence of ditch connections and more neutral water pH were associated with *P. maculata* occurrence. I did not find evidence that Euclidean distance and minimum ditch distance were associated with *P. maculata* occurrence. I also performed a 5 month field experiment where I translocated snails to previously occupied and non-occupied wetlands and measured snail survival and growth (20 wetlands from November to March). This experiment evaluated if non-occurrence during survey was more likely to be associated with unfavorable habitat conditions or dispersal limitation. Wetland pH and water hardness explained variation in *P. maculata* survival, and wetland pH best explained growth. I did not find evidence that prior occupancy affected the snail survival and growth, which suggests previously unoccupied wetlands are due to dispersal limitation. These results emphasize that man-made conduits can increase permeability of the landscape, facilitating the dispersal and introduction of nonnative species and the need for the inclusion of dispersal metrics in understanding invasive species distribution.

ACKNOWLEDGMENTS

This thesis would not have been possible without the support and patience of my thesis committee. I would like to thank Dr. Elizabeth Boughton for facilitating my field research at the MAERC and for insightful feedback and guidance throughout this project. I would like to thank Dr. David Jenkins for assisting me in developing a reasonable and robustly designed experiment, and for being a grounding force during the entire process. I will also be forever indebted to my committee chair, Dr. Pedro F. Quintana-Ascencio, not only for his mentorship and guidance, but also for his unwavering trust, encouragement and support that empowered me to pursue a project along my own interests.

I am eternally grateful to all members of staff at Buck Island Ranch and Archbold Biological Station for supporting my thesis research and I am especially thankful to Dr. Hilary Swain, Dr. Elizabeth Boughton and Mr. Gene Lollis for accommodating my fieldwork and ongoing presence at the Ranch. I also genuinely appreciate the support shown by my peers at UCF and Archbold and thank them for their contributions in strengthening my overall project – with special thanks to Christen Steele, Christopher Long, Ryan Chabot, Lina Sanchez-Clavijo, John Garrett, Diana Jaramillo, Federico Borghesi and Eric Behrens for helping with field work. I would also like to acknowledge the UCF faculty members for granting me the opportunity to attend UCF and thank them for contributing to my intellectual, professional and personal growth.

Finally, I am extremely grateful for the sacrifices, patience and support provided to me by my family and my extended family that have allowed me to undertake this journey, and the many I have yet to embark upon.

*** *CERTANT OMNES SED NON OMNIBUS PALMA* ***

TABLE OF CONTENTS

| | |
|--|------|
| LIST OF FIGURES | vii |
| LIST OF TABLES | viii |
| INTRODUCTION | 1 |
| METHODS | 5 |
| Study Species and Location | 5 |
| Wetland selection..... | 7 |
| Landscape Variables | 8 |
| Local Variables | 10 |
| Presence Survey | 10 |
| Translocation Experiment..... | 12 |
| ANALYSIS..... | 15 |
| <i>P. maculata</i> presence | 15 |
| <i>P. maculata</i> Translocation Experiment..... | 15 |
| RESULTS | 17 |
| <i>P. maculata</i> distribution and presence | 17 |
| <i>P. maculata</i> Survival..... | 20 |
| <i>P. maculata</i> Growth..... | 24 |
| DISCUSSION..... | 28 |
| Conclusion | 31 |

| | |
|---|----|
| APPENDIX A: Landscape Connectivity Methods | 32 |
| APPENDIX B: Full AICc Tables and Alternative Plausible Models | 36 |
| APPENDIX C: Model Average Results | 42 |
| APPENDIX D: Script for R Analysis (R v2.15.1)..... | 44 |
| REFERENCES | 59 |

LIST OF FIGURES

| | |
|--|----|
| Figure 1 Diagram of Euclidean (red arrow) and ditch network (purple) distances..... | 7 |
| Figure 2 Spatial distribution of <i>P. maculata</i> (2014). | 17 |
| Figure 3 Graph of probability of <i>P. maculata</i> presence across measured values of pH. . | 19 |
| Figure 4 Graph of Proportional <i>P. maculata</i> survival in response to Treatment | 20 |
| Figure 5 Predicted probability of <i>P. maculata</i> survival in response to pH. | 23 |
| Figure 6 Relative change in <i>P. maculata</i> shell width across pH..... | 26 |
| Figure 7 Relative change in <i>P. maculata</i> mass across pH. | 27 |

LIST OF TABLES

| | |
|--|----|
| Table 1. Rationale for Landscape Variable/Parameter Selection..... | 9 |
| Table 2 Rationale for selected local variable and <i>P. maculata</i> response metrics | 11 |
| Table 3 Translocation Treatments..... | 12 |
| Table 4 Abbreviated Table of AIC Model Selection for <i>P. maculata</i> presence | 18 |
| Table 5 Abbreviated Table of AIC Model Selection for <i>P. maculata</i> survival | 21 |
| Table 6 Generalized Mixed model of <i>P. maculata</i> survival as explained by pH with wetland level variation for random intercept. Coefficients with SE in parentheses..... | 21 |
| Table 7 Abbreviated Table of AIC Model Selection for Relative growth in shell width (deltwidth) with wetland as random effect | 24 |
| Table 8 Abbreviated Table of AIC Model Selection for Relative growth in mass (deltmass) with wetland as random effect..... | 24 |
| Table 9 a and b. Generalized Mixed model of <i>P. maculata</i> growth in (a) shell width and (b) live mass as explained as explained by pH with wetland level variation for random intercept. Coefficients with SE in parentheses by pH..... | 25 |

INTRODUCTION

Invasion biology exists as an individual focus of ecological study, yet a precise and comprehensive definition of biological invasion remains elusive within the scientific community (MacIsaac and Colautti 2004; Blackburn et al. 2011; Richardson et al. 2000). A mechanistic definition coalesced by Valéry, Fritz, Lefeuvre, & Simberloff (2008) poses that biological invasion occurs when the natural restrictions on a species' population expansion are removed, providing the species with a competitive advantage and facilitating the species' rapid dispersal, colonization and dominance in naïve recipient localities. Thus biological invasion is a multi-tiered process that is initiated and sustained by physical translocation of organisms into novel habitat with reduced biological constraints to the species' proliferation (Valéry et al. 2008)¹. Therefore understanding dispersal can be critical for crippling a biological invasion – for without initiatory propagule movement (i.e. dispersal) can the invasion even exist?

However, the significance of dispersal to biological invasion should be evaluated relative to underlying niche factors of the invaded habitat (Ricklefs 1987; Ricklefs 2004). Invading species do not enter into an ecological vacuum, but must overcome a suite of constraining filters that reflect a complex local legacy of biogeography, evolution and stochastic events. Therefore invasions occur when and where the barrage of propagule dispersal events intersects with hospitable environmental circumstance.

Human activity further complicates the dispersal-habitat interaction, as landscape modification reduces and fragments “natural” habitat, introduces new types of land use and alters avenues of connectivity (Bilton, Freeland, and Okamura 2001). As a result, many human modified landscapes have retained fragmented and variably isolated parcels of “natural habitat” within a mosaic of potentially favorable, tolerable and inhospitable anthropogenic land uses (Diamond 1975). In accordance with Island

¹ Debatably, invasions also occur if environmental conditions change (with the species already present) and remove

Biogeography theory², the probability of a new species invading a patch of habitat increases with patch area³, and decreases with increasing patch isolation⁴ (traditionally, Euclidean distances) from a contributory source of biota (*sensu* MacArthur and Wilson 1967). However many anthropogenic land uses linearize the landscape for human efficiency. Therefore rectilinear distances (i.e. the distance between two points constrained on a grid) between habitat patches may measure functional isolation more accurately than Euclidean distances.

Despite the importance of dispersal to biological invasion, much of invasion research focuses on the local invasion filters of the establishment phase(s), examining habitat and community interactions through the lens of Ecological Niche theory (Theoharides and Dukes 2007; Lockwood, Hoopes, and Marchetti 2007). In a literature review conducted by Puth and Post (2005) examining 873 articles across 23 major journals within 10 years, only 27% of studies examined dispersal at all and only 10% were focused on initial dispersal. As highlighted by Puth and Post (2005) this lack of focus on dispersal is somewhat surprising given that the efficacy of control is highest during initial dispersal (Pimentel et al. 2000; Simberloff 2003). Furthermore, if the species is limited by processes that restrict occupation of all amenable habitat (i.e. dispersal) the full environmental niche cannot be properly defined (and used to predict invasive distribution) (Václavík and Meentemeyer 2012). To more fully understand invasion success, factors that affect *both* dispersal and establishment should be studied in tandem.

Here, I utilize an on-going invasion of the Island Apple snail (*Pomacea maculata*) in a human modified landscape to understand the relative importance of landscape factors that affect dispersal versus local wetland variables that affect invader niche requirements. I examine the 2014 spatial distribution of *Pomacea maculata* across 171 agricultural wetlands and performed survival/growth experiments in 20 wetlands to test two predictions: (1) the occurrence of the invader is affected primarily by geospatial

² Island Biogeographic theory (MacArthur and Wilson, 1967) examines the legacy of past biological invasions (of geographic islands), and has become commonly (albeit contentiously) applied to similarly “insular” contexts.

³ Due to increased likelihood of habitat heterogeneity and increased effect of passive sampling

⁴ Due to reduced likelihood of propagule arrival with increasing distance

measures compared to local relevant abiotic variables; and (2) the absence of the invader is not indicative of unsuitable habitat during the invasion. If *P. maculata* is not present in all wetland habitats and presence/absence correlates significantly with geospatial measures of dispersal, this suggests *P. maculata* presence may be due to dispersal.

Pomacea maculata Perry (Caenogastropoda: Ampullariidae) are large dioecious freshwater snails with a broad native distribution in South America (Cowie 2002). These long-lived (1-3 years) snails have the capacity to breathe air (Carlsson 2004) and routinely extend a siphon appendage to the surface to ventilate the ctenidium (respiratory organ). Their capacity for aerial respiration allows them to thrive in waters with low dissolved oxygen and permits extended foraging above the water line. They are highly fecund, producing multiple bright pink egg clusters per breeding season (consisting of hundreds of eggs) which they oviposit on emergent structures (Morrison and Hay 2010; Kyle, Kropf, and Burks 2011; Seuffert and Martín 2009). However they are heavily dependent on calcium for shell growth and egg deposition, and low snail densities have been associated with relatively low water hardness and low water pH (Glass and Darby 2008). Established populations of non-native *Pomacea* apple snails have been documented to completely denude large swaths of commercially valuable agricultural crops in many South East Asian nations and are inferred to be a significant potential threat to nutrient dynamics in endemic freshwater ecosystems (Wada et al. 2004; Carlsson 2004; Rawlings et al. 2007b). Given their prodigious capacity for reproduction, and their potential to modify novel habitat, the IUCN's Global Invasive Species Program Database lists *Pomacea* snails among the world's most invasive species (Lowe, Browne, and Boudjelas 2004).

I predict that minimum ditch network distances (i.e. rectilinear distances) might be strongly related to *P. maculata* presence. This hypothesis is predicated on the observation that passive buoyant dispersal in the direction of water flow (as free floating individuals or attached to floating vegetative material) has been the prominent mechanism of rapid dispersal observed on the MAERC and in the literature for *P. maculata*

(Ostrom and Chesnes 2014; Cowie 2002). However, *P. maculata* could follow a more Euclidean (straight line) net dispersal pattern from initial source populations into MAERC wetlands during the peak of the wet season and following especially heavy precipitation events, when flood conditions connect wetlands that are usually separated. Alternatively, long distance dispersal has been inferred for pulmonate gastropods, where individuals hitch-hike on or are excreted alive by birds and mammals (Van Leeuwen et al. 2013; S. Wada, Kawakami, and Chiba 2012). *P. maculata* could potentially be vectored between wetlands as neonate passengers on visiting waterfowl. Examining *P. maculata* presence in relation to isolation may provide support for these alternative dispersal mechanisms.

Physiologically-relevant local variables (pH, water hardness, soil type and conductivity) may also influence *P. maculata* presence. Therefore *P. maculata* presence/absence could be due to dispersal limitation and/or habitat suitability. To differentiate unsuitable wetland habitat from inaccessible (or unaccessed) wetland habitat, I performed a five month persistence and growth field experiment. I experimentally introduced *P. maculata* snails to (1) wetlands where *P. maculata* were previously found and (2) wetlands where *P. maculata* were not found. If survival and growth are not statistically different, then *P. maculata* absence is likely due to dispersal limitation. This supports the first prediction that dispersal measures are valid predictors of *P. maculata* presence. If survival and growth in occupied wetlands significantly exceeded that in unoccupied wetlands, then local conditions would be responsible for distribution.

I expected that *P. maculata* absence is more likely due to dispersal limitation, and predicted there would not be significant differences in growth and survival across wetlands with previous *P. maculata* presence versus *P. maculata* absence. Additionally, I hypothesize that local wetland pH will be the most significant predictor of snail survival and growth based on prior information that highlights the importance of pH conditions on the growth rate and overall health of snails in genus *Pomacea* due to their calcareous protective shells (Seuffert and Martín 2013; Glass and Darby 2008)

METHODS

Study Species and Location

I selected a model system that readily provided me with the following components:

1. The spatial distribution of a relatively non-cryptic, dispersal limited organism
2. An invasive species that is not yet in equilibrium with the environment
3. A landscape with a clear documented gradient of environmental conditions
4. A landscape of fragmented habitat with different potential dispersal distances from original point sources to invadable habitat patch.

I capitalized on the current, ongoing invasion of the MacArthur Agro-Ecology Research Center (MAERC) in Lake Placid, Florida (lat 27°09'N; long 81°12'W) by the invasive apple snail *Pomacea maculata* (Ampullariidae). This invasive apple snail, native to South America (wide distribution; Argentina, Brazil and Uruguay) has been documented in Florida since the late 1990s (Hayes et al. 2012; Rawlings et al. 2007a), but was only observed in peripheral MAERC wetlands within the last 3 years. Therefore the invasion front had not completely passed through the MAERC, as the invasion was ongoing. Wetland occupation by *P. maculata* can be determined by the presence of shells (remnant or alive) of this large robust snail which forages above the waterline, as well as its highly visible egg clusters (bright pink) which are oviposited on emergent structures (Andrews, 1965; Seuffert and Martin, 2009). The only visually-similar mollusk found in the area, the native Florida apple snail (*P. paludosa*), is not documented to occur within MAERC waterway, and its egg clusters are markedly different in egg size, density and color from those of *P. maculata*.

The MAERC, is a 4170-ha working cattle ranch that encompasses >600 wetlands (0.01 to 41.9 ha) with varying levels of disturbance, spatial isolation, depth profiles and interconnectivity via a pervasive

network of ditches and irrigation structures. We hypothesize that the point sources of invasive *P. maculata* into the MAERC are nodes of connection between MAERC ditches and Harney Pond Canal (See Figure 1) which connects Lake Istokpoga and Lake Okeechobee. The wetlands themselves are embedded in a complex matrix of intensively managed and *semi-natural* pasture lands that are stocked with cattle as determined by current agricultural management practices (Bohlen et al. 2009). The intensively pasture lands are seeded with non-native Bahia grass (*Paspalum notatum*), fertilized (N only), irrigated, burned and importantly for this study, limed. The semi-natural pastures are considerably less intensively managed – with occasional burning to prevent shrub and tree encroachment and infrequent irrigation. The predominant wetland vegetation in the intensively managed pastures is *Juncus effusus*, whereas the semi-natural pasture wetlands have a wider variety of emergent macrophytes, graminoids such as *Panicum hemitomon* and a diverse wet prairie assemblage on the periphery. Please refer to Boughton et al. (2010) for further information on MAERC wetland floral assemblages.

Wetland selection

Studied wetlands were chosen via a stratified random design to encompass variation in environmental conditions and spatial coverage of the MAERC. All wetlands within MAERC property boundaries (*ca.* 600 wetlands) were ordered independently according to (1) Euclidean distances and (2) wetland ditch distances (rectilinear distance) (Figure 1) from initial point sources of *P. maculata* (calculated in ArcGIS) and stratified into quartiles. I randomly selected 200 wetlands (50 wetlands per quartile) that were examined for study suitability. Each of the 200 wetlands was surveyed at least twice between June and September 2014. Some wetlands were excluded from the presence survey due to ambiguous wetland boundaries, ambiguous ditch connectivity, excessive cattle disturbance or prohibitively large survey area. As a result presence/absence data was collected for 171 wetlands that were thoroughly surveyed for *P. maculata* presence. However no wetland biophysical measurements were taken if water level was below ~ 30cm depth due to inconsistent probe readings. Therefore the final sample size for water chemistry analysis was 95 wetlands (approx. 1/6 of MAERC wetlands).

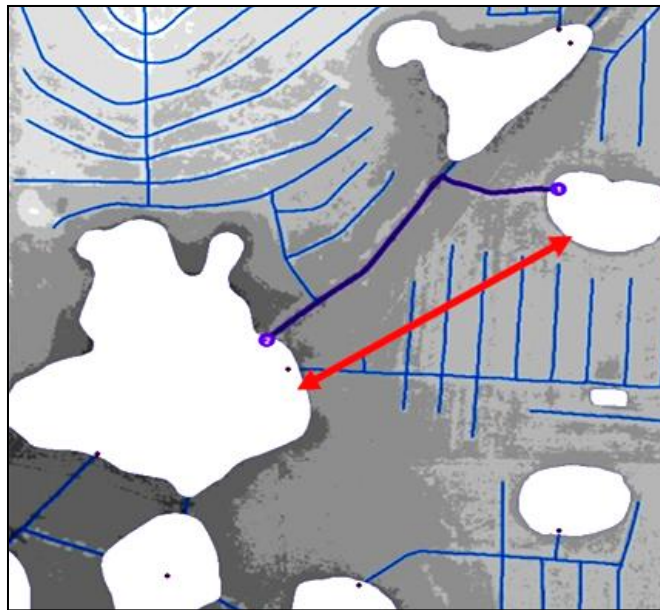


Figure 1 Diagram of Euclidean (red arrow) and ditch network (purple) distances

Landscape Variables

Buck Island Ranch (MAERC) GIS shapefiles (wetlands, roads and ditches), LiDAR Digital Elevation Model (DEM) and color aerial orthoimages were obtained from Archbold Biological Station GIS database. Perimeter and area calculations are contained in the attribute table of the shapefiles, calculated with the *Calculate Geometry* tool from the digitized wetlands. The MAERC ditch network shapefile was projected over the orthoimages to clean up the ditch network connectivity. Ditches that were found to be missing (via viewing the aerial images or ground truthing) were digitized when necessary and connectivity of the ditches was corrected for analysis. Ditch network and wetland shapefiles were used to calculate Euclidean and ditch network distance metrics from Harney Pond Canal sources of *P. maculata* (Table 1). Comprehensive landscape metric methodology can be found in Appendix I.

Table 1. Rationale for Landscape Variable/Parameter Selection

| Variable Description | Rationale for inclusion | *Variable Name |
|--|--|-----------------|
| Count of ditch entry points into wetland | The number of entry points to specified wetland (ditches entering wetland) may influence propagule pressure | WetInfloCount |
| Wetland ditch presence | Binary categorical: Wetland has ditch (Yes or No) | Xinflo |
| Minimum Euclidean distance from Harney Pond Canal inflows | Euclidean nearest neighbor distance between originating point source on Harney Pond and the focal wetlands. | MinEuc |
| Minimum elevation of wetland inflows or perimeter | The elevation of the wetland. This influences the water flow direction and volume from originating point source. Elevation of inflow points used for wetlands with ditches. For wetlands without ditches, 10 random perimeter elevation points selected from which the minimum and average extracted.(max std. dev for 10 points = 0.3m) | MinElev |
| Average elevation of the wetland inflows or perimeter | | AveElev |
| Minimum ditch distance from point source to wetland (“rectilinear” nearest neighbor) | Distances via ditch network between the originating point source and the recipient wetland. | MinDitchDist |
| Average ditch distance across all possible routes to wetland | Wetlands at closer distance to point source should be more likely to receive propagules. | AveDitchDist |
| Average total distance for all possible ditches to wetland | A value of 0.0 indicates no ditches from point source to recipient wetland – and NOT that the recipient wetland is really close/attached to the source. | AveSumDitchDist |
| Minimum total distance for all possible ditches to wetland | | MinSumDitchDist |
| Perimeter of wetland | An estimate of the edge area/littoral habitat which is preferred by genus <i>Pomacea</i> | Perimeter |
| Wetland area in hectares | Area available for plant growth and snail occupation. | AreaHA |
| Interwetland distances | Measurement of Euclidean inter-wetland distances which is a commonly used metric for the effects of wetland proximity on wetland composition. | Hanski Index |
| Minimum Ditch Distance x Perimeter/Area | Minimum ditch distance multiplied by the Shoreline complexity (Perimeter/Area) as a measure of the littoral habitat preferred by snails | MyIndex |

*Variable Name column include to facilitate understanding of R script used for analysis

Local Variables

Prior to conducting *P. maculata* presence surveys, I collected the following wetland biophysical parameters using YSI Professional Series Probe (equipped with Quattro sonde): pH, Conductivity, temperature and dissolved oxygen. Measured variables were within the ranges found in other Florida wetlands (Reiss 2006) and long term MAERC water quality datasets. YSI probe measurements and complementary grab water samples were taken only when standing water exceeded 30cm. Grab samples were preserved in the field (2mL HNO₃ per sample) and maintained around 4°C. These samples were later prepared and analyzed for water hardness (combined calcium and magnesium content) using YSI 9500 EcoSense photometer and Palintest Water Hardness Test (Hardicol) reagents.

Presence Survey

Survey protocol consisted of traversing the entire wetland perimeter looking for the bright pink *P. maculata* egg clusters on emergent structures, while simultaneously “trawling” a D-frame invertebrate dip net at approximately 30cm depth, until evidence of *P. maculata* presence was observed. The dip net was examined approximately every 10m, or whenever resistance from collected debris impeded easy movement. Two transects were conducted perpendicular to the bathymetric gradient⁵ through any central emergent wetland vegetation (haphazard direction). Sightings of egg clusters (or remnants thereof), empty shells or intact *P. maculata* snails (dead or alive) in the wetland, in the dip net or within 2m of the perimeter were accepted as evidence of *P. maculata* presence in the wetland. Shells had to be intact and not clustered (separated by at least 10m) to avoid predation middens, where snails collected from other wetlands may have been eaten, and their shells deposited. No snails or other biota were removed from the wetlands during surveying.

⁵ South Florida landscape has relatively limited topographical relief. Thus bathymetric gradient is shallow

Table 2 Rationale for selected local variable and *P. maculata* response metrics

| Response metric description | Rationale for use | *Variable Name |
|---|---|----------------|
| Survival | Survival in response to enclosure wetland conditions | alive |
| Relative growth (width) | Increase in shell perpendicular to collumellar axis attributed to enclosure wetland conditions | deltwidth |
| Relative growth (mass) | Increase in intact snail (blotted dry) mass attributed to enclosure wetland conditions | deltmass |
| Variable Description | Rationale for inclusion | *Variable Name |
| Wetland water pH prior to enclosure snail introduction | Wetland water pH conditions measured prior to snail introduction. Snail health and calcareous shell deposition and erosion affected by lower pH | phpre |
| Estimate of water hardness | The availability of dissolved calcium for snail uptake may influence snail shell deposition and growth ; buffering capacity of water | calc |
| Pasture type | Wetland in intensively managed pastures may have higher nutrient load and calcium content than semi-natural pasture | pastype |
| Soil Category | Categorization of wetlands according to soil type. Wetland substrate may influence aquatic conditions and ability to aestivate | soilcat |
| Conspecific snail presence prior to enclosure placement | The previous presence of <i>P. maculata</i> . The prior presence of conspecifics may induce growth effects on enclosure snails | presnails |
| Wetland Identification number | Included to highlight if there is an unidentified wetland variable that may have explanatory power | wetid |

*Variable Name column included to facilitate understanding of R script used for analysis

Translocation Experiment

This experiment evaluated if *P. maculata* absence was better explained by habitat or by dispersal limitation. Local wetland variables considered for investigation were (1) pH, (2) estimated water hardness, (3) previous presence/current occupation by conspecific apple snails, (4) pasture type, (5) soil type and (6) wetland identification number (Table 2). I split the surveyed wetlands into four (4) treatments according to *P. maculata* presence (*present* or *absent* (control); as determined by presence surveys) and pasture type (*semi-natural* or *intensively managed*). Within each treatment, I randomly selected six wetlands from a stratification of pH values, measured during survey (

Table 3). I built completely enclosed, rectangular wire mesh enclosures (1.0 x 0.5m) that were placed into each of these 24 wetlands. The wire mesh retained snails in a quarantined area away from large predators, provided access to environmental conditions, and prevented permanent introduction of *P. maculata* to previously unoccupied wetlands. A representative sample of neighboring wetland vegetation that would have been displaced by the enclosure was placed in the enclosure.

Table 3 Translocation Treatments

| VARIABLE and LEVELS | Recipient Site | Pasture Type | pH |
|---------------------|--------------------|--------------|---------|
| | Previously present | Improved | High pH |
| Replicates: 3 | Previously absent | Semi-Native | Low pH |
| n = 24 wetlands | 2 | 2 | 2 |

A maximum density of 1 snail per 8 liter volume is recommended in captive breeding repopulation programs to avoid significant density dependent growth effects within this genus (Conner, Pomory, and Darby 2008). The submerged volume of each enclosure would therefore allow for a maximum of 30 snails (under laboratory conditions) without density dependent effects. I reduced the potential for density dependent effects by placing 3 snails in each enclosure. All experimentally placed *P. maculata* were reared from MAERC egg clusters (7 clusters collected in the field). All snails selected for the experiment were estimated to be roughly the same age, as neonate emergence from all clusters occurred within a period of 2 weeks. All snails were kept in equal conditions for 8 months prior to wetland enclosure introduction and were larger than enclosure mesh size at experimental start. All captive born snails remained naïve to wetland vegetation until their introduction to enclosures.

I measured snail morphometry using standardized metrics as suggested by (Youens and Burks 2008) to establish baseline condition prior to wetland introduction. To facilitate identification of individual snails, the snails' shells were marked with identifying numbers using a non-toxic liquid correction pen ("white out") and cyanoacrylate sealant. I measured shell width, and shell length using a digital micrometer and snail mass (blotted wet live weight; in g) using a digital balance. I used shell width, as the preferred linear measurement (operculum width in Burks, Hensley, and Kyle 2011) and mass for analysis to facilitate comparison across studies. Shell width (21.6 \pm 4.7mm; mean \pm SD) of the reared snails displayed less variation than mass (14.6 \pm 8.6g; mean \pm SD).

There was no standardized size-maturity class assignment for *P. maculata* (Burks, Hensley, and Kyle 2011). However in accordance with the morphometric work of (Youens and Burks 2008) the snails selected for use were classified as juvenile *individuals*, with "early" juveniles (<21 mm shell width;) and "late juveniles (> 21mm). No egg clusters were observed during the course of this study, which supported the assertion that snails were all juveniles.

The three snails introduced into each of the enclosures (72 total) were haphazardly selected from size classes to achieve standardization of total snail biomass across enclosures ($43.6 + 8.43\text{g}$ (mean +SD)). Enclosures were checked biweekly for egg mass deposition and to ensure the enclosures remained intact and upright. Snail growth and survival were assessed after five months (October through February), after the coldest weather (frost) of the 2014 South Florida winter season. Enclosures were opened and the vegetative and soil contents were sifted through until snails were located. Closing or further withdrawal of closed operculum when prodded indicated survival. All previous growth measurements (including blotted wet weight, where possible) were repeated with collected snails. Change in measurement from baseline was indicative of growth.

ANALYSIS

For each model evaluated, residuals of the parameters were plotted and inspected to ensure homogeneity of variance. Correlation plots were examined to ensure no collinearity of variables. All statistical analyses were performed using the R software package (R Development Core Team, 2010, v2.15.1) and all plots were generated using the ggplot2 R package (Wickham 2008). All models were designed to identify if local variables and landscape metrics influenced *P. maculata* presence in wetlands, and test hypotheses determined to be important from the literature.

P. maculata presence

I used logistic regression to assess the probability of *P. maculata* presence as a function of connectivity metrics and local variables in the surveyed wetlands. All models evaluating presence were general linear models with binomial errors and a logit link, using the lme4 package in R (Bates, Maechler, and Bolker 2013). Twenty (20) alternative models using predictor variables summarized in Tables 1 & 2 were compared against the null model using information-theoretic model selection based on the corrected Akaike Information Criterion and utilizing the AICcmodavg package in R (Marc J. Mazerolle 2015). Exploratory investigations showed ditch presence (as a geospatial variable) influenced the effect of pH on snail presence. The only interactive models considered examined the interaction between ditch presence and other local wetland variables.

P. maculata Translocation Experiment

I used AICc-based model selection of logistic regressions to determine which experimental variables (Table 2) best accounted for survival probability of *P. maculata*. Logistic regressions were generalized mixed models (with binomial errors and a logit link) using the nlme R package (Bliese 2005). The null model was included for comparison and 10 models were considered. Given the importance of pH and

calcium from the literature, additive effects were considered between pH, calcium and other remaining local variables.

I evaluated the effect of pH, water hardness, pasture type and soil type on snail growth with a model selection framework (as above) to predict growth using a linear mixed models (with Gaussian errors), where wetland was a random effect. These analyses used the nlme R package (Bliese 2005). The null model was included for comparison.

RESULTS

P. maculata distribution and presence

My survey of wetlands encompassed roughly $\frac{1}{4}$ of MAERC wetlands. Of the 171 wetlands included in the presence survey, 43% (73) wetlands indicated presence of *Pomacea maculata* (Figure 2).

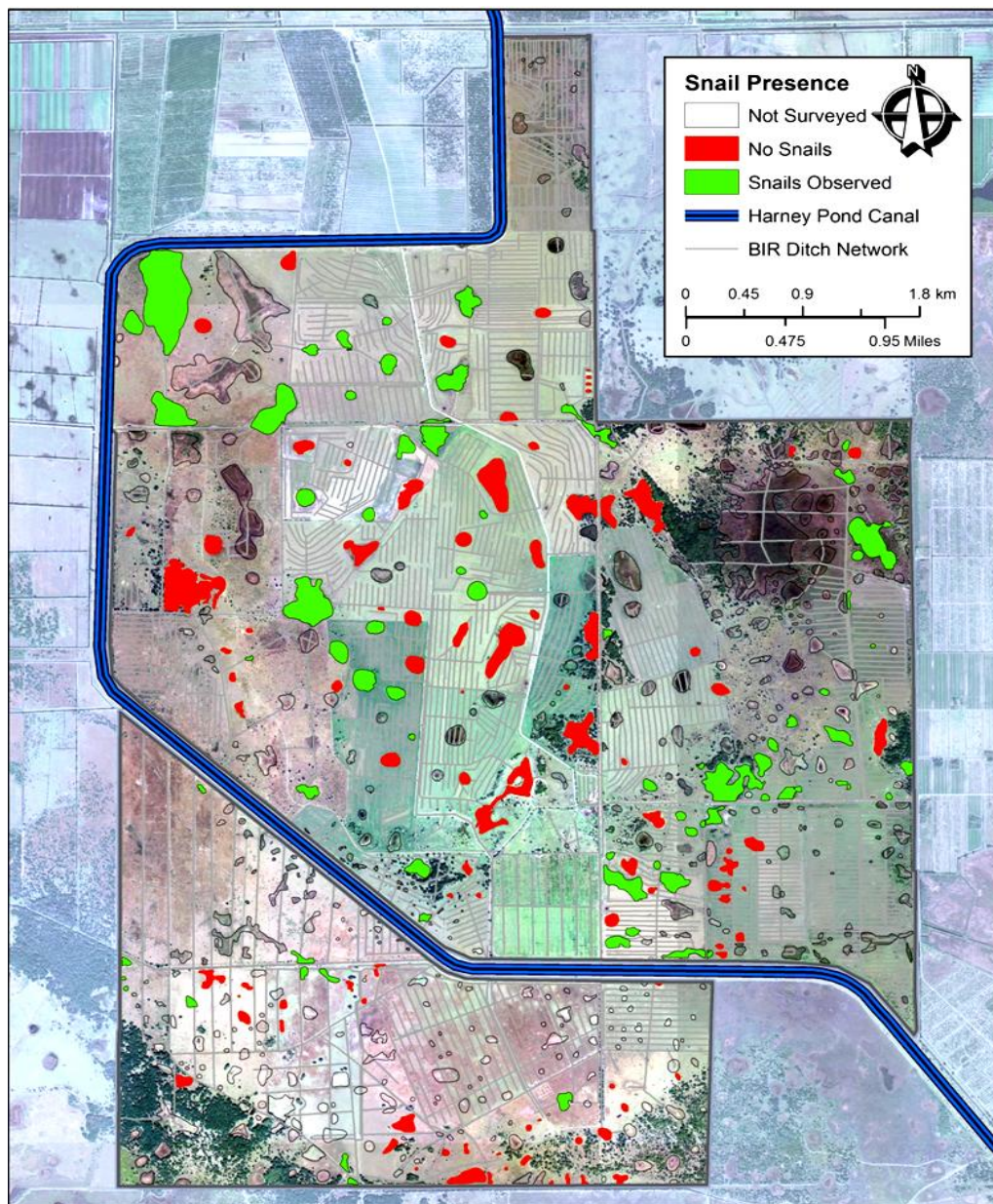


Figure 2 Spatial distribution of *P. maculata* (2014).

Results from the AICc model selection revealed that the most plausible models for *P. maculata* presence included ditch presence (

Table 4; for full table see Appendix B)

Table 4 Abbreviated Table of AIC Model Selection for *P. maculata* presence

| | Model Names | K | AICc | Delta_AICc | AICcWeight |
|---|--|---|--------|------------|------------|
| | Presence ~ Ditch+pH | 3 | 102.56 | 0.00 | 0.68 |
| | Presence ~ Ditch*pH | 4 | 104.16 | 1.60 | 0.30 |
| | Presence ~ Ditch+Conductivity | 3 | 113.06 | 10.50 | 0.00 |
| | Presence ~ Ditch | 2 | 113.28 | 10.73 | 0.00 |
| * | Presence ~ Ditch + Ditch:MinimumDitchDist | 3 | 113.98 | 11.42 | 0.00 |
| | Presence ~ 1 | 1 | 133.73 | 31.17 | 0.00 |

*Not all wetlands have ditches. Xinflo + MinDitchDist is specified as Xinflo + Xinflo:MinDitchDist

Roughly 1/3 of all MAERC wetlands do not have connection to the ditch network (32.7% according to the criteria of this study). The sampled wetlands also approximate this ratio – 95 wetlands observed extensively, with 28 wetlands lacking a direct connection to the ditch network (29.4%). Of the 28 wetlands without direct ditch connectivity, 4 of these wetlands showed evidence of *P. maculata* presence (14.2%). This contrasts with the 67 wetlands with direct ditch connectivity, of which 44 wetlands (67%) showed evidence of *P. maculata* presence. Euclidean and minimum ditch distances from point sources were not significant predictors for *P. maculata* presence in this study.

Wetlands without ditches had a lower probability of *P. maculata* occurrence compared to wetlands with ditches (upper curve; Figure 3). The probability of *P. maculata* presence decreased as wetland acidity increased, with observed individuals found only in wetlands with pH higher than 4.0. The range in pH observed in this study is representative of water samples taken previously within Buck Island Ranch and is comparable with other Florida wetland pH studies (Reiss 2006).

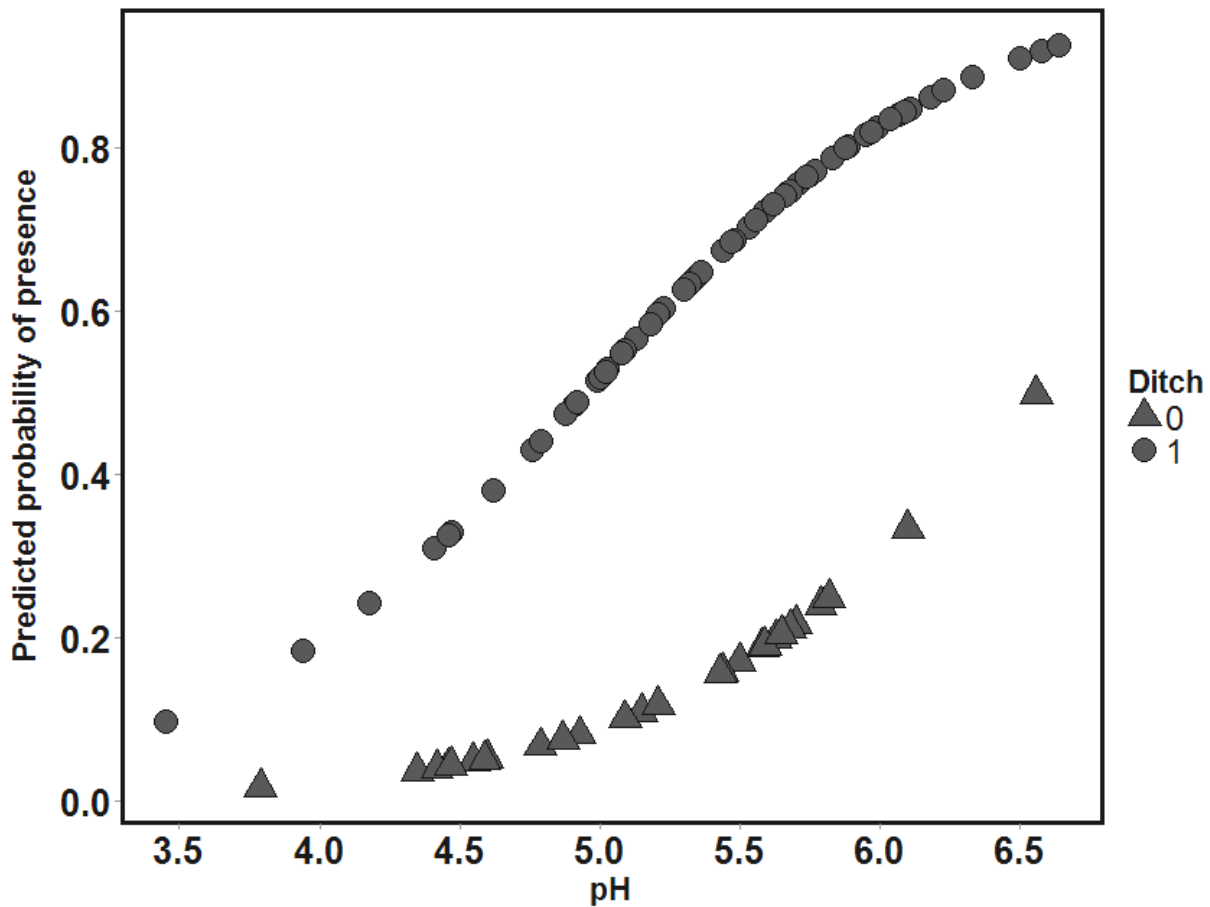
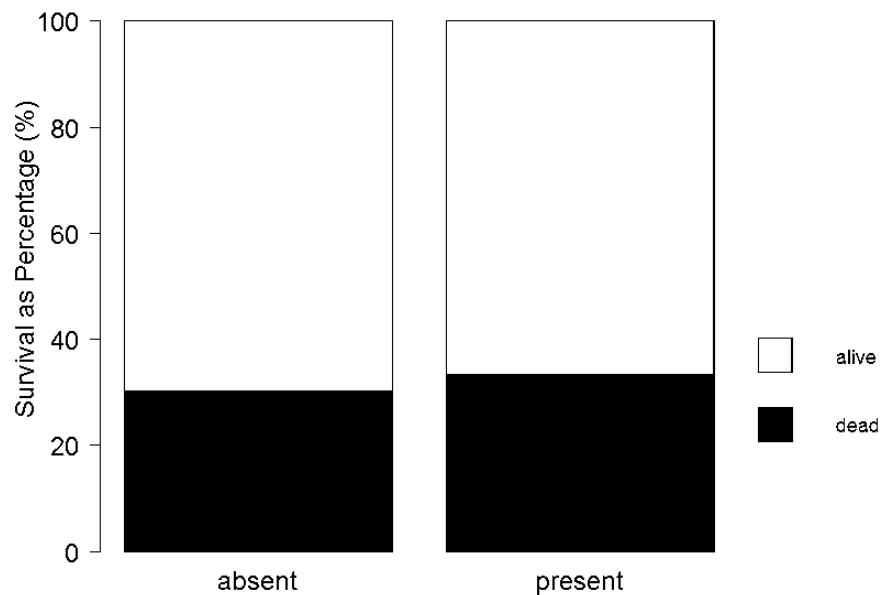


Figure 3 Graph of probability of *P. maculata* presence across measured values of pH. .

The probability of snail presence also increases with wetland pH. Wetlands without ditches (filled triangles) had a lower likelihood of snail occurrence than wetlands with ditches (filled circles).

P. maculata Survival

I recovered 20 cages without damage (4 cages were damaged by cattle) that contained 60 snails in total, 41 of which were found alive at the end of the enclosure experiment (Figure 4). Three individuals were not present in intact enclosures when checked. I presumed these snails died and all traces of their shells to be consumed. Sixteen other snail deaths as evidenced by empty shells. Seven of these snails were dead on the substrate surface, with attached operculum and the soft body tissue retained within intact shell. As crayfish (often found trapped within cages), and conspecific apple snails will readily scavenge the rapidly decomposing soft tissues, these snails were considered to have died within a very short period preceding cage removal. It is assumed that these snails died as the result of a frost event prior to data collection.



| | Wetlands without snails | Wetlands with snails |
|---|-------------------------|----------------------|
| Recovered Alive | 23 | 18 |
| Recovered Dead | 10 | 09 |
| Total Recovered | 33 | 17 |

Figure 4 Graph of Proportional *P. maculata* survival in response to Treatment

AICc Model selection of *P. maculata* survival revealed that “wetland pH” and “wetland pH and water hardness” were almost equally plausible predictors for *P. maculata* survival (Table 5). Examination of the model averaged coefficients for all plausible models (Delta AICc less than 2) indicated that pH was the only variable with a coefficient that was statistically different from 0. pH was 12 times more important than hardness, and 4 times more important than previous snail presence (APPENDIX C: Model Average Results). All other plausible models contained pH, so for parsimony I chose to examine “wetland pH” as the explanatory variable. The summary of the “wetland pH” model is provided below (Table 6). Summary of the alternatively plausible model, “wetland pH and water hardness” is provided in Appendix B.

Table 5 Abbreviated Table of AIC Model Selection for *P. maculata* survival (with random effect of wetland)

| Model Names | K | AICc | Delta_AICc | AICcWeight |
|--|---|------|------------|------------|
| alive ~ pH + random | 3 | 65.9 | 0.00 | 0.30 |
| alive ~ pH + hardness + random | 4 | 66.0 | 0.13 | 0.28 |
| alive ~ pH + previous snails + random | 4 | 67.4 | 1.47 | 0.14 |
| alive ~ pH + pasture type+ random | 4 | 67.8 | 1.90 | 0.12 |
| alive ~ pH + pasture type+ calc + random | 5 | 67.9 | 2.04 | 0.11 |

Table 6 Generalized Mixed model of *P. maculata* survival as explained by pH with wetland level variation for random intercept. Coefficients with SE in parentheses

| Parameter | Estimate using REML |
|----------------------------------|---------------------------|
| Fixed intercept | -8.6 ^{**} (1.05) |
| Fixed slope of pH | 1.76 ^{**} (0.58) |
| Variance due to random intercept | 0.37 |
| Residual | 0.61 |
| AIC | 65.47 |
| BIC | 71.76 |
| Observations | 60 |

Note: * p<0.1; ** p<0.05; *** p<0.01

The graphical representation of probability of *P. maculata* survival with pH (

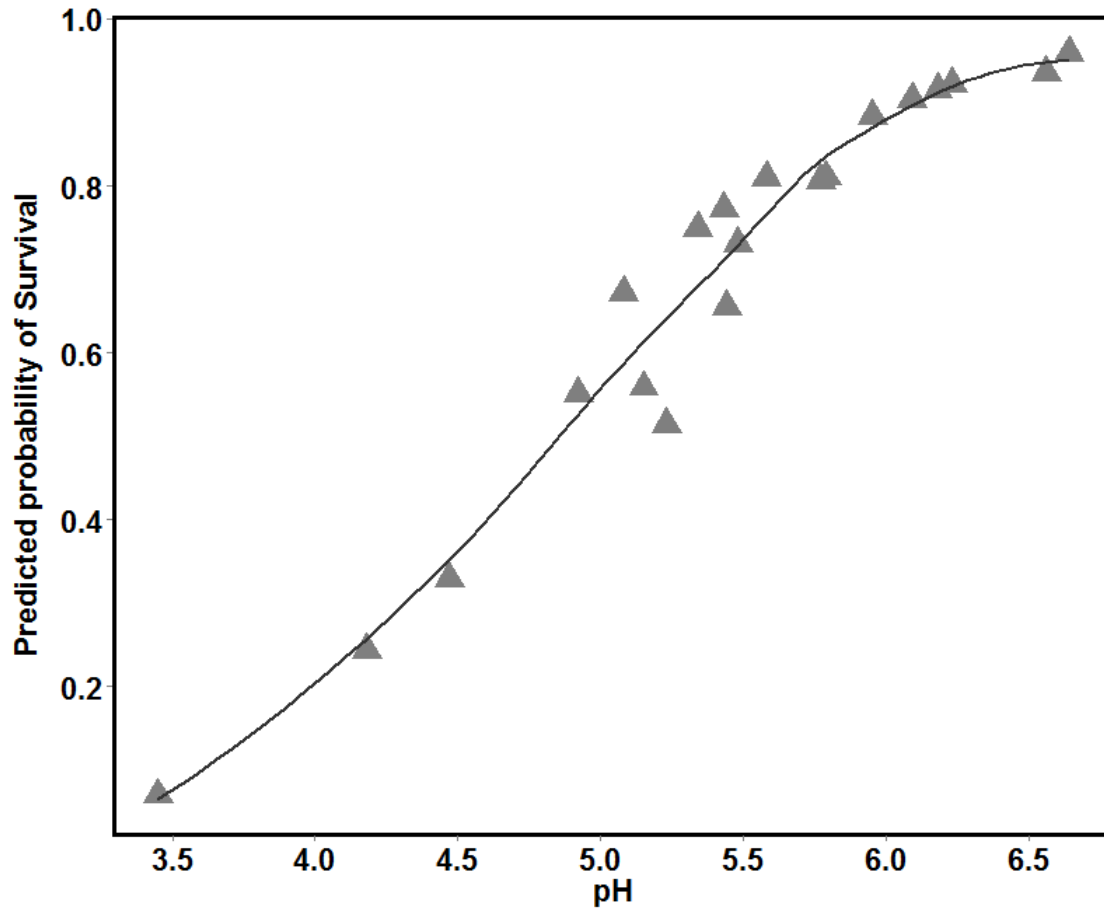


Figure 5) shows probability of survival to be increased at more neutral wetland pH. The omega coefficient, Ω_0^2 (Xu 2003), an estimate of the dependent variance accounted for by the independent variable within the mixed model for survival (i.e., the fit; comparable to R^2) was 0.42.

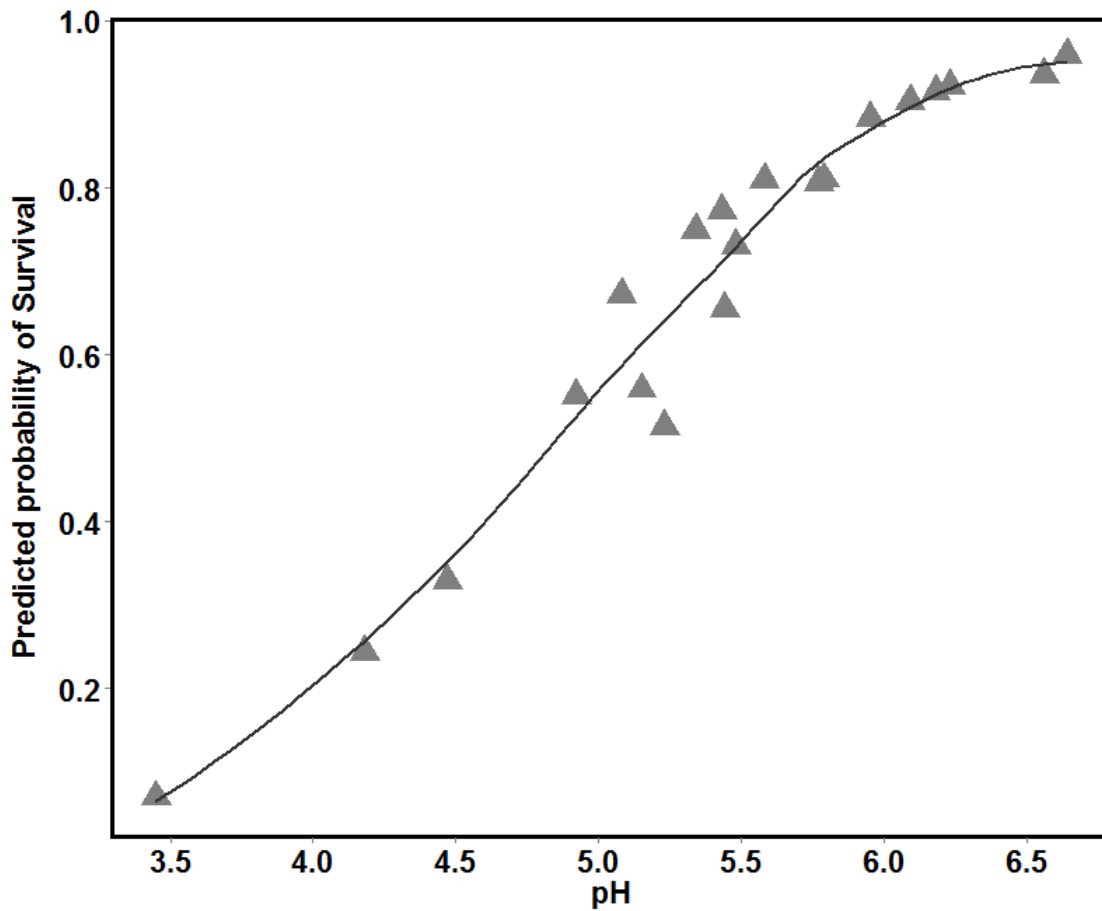


Figure 5 Predicted probability of *P. maculata* survival in response to pH.

Triangles indicate the predicted probability of survival at recorded wetland pH values. The fixed mean effect is represented by the line and the random effect of the wetland is displayed as the deviation of the triangles from the line. Ω_0^2 for this model (comparable to R^2 (Xu 2003)) was 0.42 .

P. maculata Growth

Snail mass and shell width were used to evaluate growth (n = 41) after 5 months in response to local wetland conditions. Models evaluated by AICc model selection were generalized mixed models with wetland as random effect and Gaussian errors. According to AICc Model selection, wetland pH was the best overall predictor of *P. maculata* shell width increase and mass increase (Table 7 and Table 8).

Summaries of the most explanatory models for growth in shell width and mass respectively are provided below (

Table 9a & b).

Table 7 Abbreviated Table of AIC Model Selection for Relative growth in shell width (deltwidth) with wetland as random effect

| Model Names | K | AICc | Delta_AICc | AICcWeight |
|-----------------------------------|---|------|------------|------------|
| width ~pH+ random | 4 | 7.67 | 0,00 | 0.24 |
| width ~null + random | 3 | 8.45 | 0.79 | 0.16 |
| width ~ pH + pasture type+ random | 5 | 9.58 | 1.92 | 0.09 |
| width ~ pH+ soil type+ random | 5 | 9.69 | 2.03 | 0.09 |
| width ~pasture type+ random | 4 | 9.85 | 2.18 | 0.08 |

Table 8 Abbreviated Table of AIC Model Selection for Relative growth in mass (deltmass) with wetland as random effect

| Model Names | K | AICc | Delta_AICc | AICcWeight |
|--|---|--------|------------|------------|
| mass ~pH +random | 4 | 102.91 | 0.00 | 0.29 |
| mass ~pH + pasture type + random | 5 | 104.66 | 1.75 | 0.12 |
| mass ~pH + prior snail presence + random | 5 | 104.78 | 1.87 | 0.11 |
| mass ~pH+ soil type + random | 5 | 105.04 | 2.14 | 0.10 |
| mass ~ null + random | 3 | 105.16 | 2.26 | 0.09 |

Table 9 (a) Generalized Mixed model of *P. maculata* growth in shell width and (b) generalized mixed model for change in live mass.

Both models include pH and wetland level variation for random intercept. Coefficients with SE are in parentheses

| (a) | Shell Width | (b) | Live Mass |
|---------------------------|-----------------------------|---------------------------|-----------------------------|
| Parameter | Estimate using REML | Parameter | Estimate using REML |
| <i>Fixed intercept</i> | -0.43 (0.49) | <i>Fixed intercept</i> | -2.30 (1.43) |
| <i>Fixed slope</i> | 0.16* (0.09) | <i>Fixed slope</i> | 0.56** (0.25) |
| Variance Random Intercept | 0.19 | Variance Random Intercept | 0.44 |
| Residual | 0.08 | Residual | 0.65 |
| AIC | 13.05 | AIC | 101.80 |
| BIC | 19.71 | BIC | 108.65 |
| Observations | 41 | Observations | 41 |
| <i>Note:</i> | *p<0.1; **p<0.05; ***p<0.01 | <i>Note:</i> | *p<0.1; **p<0.05; ***p<0.01 |

Growth of both metrics of *P. maculata* (Figure 6 and Figure 7) indicated significant variation due to the specific wetlands; however overall, growth was best predicted by wetland pH. We did not find evidence of any effect of prior presence/absence on *P. maculata* growth (denoted as diamond and crosshair symbols respectively in both models). Estimates of the dependent variance accounted for by the independent variable within the mixed models (i.e., omega coefficients, Ω_0^2 , comparable to R^2 , (Xu 2003)) were 0.68 for increase in shell width and 0.54 for increase in mass.

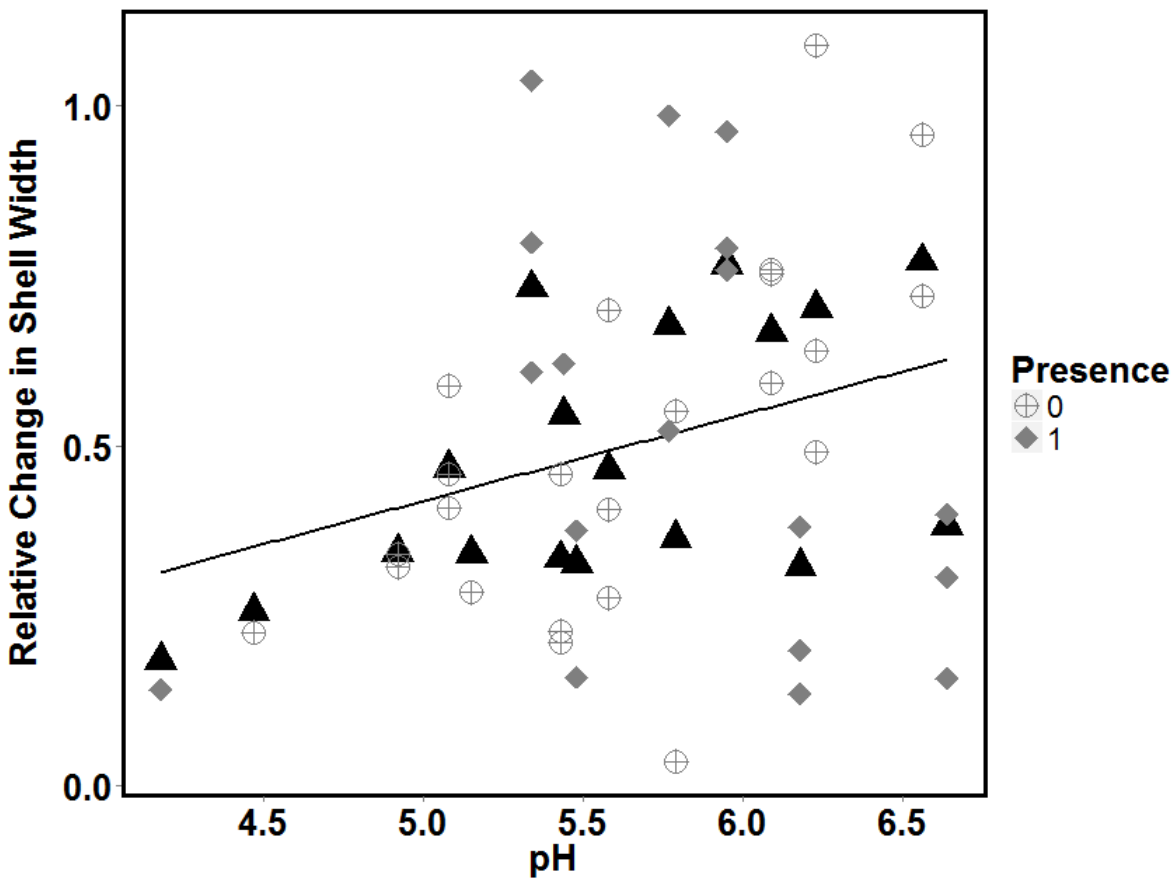


Figure 6 Relative change in *P. maculata* shell width across pH. Black triangles indicate the predicted probability of relative shell width increase for recorded wetland pH values. The fixed mean effect is represented by the black line and the random effect of the wetland is displayed as the deviation of the black triangles from the line. The crosshair symbols indicate relative change in shell width (actual not predicted) in wetlands where snails were not present. The diamond symbols indicate relative change in shell width in wetlands where snails were present. Ω_0^2 for this model (comparable to R^2 (Xu 2003)) was 0.68

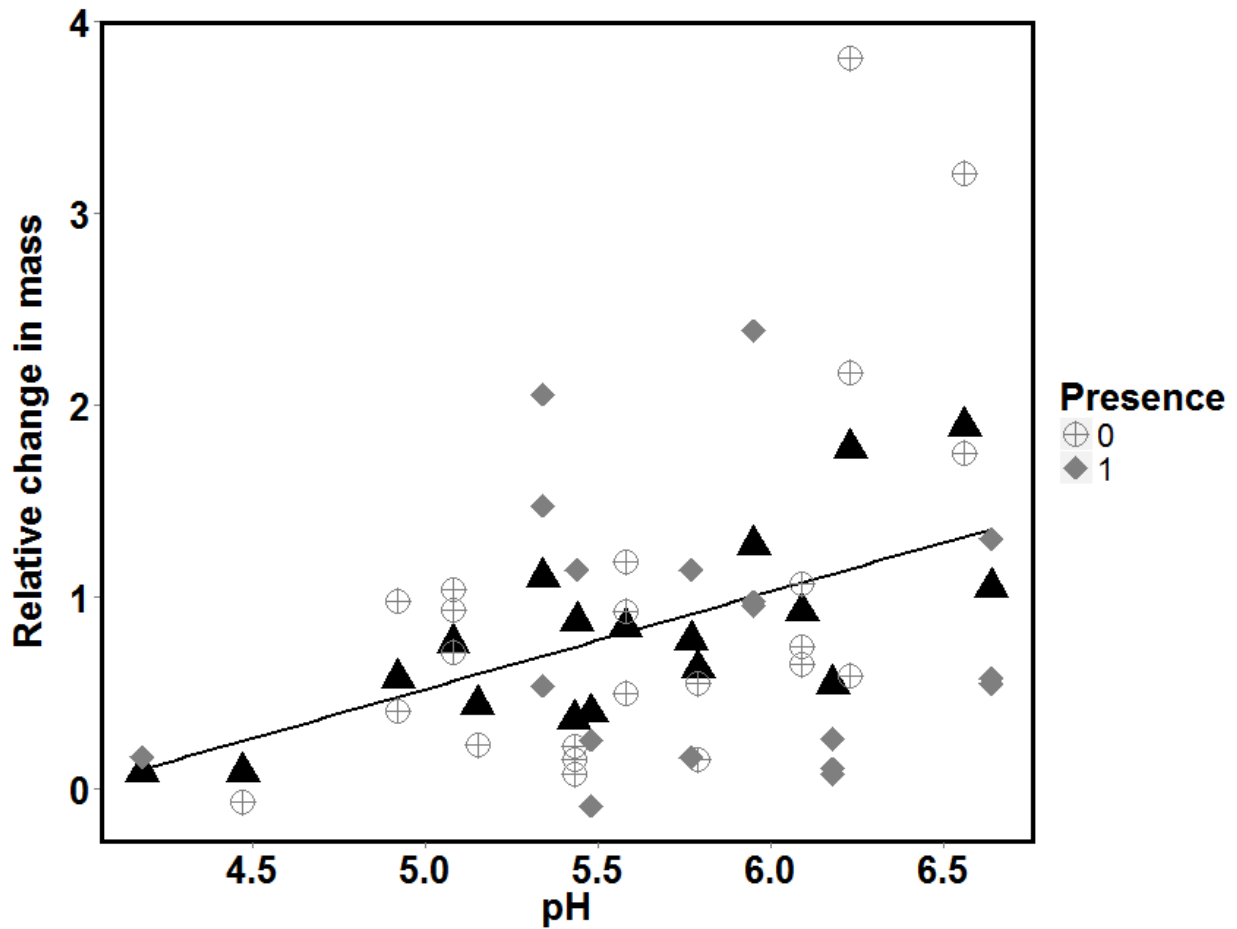


Figure 7 Relative change in *P. maculata* mass across pH.

The black triangles indicate predicted probability of relative mass increase for recorded wetland pH values. The fixed mean effect is represented by the black line and the random effect of the wetland is displayed as the deviation of the black triangles from the line. The crosshair symbols indicate relative change in mass in wetlands where snails were not present (actual not predicted). The diamond symbols indicate relative change in mass in wetlands where snails were present. Ω_0^2 for this model was 0.54.

DISCUSSION

Most invasion research focuses on the local invasion filters of the establishment phase(s) (Puth and Post 2005), however understanding dispersal is critical to understanding habitat invasibility (Vicente et al. 2010). In this study, I provide evidence that both dispersal and niche requirements influence invasive species distribution, but dispersal was essential to understanding the occurrence of the invasive species. The presence of the invader was predicted by geospatial measures of dispersal and local wetland characteristics; and I did not find evidence that the absence of the invader is indicative of unsuitable habitat. The fact that translocated snails survived and grew equally well in both previously occupied and non-occupied wetlands suggests dispersal limitation is a barrier that prevents the snail from occupying many wetlands.

Ditch presence was an important predictor of snail occurrence in my study; however Euclidean and rectilinear distances to initial source were not. Although shallow and seasonally inundated, ditches themselves are tolerable habitat as *P. maculata* can survive extended dry down conditions (Rawlings et al. 2007b; Hayes et al. 2012). Wetlands and shallow ditches may be functioning as secondary population point sources, masking the association of *P. maculata* occurrence with Euclidean and rectilinear proximity to initial point sources. My study could be strengthened by incorporating a meta-population patch dynamic model that treats all occupied wetlands as propagule sources. Additionally, examining multiple dispersing species across taxonomic assemblages within my study system could highlight when and how ditches might be important. Furthermore, I use linear distances as proxies for dispersal to predict presence, but a longer term study that incorporates telemetry or radiolabeling techniques could quantify dispersive migration empirically.

Water pH was an important predictor of snail occurrence, and results showed pH also explained variation in survival and growth. This is consistent with the results of Glass and Darby (2008) that evaluated growth of *Pomacea paludosa* in response to pH and dissolved calcium. Given the calcareous nature of

their protective shells, low pH results in thin eroded shells, increases demand for calcium to perform shell repair and can arrest growth even with high calcium availability (Glass and Darby 2008; Hunter 1990) . Overall, the interaction between ditch presence and pH suggests that the ditches predict the probability of snail introduction to wetlands and pH explains variation in snail persistence after introduction. The fact that snails survived and grew equally well in previously occupied and non-occupied wetlands demonstrates that absence is likely due to dispersal limitation and not due to unsuitable habitat.

Water hardness by itself was not a predictor of occurrence or growth, but water hardness and pH was a plausible alternative model for snail survival (Table 5). Plotting of this alternative model suggests the hardness explains some variation across pH, but water hardness was not statistically significant and the pH model was selected on parsimony. Hardness is often strongly correlated with pH in natural conditions (Glass and Darby 2008) but a strong correlation was not observed in this study, potentially reflecting the effect of intensive pasture management. A greater sample size of wetlands would better show response to water hardness across pH.

Although it is often a relevant factor influencing invertebrate presence in wetland studies (Steinman et al. 2003), pasture type, as a proxy for management intensity, was also not an important predictor in my study. Pulses of nutrients from direct addition, disturbance of substrate or burning of biomass could potentially influence apple snail health and survivability (Glass and Darby 2008). The periodic application of lime at the MAERC might have resulted in differential availability of calcium between intensively managed and semi-natural pasture wetlands. However, I suspect that my survey and survival/growth experiments fell outside of the window of effect of the previously applied lime, as pastures were limed in the growing season subsequent to my experimental procedures. Therefore although I found no comprehensive evidence to support the effect of management on this occasion, it is possible that results may be different post liming or even following a major prescribed burn. I hypothesize that future examination of the intensity and periodicity of management events relative to the reproductive

timing of *P. maculata* will prove crucial for understanding its population dynamics and potential environmental impacts.

Although I did not find any current evidence of negative environmental impact by *P. maculata* within the pastoral setting of my study sites, stormwater treatment areas (STAs) downstream of the MAERC experienced unprecedented defoliation of submerged aquatic vegetation by populations of *P. maculata* (Andreotta et al 2015). Due to the intensity of the *P. maculata* herbivory, the sediment and nutrient load of the STA outflow stream increased almost four-fold (Andreotta et al 2015). Therefore the proliferation of these snails directly threatens costly management efforts currently aimed at restoring the historical oligotrophy of the Everglades region and the health of its associated biota. These outcomes would infer that wetland occupation by *P. maculata* should be discouraged, and to reduce snail access, wetlands should remain unditched, or at least disconnected from the broader ditch networks.

Conversely, my examination of *P. maculata* presence also applies to understanding food availability in marginal habitats for the endangered Florida Everglades snail kite, *Rostrhamus sociabilis*, a specialist bird that feeds almost exclusively on apple snails. Most work on *P. maculata* in this context has taken place on permanent large water bodies (lakes) known to host foraging snail kites, but my study examined their presence in seasonally flooded wetlands and documents successful survival of *P. maculata* in ephemeral water bodies (that are not favored by the declining endemic Florida apple snail, *P. paludosa*). While not a component of my study, I frequently observed Florida Everglades snail kites foraging at my study sites during drydown and recent telemetry work confirms snail kite visitation of ranchland, previously labeled as “peripheral” habitat (Meyer et al. 2011). The juxtaposition of the potential environmental degradation caused by burgeoning *P. maculata* populations against the role of *P. maculata* in the recovery of the endangered Florida Everglades snail kite represents an inherent challenge for land managers that I do not seek to address here.

The importance of dispersal and dispersal limitation as relates to understanding invasion is well documented in the literature, but less empirically tested. Jenkins & Buikema (1998) highlight that rates of dispersal attenuated factors influencing zooplankton community assembly within mesocosms. Cáceres & Soluk (2002) indicated that Euclidean distances between experimental mesocosms were better predictors of zooplankton community homogeneity than differential access by vector animals and advocate for increased focus on dispersal limitation. Similarly to Jenkins & Buikema (1998) and Cáceres & Soluk (2002), my study used combinations of correlative dispersal measures and measured local habitat. However their results are referenced in terms of community assembly (which itself is a product of past invasions) within mesocosms, instead of invasion in natural systems (Puth and Post 2005). Havel, Shurin, & Jones (2002) evaluated an invasive cladoceran in a series of lakes to estimate dispersal and found that dispersal and local factors collectively constrain colonization by this invader. My study goes beyond correlation, and experimentally determines that invader absence was more likely to be associated with dispersal limitation than unfavorable habitat conditions.

Conclusion

My results emphasize (1) that man-made conduits (i.e. ditches) can increase permeability of the landscape, facilitating the dispersal and introduction of nonnative species; and (2) the need for the inclusion of dispersal or dispersal limitation metrics in understanding invasive species distribution. Examining habitat at the expense of dispersal is not reflective of reality and weakens our understanding of invasive processes. To understand if the dispersal of propagules will have any tangible effect, research on the habitat and its influences on persistence and colonization is necessary. But as the process of biological invasion is contingent on propagule movement (i.e. dispersal) for initiation and for expansion, biological invasion ceases to exist without dispersal.

The destination is important... but the journey also matters.

APPENDIX A:
Landscape Connectivity Methods

Landscape /Connectivity Methods

Connectivity to original propagule source (Harney Pond Canal)

Perimeter and Area calculations are contained in the attribute table of the shapefiles, calculated with the *Calculate Geometry* tool from the digitized wetlands.

BIR connectivity variables are defined as those variables that are assumed to be explanatory for snail presence at a specified wetland. For ditch connectivity analysis, wetland polygons were intersected with the BIR ditch network polylines at 10m tolerance. This created intersection nodes (points) which represent inflow points into the wetlands via the ditches. The tolerance range is a conservative buffer range between wetland and ditches – if a ditch falls within 10m of the wetland periphery, an intersection node is created.

The 10m tolerance accounts for potential wetland edge expansion during higher water levels, digitizing errors (if ditch polyline was not digitized into the wetland correctly) and is within the terrestrial mobility limitations of the snails – i.e. if propagule has a route to within 10m of a wetland, the propagule has effectively invaded the wetland. A Harney Pond Canal polyline was intersected with the BIR ditch network polylines to create intersection nodes representing *propagule point sources* for BIR wetlands.

The wetland-ditch intersection nodes (henceforth called *wetland inflow points*), BIR ditch polylines and a Harney Pond Canal *propagule point sources* were used as input to create a *Network Dataset*. This Network Dataset was analyzed using the *Origin-Destination Cost Matrix* tool to determine the distances between every propagule point source and every wetland inflow point. The resulting output table of distances was exported and condensed into pivot table (Microsoft Excel). From the pivot table (organized by the corresponding wetland), all ditch connectivity metrics (Average,

Minimum, Average Total and Minimum Total ditch distances) were compiled and attached to the wetland shapefile attribute tables.

Wetlands were identified that do not have any connection to the network of ditches. These wetlands generated Near Table values of “0” for all ditch connectivity metrics. These “0” values were converted to “NA” as these wetlands did not have routes connecting them to Harney Pond Canal (and therefore distances were not available). The valid interpretation of a “0.0m” distance is that a wetland is very close or attached to Harney Pond Canal.

Euclidean Distance Metrics

The minimum Euclidean distance (straight-line) distance between the periphery of each wetland polygon and the nearest node of the Harney Pond Canal polyline was calculated for all wetlands using the *Generate Near Table* tool. All wetlands have a calculated Euclidean distance. The compiled Near Table was exported to Microsoft Excel for further analysis.

Elevation

Wetland inflow points are assumed to be low points on the wetland perimeter (as they drain into or out of the wetland). The wetland inflow points were used to extract the elevation data for the wetland periphery.

For wetlands without inflow points, the wetland polygons were converted to polyline features (outline of the perimeter), and 10 randomly selected points on the polyline were used to extract elevation data. Elevation data was extracted from the BIR LiDAR DEM using the *Extract by Points tool (Spatial Analyst)* with the aforementioned points as input.

Hanski Isolation Index

This index was previously calculated for all BIR wetlands for use in study by Boughton et al. (2009) and was obtained from Archbold Biological Station MAERC database

My Isolation Index

This index was calculated as the product of the minimum Ditch Distance multiplied by the Shoreline complexity (Perimeter/Area) as a estimated measure of the littoral habitat, which is preferred by snails.

APPENDIX B:
Full AICc Tables and Alternative Plausible Models

AICc Model Selection table for Presence

| Model Names | K | AICc | Delta_AICc | AICcWeight | Cumulative Weight |
|---------------------------------------|---|--------|------------|------------|-------------------|
| Presence ~ Xinflo+pH | 3 | 102.56 | 0 | 0.68 | 0.68 |
| Presence ~ Xinflo*pH | 4 | 104.16 | 1.6 | 0.30 | 0.98 |
| Presence ~ Xinflo+Cdty | 3 | 113.06 | 10.5 | 0.00 | 0.99 |
| Presence ~ Xinflo | 2 | 113.28 | 10.73 | 0.00 | 0.99 |
| Presence ~ Xinflo+Xinflo:MinDitchDist | 3 | 113.98 | 11.42 | 0.00 | 0.99 |
| Presence ~ Xinflo+AREA | 3 | 115.24 | 12.69 | 0.00 | 0.99 |
| Presence ~ Xinflo+MinElev | 3 | 115.3 | 12.75 | 0.00 | 1 |
| Presence ~ Xinflo+MinEucWet | 3 | 115.41 | 12.85 | 0.00 | 1 |
| Presence ~ Xinflo+MyIsoIndex | 3 | 115.41 | 12.86 | 0.00 | 1 |
| Presence ~ Inflo | 4 | 118.7 | 16.14 | 0.00 | 1 |
| Presence ~ pH | 2 | 118.87 | 16.32 | 0.00 | 1 |
| Presence ~ MyIsoIndex | 2 | 129.35 | 26.79 | 0.00 | 1 |
| Presence ~ Cdty | 2 | 129.84 | 27.29 | 0.00 | 1 |
| Presence ~ Hanski | 2 | 130.24 | 27.68 | 0.00 | 1 |
| Presence ~ BIWET04ID | 2 | 131.03 | 28.47 | 0.00 | 1 |
| Presence ~ PERIMETER | 2 | 132.52 | 29.96 | 0.00 | 1 |
| Presence ~ AREA | 2 | 132.72 | 30.16 | 0.00 | 1 |
| Presence ~ 1 | 1 | 133.73 | 31.17 | 0.00 | 1 |
| Presence ~ AveElev | 2 | 135.12 | 32.56 | 0.00 | 1 |
| Presence ~ MinEucWet | 2 | 135.81 | 33.25 | 0.00 | 1 |

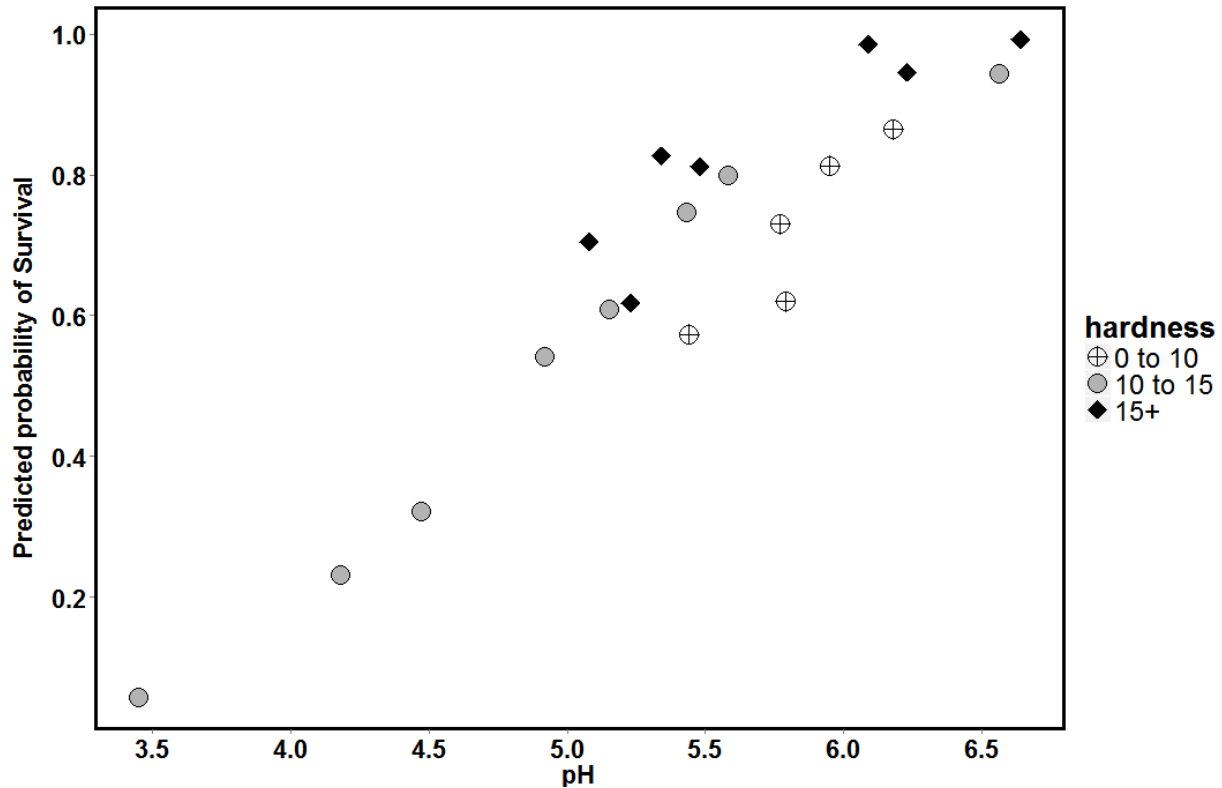
*Not all wetlands have ditches. Xinflo + MinDitchDist is specified as Xinflo + Xinflo:MinDitchDist

AICc Model Selection table for Survival

| Model Names | K | AICc | Delta_AICc | AICcWeight |
|---|---|------|------------|------------|
| alive ~ phpre + (1 wetland) | 3 | 65.9 | 0.00 | 0.30 |
| *alive ~ phpre + calc + (1 wetland) | 4 | 66.0 | 0.13 | 0.28 |
| **alive ~ phpre + presnails + (1 wetland) | 4 | 67.4 | 1.47 | 0.14 |
| alive ~ phpre + pastimprov+ (1 wetland) | 4 | 67.8 | 1.90 | 0.12 |
| alive ~ phpre + pastimprov+ calc + (1 wetland) | 5 | 67.9 | 2.04 | 0.11 |
| alive ~ phpre + pastimprov+ presnails + (1 wetland) | 5 | 69.5 | 3.61 | 0.05 |
| alive ~ 1 + (1 wetland) | 2 | 75.1 | 9.21 | 0.00 |
| alive ~ calc + (1 wetland) | 3 | 75.1 | 9.25 | 0.00 |
| alive ~ pastimprov+ (1 wetland) | 3 | 77.0 | 11.08 | 0.00 |
| alive ~ presnails + (1 wetland) | 3 | 77.3 | 11.39 | 0.00 |

*model is within limits of plausibility, but less parsimonious and calc is not significant

**model is within limits of plausibility, but less parsimonious and the direction of the coefficient is in opposite direction what would be expected if prior occupancy indicated unsuitable habitat.



Alternative plausible model of predicted probability of survival in response to pH and water hardness

Generalized Mixed model of *P. maculata* survival as explained by pH and hardness with wetland level variation for random intercept. Coefficients with SE in parentheses

| Parameter | Estimate using REML |
|---------------------------|---------------------|
| Fixed intercept | -10.24* (4.25) |
| Fixed slope of pH | 1.95** (0.73) |
| Hardness 10 to 15 | 0.80 (1.04) |
| Hardness 15+ | 0.91 (0.93) |
| Variance Random Intercept | 0.21 |
| Residual | 0.46 |
| AIC | 68.51 |
| BIC | 78.98 |
| Observations | 60 |

Note: * p<0.1; ** p<0.05; *** p<0.01

AICc Model selection table for Relative growth in shell width (deltwidth) with wetland as random effect

| Model Names | K | AICc | Delta_AICc | AICcWeight |
|--|---|---------|------------|------------|
| deltwidth ~phpre, random = ~1 wetland | 4 | 7.6684 | 0 | 0.2428 |
| deltwidth ~1, random = ~1 wetland | 3 | 8.4537 | 0.7852 | 0.1639 |
| deltwidth ~ phpre + pastimprov, random = ~1 wetland | 5 | 9.5839 | 1.9154 | 0.0932 |
| deltwidth ~ phpre+soil, random = ~1 wetland | 5 | 9.6945 | 2.0261 | 0.0881 |
| deltwidth ~pastimprov, random = ~1 wetland | 4 | 9.8478 | 2.1793 | 0.0816 |
| deltwidth ~phpre+calc, random = ~1 wetland | 5 | 10.2664 | 2.5980 | 0.0662 |
| deltwidth ~phpre+presnails, random = ~1 wetland | 5 | 10.2696 | 2.6012 | 0.0661 |
| deltwidth ~calc, random = ~1 wetland | 4 | 10.8278 | 3.1594 | 0.0500 |
| deltwidth ~presnails, random = ~1 wetland | 4 | 10.8689 | 3.2005 | 0.0490 |
| deltwidth ~soil, random = ~1 wetland | 4 | 10.9063 | 3.2378 | 0.0481 |
| deltwidth ~calc+pastimprov, random = ~1 wetland | 5 | 12.3769 | 4.7085 | 0.0231 |
| deltwidth ~calc+presnails, random = ~1 wetland | 5 | 13.3763 | 5.7078 | 0.014 |
| deltwidth ~calc+soil, random = ~1 wetland | 5 | 13.3959 | 5.7275 | 0.0139 |

AICc Model selection table for Relative growth in Mass (deltmass) with wetland as random effect

| Model Names | K | AICc | Delta_AICc | AICcWeight |
|---|---|----------|------------|------------|
| deltmass ~phpre, random = ~1 wetland | 4 | 102.9065 | 0.0000 | 0.2856 |
| deltmass ~phpre+pastimprov, random = ~1 wetland | 5 | 104.6568 | 1.7503 | 0.1190 |
| deltmass ~phpre+presnails, random = ~1 wetland | 5 | 104.7810 | 1.8745 | 0.1119 |
| deltmass ~phpre+soil, random = ~1 wetland | 5 | 105.0417 | 2.1353 | 0.0982 |
| deltmass ~ 1, random = ~1 wetland | 3 | 105.1639 | 2.2575 | 0.0924 |
| deltmass ~ phpre+calc, random = ~1 | 5 | 105.5096 | 2.6032 | 0.0777 |
| deltmass ~soil, random = ~1 wetland | 4 | 105.9744 | 3.0680 | 0.0616 |
| deltmass ~pastimprov, random = ~1 wetland | 4 | 106.3232 | 3.4167 | 0.0517 |
| deltmass ~presnails, random = ~1 wetland | 4 | 107.3602 | 4.4537 | 0.0308 |
| deltmass ~calc, random = ~1 wetland | 4 | 107.4296 | 4.5231 | 0.0298 |
| deltmass ~calc+soil, random = ~1 wetland | 5 | 108.5654 | 5.6589 | 0.0169 |
| deltmass ~calc+pastimprov, random = ~1 wetland | 5 | 108.7517 | 5.8452 | 0.0154 |
| deltmass ~calc+presnails, random = ~1 wetland | 5 | 109.7860 | 6.8795 | 0.0092 |

APPENDIX C: Model Average Results

Survival

Model-averaged coefficients:

| | Estimate | Std. Error | z value | Pr(> z) | |
|------------------|----------|------------|---------|----------|----|
| (Intercept) | -8.7423 | 3.2014 | 2.731 | 0.00632 | ** |
| phpre | 1.7847 | 0.5899 | 3.025 | 0.00248 | ** |
| presnails | -0.6572 | 0.6977 | 0.942 | 0.34623 | |
| pastimprov | 0.4517 | 0.7120 | 0.634 | 0.52581 | |
| hardness10 to 15 | 0.7958 | 1.0449 | 0.762 | 0.44627 | |
| hardness15+ | 0.9066 | 0.9321 | 0.973 | 0.33075 | |

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

Full model-averaged coefficients (with shrinkage):

| (Intercept) | phpre | presnails | pastimprov | hardness10 to 15 | hardness15+ |
|-------------|----------|-----------|------------|------------------|-------------|
| -8.742270 | 1.784666 | -0.155627 | 0.086354 | 0.061402 | 0.069948 |

Relative variable importance:

| phpre | presnails | pastimprov | hardness |
|-------|-----------|------------|----------|
| 1.00 | 0.24 | 0.19 | 0.08 |

Growth in Mass

Model-averaged coefficients:

| | Estimate | Std. Error | Adjusted SE | z value | Pr(> z) |
|-------------|----------|------------|-------------|---------|----------|
| (Intercept) | -2.2809 | 1.4599 | 1.5395 | 1.482 | 0.1385 |
| phpre | 0.5444 | 0.2554 | 0.2769 | 1.966 | 0.0493 * |
| pastimprov | -0.2756 | 0.3076 | 0.3345 | 0.824 | 0.4099 |
| presnails1 | -0.2551 | 0.3057 | 0.3324 | 0.767 | 0.4429 |
| soil | 0.2823 | 0.4274 | 0.4648 | 0.607 | 0.5436 |

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

Full model-averaged coefficients (with shrinkage):

| (Intercept) | phpre | pastimprov | presnails1 | soil |
|-------------|----------|------------|------------|----------|
| -2.280947 | 0.544409 | -0.053373 | -0.046420 | 0.045095 |

Relative variable importance:

| phpre | pastimprov | presnails | soil |
|-------|------------|-----------|------|
| 1.00 | 0.19 | 0.18 | 0.16 |

APPENDIX D:
Script for R Analysis (R v2.15.1)

R Code

```
###Part I: Preparing the data

rm(list=ls()) ##Ctrl+L clears everything from console
detach(orig_data)

## read the data from file

orig_data <- snailgrow3R

attach(orig_data) ##will be masked if previously attached
#names(orig_data) ##all column names must have no spaces

library(AICcmodavg)
library(ggplot2)

Data checks
## qqnorm(x)
# qqline(x)
# hist(x)

libs <- c('ggplot2', 'latticeExtra', 'gridExtra', 'MASS',
          'colorspace', 'plyr', 'Hmisc', 'scales')
lapply(libs, require, character.only = T)

#R does not like 0 as a name, even if factored

#-----snail survival-----#

ms <- c(
  "alive ~ 1+ (1|wetland) ", #1
  "alive ~ pastimprov + (1|wetland)", #2
  "alive ~ presnails + (1|wetland)", #3
  "alive ~ phpre + (1|wetland)", #4y
  "alive ~ calc + (1|wetland)", #5y
  "alive ~ phpre + pastimprov+ (1|wetland)", #6 y
  "alive ~ phpre + presnails + (1|wetland)", #7y
  "alive ~ phpre + calc + (1|wetland)", #8y
  "alive ~ phpre + pastimprov+presnails + (1|wetland)", #9
  "alive ~ phpre + pastimprov+calc + (1|wetland)" # 10

  #no comma at end!
)

Cand.models<-list()
for (i in 1:length(ms)) {
  Cand.models[[i]] <- glmer(as.formula(ms[i] ), family=binomial, data=orig_data)
}

Modnames<-paste("model", 1:length(Cand.models), sep="")
```

```

print(aictab(cand.set = Cand.models, modnames = ms, sort =
TRUE),digits = 4, LL = TRUE)

#Model average#
library(glmulti)
library(MuMIn)
library(AICcmmodavg)

try1 <-glmer(alive ~ phpre + (1|wetland), family=binomial, data=orig_data)
try2 <-glmer(alive ~ phpre + hardness+ (1|wetland), family=binomial, data=orig_data)
try3 <-glmer(alive ~ phpre + presnails+ (1|wetland), family=binomial, data=orig_data)
try4 <-glmer(alive ~ phpre + pastimprov+ (1|wetland), family=binomial, data=orig_data)

aved <- model.avg(try1, try2, try3, try4)
summary (aved)

library(car)

summary (try1)
summary (try2)

require(gridExtra)
Ace <- aictab(cand.set = Cand.models, modnames = ms, sort = TRUE)
aictab <- data.frame (Ace)

grid.table(aictab,
  gpar.coretext= gpar(fontsize = 12),
  gpar.coltext = gpar(fontsize = 12),
  gpar.rowtext = gpar(fontsize = 12),
  gpar.corefill = gpar(fill = "cornflowerblue", alpha = 0.5, col = NA),
  h.even.alpha = 0.5,
  equal.width = FALSE,
  show.rownames = FALSE,
  show.vlines = TRUE,
  padding.h = unit(6, "mm"),
  padding.v = unit(6, "mm")
)

summary(Cand.models[[4]])

#install.packages("stargazer") #Use this to install it, do this only once
library(stargazer)

#stargazer(Cand.models[[4]], type="html",
  title="", dep.var.labels=c("Survival"),
  covariate.labels=c("pH","Intercept"),
  out="survival_pH.htm")

require(ggplot2)

```

```

require(reshape2)
require(lme4)
require(compiler)
require(parallel)
require(boot)

Cands <- list(m1,m2,m3,m4,m5,m6,m7,m8,m9,m10,m11,m12)
Model.names <- c(1:12)
aictab(cand.set = Cands, modnames = Model.names, sort = TRUE)

par(mfrow=c(1,1))
#Prdt is right
prdt<-predict(glmer(alive~phpre+ (1|wetland),family=binomial, data=orig_data),
              type = "response")

prdtplaus<-predict(glmer(alive~phpre + calc + (1|wetland),family=binomial, data=orig_data),
                  type = "response")

plot(phpre[presnails==1], prdt[presnails==1], col="green",pch=16,ylim=c(0,1), xlim =c(3,7))
points(phpre[presnails==0], prdt[presnails==0], col="red",pch=16)

plot(phpre[calc<10], prdt[calc<10], col="red",pch=16,ylim=c(0,1), xlim =c(3,7))
points(phpre[calc>=10 & calc <15], prdt[calc>=10 & calc <15], col="blue",pch=16)
points(phpre[calc>=15], prdt[calc>=15], col="yellow",pch=16)

#color
snailalive <- ggplot(orig_data,aes(phpre,prdt, color=hardness))+ labs(title = 'Probability of Snail Survival with
pH')+
  scale_color_manual( values = c("red","blue","yellow"))+ geom_point(size = 12, shape = 18, position =
position_jitter(w = 0, h = 0.0))+ stat_smooth(method="lm", se=FALSE, size =0.8, color = 'blue')+
snailalive <- snailalive + theme(panel.background = element_rect(fill= 'black'), panel.grid.minor =
element_line(colour = "black"), panel.grid.major = element_line(colour = "grey25"))

snailalive <-snailalive +theme(plot.title = element_text(size = 30, face='bold', vjust=2))+
  labs(x="pH", y="Predicted probability of Survival")
snailalive <- snailalive + scale_y_continuous(breaks=pretty_breaks(n=4))+
  scale_x_continuous(breaks=pretty_breaks(n=6))+ theme(legend.text = element_text(size = 30), legend.title =
element_text(size = 26))

snailalive <- snailalive + theme(panel.background = element_rect(fill= 'black'), panel.grid.minor =
element_line(colour = "black"), panel.grid.major = element_line(colour = "grey25")) +
  theme(axis.text.y=element_text(size=30, vjust=0.5, color = "black", face = 'bold')) +
  theme(axis.text.x=element_text(size=30, vjust=0.2, color = "black",face = 'bold')) +
  theme(axis.title.y=element_text(size=30, vjust=0.2, color = "black", face = 'bold'),
axis.title.x=element_text(size=30, vjust=0.5, face = 'bold'))
snailalive

#b&w
snailalive <- ggplot(orig_data,aes(phpre,prdt))+
  geom_point(size = 8, shape = 17,color = "grey 50", position = position_jitter(w = 0, h = 0.0))+
  stat_smooth(method="lm", se=FALSE, size =0.8, color = 'grey20')

```



```

snailalive <- snailalive + theme(panel.background = element_rect(fill= 'white'), panel.grid.minor =
element_blank(), panel.grid.major = element_blank()) +
  theme(panel.background = element_rect(colour = "black", size=2, fill=NA))

snailalive <-snailalive +theme(plot.title = element_text(size = 22, face='bold', vjust=2))+
  labs(x="pH", y="Predicted probability of Survival")
snailalive <- snailalive + scale_y_continuous(breaks=pretty_breaks(n=4))+
  scale_x_continuous(breaks=pretty_breaks(n=6))+ theme(legend.text = element_text(size = 30), legend.title =
element_text(size = 26))

snailalive <- snailalive +
  theme(axis.text.y=element_text(size=22, vjust=0.5, color = "black", face = 'bold')) +
  theme(axis.text.x=element_text(size=22, vjust=0.2, color = "black",face = 'bold')) +
  theme(axis.title.y=element_text(size=22, vjust= 0.2, color = "black", face = 'bold'),
axis.title.x=element_text(size=22, vjust=0.5, face = 'bold'))
snailalive

#b&w plausible model
snailalive <- ggplot(orig_data,aes(phpre,prdtplaus, shape = hardness))+ scale_shape_manual( values =
c(10,21,18))+

  geom_point(size = 8,fill = "grey70", position = position_jitter(w = 0, h = 0.0))
snailalive <- snailalive + theme(panel.background = element_rect(fill= 'white'), panel.grid.minor =
element_blank(), panel.grid.major = element_blank()) +
  theme(panel.background = element_rect(colour = "black", size=2, fill=NA))

snailalive <-snailalive +theme(plot.title = element_text(size = 22, face='bold', vjust=2))+
  labs(x="pH", y="Predicted probability of Survival")
snailalive <- snailalive + scale_y_continuous(breaks=pretty_breaks(n=4))+
  scale_x_continuous(breaks=pretty_breaks(n=6))+ theme(legend.text = element_text(size = 24), legend.title =
element_text(size = 26))
#snailalive

snailalive <- snailalive +
  theme(axis.text.y=element_text(size=22, vjust=0.5, color = "black", face = 'bold')) +
  theme(axis.text.x=element_text(size=22, vjust=0.2, color = "black",face = 'bold')) +
  theme(axis.title.y=element_text(size=22, vjust= 0.2, color = "black", face = 'bold'),
axis.title.x=element_text(size=22, vjust=0.5, face = 'bold'))
snailalive

names (orig_data)

# Bar graphs of data.
#bar plot of survival
snailalivebypre <- table(orig_data$alive, orig_data$presnails )
snailalivebypre[1:2] <- snailalivebypre[1:2]/sum(snailalivebypre[1:2]) *100
snailalivebypre[3:4] <- snailalivebypre[3:4]/sum(snailalivebypre[3:4]) *100
snailalivebypre

par(xpd=T, mar=par()$mar+c(0,0,0,6))
barplot(as.matrix(snailalivebypre), ylab = "Survival as Percentage (%)", names.arg = c("absent","present"),
beside = FALSE, col = rainbow (3), cex.axis=1.5, cex.lab =1.5,cex.names = 1.5, las= 1, ylim=c(0,110))
legend(2.4,50, c("alive","dead"), bty = "n", cex = 1.1, fill = c("green","red"))

```

```

par(mfrow=c(1,1))

#bar plot of delta growth in length
snaillen <- subset(orig_data,!is.na(deltlength))
liveo<- subset(snaillen$deltlength, snaillen$presnails==1)
deado <- subset(snaillen$deltlength,snaillen$presnails==0)

#-----snail growth shell width-----#
names(orig_data)

library(nlme)
dt<- subset(orig_data,!is.na(deltwidth) & !is.na(deltmass))

m0<- lme(deltwidth ~ 1, random = ~1|wetland, data=dt,method ="ML")
m1<- lme(deltwidth ~phpre, random = ~1|wetland, data=dt,method ="ML")
m2<- lme(deltwidth ~calc, random = ~1|wetland, data=dt,method ="ML")
m3<- lme(deltwidth ~soil, random = ~1|wetland, data=dt,method ="ML")
m4<- lme(deltwidth ~presnails, random = ~1|wetland, data=dt,method ="ML")
m5<- lme(deltwidth ~pastimprov, random = ~1|wetland, data=dt,method ="ML")
m6<- lme(deltwidth ~phpre+calc, random = ~1|wetland, data=dt,method ="ML")
m7<- lme(deltwidth ~phpre+soil, random = ~1|wetland, data=dt,method ="ML")
m8<- lme(deltwidth ~phpre+presnails, random = ~1|wetland, data=dt,method ="ML")
m9<- lme(deltwidth ~phpre+pastimprov, random = ~1|wetland, data=dt,method ="ML")
m10<- lme(deltwidth ~calc+soil, random = ~1|wetland, data=dt,method ="ML")
m11<- lme(deltwidth ~calc+presnails, random = ~1|wetland, data=dt,method ="ML")
m12<- lme(deltwidth ~calc+pastimprov, random = ~1|wetland, data=dt,method ="ML")

Cands <- list(m0,m1,m2,m3,m4,m5,m6,m7,m8,m9,m10,m11,m12)
Model.names <- c(0:12)
aictab(cand.set = Cands, modnames = Model.names, sort = TRUE)

print(aictab(cand.set = Cands, modnames = Model.names, sort =
TRUE),digits = 4, LL = TRUE)

m1weighted <- lme(deltwidth ~ phpre, random = ~1|wetland, data = dt, method ="REML")
summary(m1weighted)

F0<- fitted(m1weighted, level= 0)
F1<- fitted(m1weighted, level= 1)

#install.packages("tidyr")
#library(tidyr)
#library(dplyr)

###pretty ggplot of snail shell width### B&W

```

F1

```
dt$presnails<- as.factor(dt$presnails)
dt$change <-as.numeric(F1)
snailgro <- ggplot(dt,aes(phpre,change))+ stat_smooth(method="lm", se=FALSE, size =0.8, color = 'forest
green')+
geom_point(size = 8, shape = 24,fill = 'black', position = position_jitter(w = 0, h = 0.0))
```

```
snailgro <-snailgro +theme(plot.title = element_text(size = 26, face='bold', vjust=2))+
labs(x="pH", y=("Relative Change in Shell Width"))+
scale_x_continuous(breaks=pretty_breaks(n=6)) +
scale_y_continuous(breaks=pretty_breaks(n=4))+
theme(axis.text.y=element_text(size=12, vjust=0.5, face = 'bold', colour = 'black')) +
theme(panel.background = element_rect(colour = "black", size=2, fill=NA))+
theme(legend.text = element_text(size = 22), legend.title = element_text(size = 26)) +
theme(axis.text.x=element_text(size=26, vjust=0.5, face = 'bold', colour = 'black'))+
theme(axis.text.y=element_text(size=26, vjust=0.5, face = 'bold', colour = 'black'))+
theme(axis.title.y=element_text(size=26, vjust= 0.2, face = 'bold'), axis.title.x=element_text(size=26,
vjust=0.5, face = 'bold'))+
theme(panel.background = element_rect(fill= "white")) +
theme(panel.grid.major = element_blank(), panel.grid.minor = element_blank())
snailgro
```

Presence <- dt\$presnails

```
snailgro <- snailgro + geom_point(aes(phpre,deltwidth,shape = Presence, color = Presence) , size = 8)+
scale_shape_manual( values = c(10,18))+ scale_color_manual( values = c("red","blue"))
```

snailgro

###pretty ggplot of snail shell width### color

#line of selected

```
snailgro <- ggplot(dt,aes(phpre,change))+ stat_smooth(method="lm", se=FALSE, size =0.8, color = 'blue')+
geom_point(size = 0, shape = 24,fill = 'black', position = position_jitter(w = 0, h = 0.0))
snailgro
```

#predicted

```
snailgro <- ggplot(dt,aes(phpre,change))+ stat_smooth(method="lm", se=FALSE, size =0.8, color = 'blue')+
geom_point(size = 10, shape = 24,fill = 'red', position = position_jitter(w = 0, h = 0.0))
snailgro
```

#graph format

```
snailgro <-snailgro +theme(plot.title = element_text(size = 30, face='bold', vjust=2))+
labs(x="pH", y=("Relative Change in Shell Width"))+
scale_x_continuous(breaks=pretty_breaks(n=6)) +
scale_y_continuous(breaks=pretty_breaks(n=4))+
theme(axis.text.y=element_text(size=30, vjust=0.5, face = 'bold', colour = 'black')) +
theme(axis.text.x=element_text(size=30, vjust=0.5, face = 'bold', colour = 'black'))+
theme(legend.text = element_text(size = 20), legend.title = element_text(size = 20)) +
theme(axis.title.y=element_text(size=30, vjust= 0.2, face = 'bold'), axis.title.x=element_text(size=30,
vjust=0.2, face = 'bold'))+
theme(panel.background = element_rect(fill= 'black'), panel.grid.minor = element_line(colour = "black"),
panel.grid.major = element_line(colour = "black"))
```

```
snailgro
```

```
snailgro <- snailgro +  
  geom_point(aes(phpre,deltwidth,color = presnails) , shape = 46, size = 0)+  
  scale_color_manual( values = c("black","black"), labels = c("Yes","No"), name = "Snails prior")+  
  theme(legend.key=element_rect(fill='black'))
```

```
snailgro
```

```
# actual data points  
snailgro <- snailgro +  
  geom_point(aes(phpre,deltwidth,color = presnails) , shape =10, size = 14)+  
  scale_color_manual( values = c("yellow","cyan"), labels = c("Yes","No"), name = "Snails prior")+  
  theme(legend.key=element_rect(fill='black'))
```

```
snailgro
```

```
#-----snail growth mass-----#
```

```
names(orig_data)
```

```
library(nlme)  
excel <- subset(orig_data,!is.na(deltmass))  
attach(excel)  
#massy$deltmass<- as.numeric(levels(massy$deltmass))[massy$deltmass] #function to convert factor to  
numeric without loss  
excel$presnails<- as.factor(excel$presnails)  
excel$change <-as.numeric(F1)
```

```
m0b<- lme(deltmass ~ 1, random = ~1|wetland, data=excel , method ="ML")  
m1b<- lme(deltmass ~phpre, random = ~1|wetland, data=excel , method ="ML")  
m2b<- lme(deltmass ~calc, random = ~1|wetland, data=excel , method ="ML")  
m3b<- lme(deltmass ~soil, random = ~1|wetland, data=excel , method ="ML")  
m4b<- lme(deltmass ~presnails, random = ~1|wetland, data=excel , method ="ML")  
m5b<- lme(deltmass ~pastimprov, random = ~1|wetland, data=excel , method ="ML")  
m6b<- lme(deltmass ~phpre+calc, random = ~1|wetland, data=excel , method ="ML")  
m7b<- lme(deltmass ~phpre+soil, random = ~1|wetland, data=excel , method ="ML")  
m8b<- lme(deltmass ~phpre+presnails, random = ~1|wetland, data=excel , method ="ML")  
m9b<- lme(deltmass ~phpre+pastimprov, random = ~1|wetland, data=excel , method ="ML")  
m10b<- lme(deltmass ~calc+soil, random = ~1|wetland, data=excel , method ="ML")  
m11b<- lme(deltmass ~calc+presnails, random = ~1|wetland, data=excel , method ="ML")  
m12b<- lme(deltmass ~calc+pastimprov, random = ~1|wetland, data=excel , method ="ML")
```

```
#ask why are these different
```

```
Cands <- list(m0b,m1b,m2b,m3b,m4b,m5b,m6b,m7b,m8b,m9b,m10b,m11b,m12b)
```

```
Model.names <- c(0:12)
```

```
aictab(cand.set = Cands, modnames = Model.names, sort = TRUE)
```

```
print(aictab(cand.set = Cands, modnames = Model.names, sort =  
TRUE),digits = 4, LL = TRUE)
```

```

#model average
avedm <- model.avg(m1b, m9b, m8b, m7b)
summary(avedm)

plot(m1b)
summary(m1b)

#Variance is associated with the variation of pH, does not have homogeneity of variances, by estimating the
(Zuur et al)
m4 <- lme(deltmass ~ phpre, random = ~1|wetland, weights="phpre", data = excel, )

F0<- fitted(m4, level= 0)
F1<- fitted(m4, level= 1)

F1
excel$change <-as.numeric(F1)
snailmass <- ggplot(excel,aes(phpre,change))+ stat_smooth(method="lm", se=FALSE, size =0.8, color =
'black')+
  geom_point(size = 8, shape = 24,fill = 'black', position = position_jitter(w = 0, h = 0.0))

snailmass <-snailmass +theme(plot.title = element_text(size = 26, face='bold', vjust=2))+
  labs(x="pH", y=("Relative change in mass"))+
  scale_x_continuous(breaks=pretty_breaks(n=6)) +
  scale_y_continuous(breaks=pretty_breaks(n=6))+
  theme(panel.background = element_rect(colour = "black", size=2, fill=NA))+
  theme(axis.text.y=element_text(size=26, vjust=0.5, face = 'bold', colour = 'black')) +
  theme(axis.text.x=element_text(size=26, vjust=0.5, face = 'bold', colour = 'black'))+
  theme(legend.text = element_text(size = 22),legend.title = element_text(size = 26)) +
  theme(axis.title.y=element_text(size=26, vjust= 0.2, face = 'bold'), axis.title.x=element_text(size=26,
vjust=0.5, face = 'bold'))+
  theme(panel.background = element_rect(fill= 'white')) +
  theme(panel.grid.major = element_blank(), panel.grid.minor = element_blank())
snailmass

Presence <- excel$presnails
snailmass <- snailmass + geom_point(aes(phpre,deltmass,shape = Presence) , colour = "grey50", size = 8)+
scale_shape_manual( values = c(10,18))
snailmass

###pretty ggplot of snail mass### color
snailmass <- ggplot(excel,aes(phpre,change))+
  geom_point(size = 14, shape = 24,fill = 'red', position = position_jitter(w = 0, h = 0.0))

snailmass <-snailmass +theme(plot.title = element_text(size = 30, face='bold', vjust=2))+
  labs(x="pH", y=("Relative Change in P. maculata Mass"))+
  scale_x_continuous(breaks=pretty_breaks(n=6)) +
  scale_y_continuous(breaks=pretty_breaks(n=4))+
  theme(axis.text.y=element_text(size=30, vjust=0.5, face = 'bold', colour = 'black')) +
  theme(axis.text.x=element_text(size=30, vjust=0.5, face = 'bold', colour = 'black'))+
  theme(legend.text = element_text(size = 30), legend.title = element_text(size = 26)) +

```

```

  theme(axis.title.y=element_text(size=30, vjust= 0.2, face = 'bold'), axis.title.x=element_text(size=30,
vjust=0.2, face = 'bold'))+
  theme(panel.background = element_rect(fill= "black"), panel.grid.major = element_line(colour = "grey28"),
panel.grid.minor = element_line(colour = "grey18"))
snailmass

snailmass <- snailmass + geom_point(aes(phpre,deltmass,color = presnails), shape =10, size = 18)+
stat_smooth(method="lm", se=FALSE, size =0.8, color = 'blue')+
  geom_point(aes(phpre,deltmass,color = presnails), shape =20, size = 8)
snailmass

#line of selected
snailmass <- ggplot(excel,aes(phpre,change))+ stat_smooth(method="lm", se=FALSE, size =0.8, color =
'blue')+
  geom_point(size = 0, shape = 24,fill = 'black', position = position_jitter(w = 0, h = 0.0))
snailmass

#predicted
snailmass <- ggplot(excel,aes(phpre,change))+ stat_smooth(method="lm", se=FALSE, size =0.8, color =
'blue')+
  geom_point(size = 10, shape = 24,fill = 'red', position = position_jitter(w = 0, h = 0.0))
snailmass

# graph format
snailmass <-snailmass +theme(plot.title = element_text(size = 30, face='bold', vjust=2))+
  labs(x="pH", y=("Relative Change in Mass"))+
  scale_x_continuous(breaks=pretty_breaks(n=6)) +
  scale_y_continuous(breaks=pretty_breaks(n=4))+
  theme(axis.text.y=element_text(size=30, vjust=0.5, face = 'bold', colour = 'black')) +
  theme(axis.text.x=element_text(size=30, vjust=0.5, face = 'bold', colour = 'black'))+
  theme(legend.text = element_text(size = 20), legend.title = element_text(size = 20)) +
  theme(axis.title.y=element_text(size=30, vjust= 0.2, face = 'bold'), axis.title.x=element_text(size=30,
vjust=0.2, face = 'bold'))+
  theme(panel.background = element_rect(fill= "black"), panel.grid.major = element_line(colour = "black"),
panel.grid.minor = element_line(colour = "black"))
snailmass

snailmass <- snailmass +
  geom_point(aes(phpre,deltmass,color = presnails), shape =46, size = 0)+
  scale_color_manual( values = c("black","black"), labels = c("Yes","No"), name = "Snails prior")+
  theme(legend.key=element_rect(fill='black'))

snailmass

#actual data points

snailmass <- snailmass +
  geom_point(aes(phpre,deltmass,color = presnails), shape =10, size = 14)+
  scale_color_manual( values = c("yellow","cyan"), labels = c("Yes","No"), name = "Snails prior")+
  theme(legend.key=element_rect(fill='black'))

snailmass

```

```
#####
library(plot3D)
summary(Cand.models[[4]])
```

Connectivity and Presence

```
attach(orig_data)
names(orig_data)
pairs (orig_data[15:26] )
subs <- subset(orig_data,Clean==4)
```

```
##will be masked if previously attached
##all column names must have no spaces
```

```
subspres <- subset(subs, Pres==2)
subsnopres <- subset(subs, Pres==1)
dim(subspres)
dim(subsnopres)
length(subs$Xinfo[subspres$Xinfo==1 & subspres$Presence==0])
```

```
length(orig_data$Xinfo)
length(orig_data$Xinfo[orig_data$Xinfo==0])
length(orig_data$Xinfo[orig_data$Xinfo==0 & orig_data$Presence==0])
```

```
ditch <- length(subs$pH[subspres$Xinfo==1])
noditch <- length(subs$pH[subsnopres$Xinfo==0])
```

```
subs$WetInfoCount <-factor(subs$WetInfoCount)
s <- c(1:9,12,15:17,21:26)
small <- subs[,s]
names(subs)
```

```
library(AICcmodavg)
#R does not like 0 as a name, even if factored
```

```
ms <- c(
"Presence ~ 1 ", #1
"Presence ~ AREA ", #2
"Presence ~ PERIMETER", #3
"Presence ~ BIWET04ID", #4
"Presence ~ Hanski", #5
"Presence ~ Inflo", #6
"Presence ~ MinEucWet", #7
"Presence ~ MinElev", #8
"Presence ~ AveElev",
"Presence ~ InfloCountReal", #10
"Presence ~ MyIsoIndex", #
"Presence ~ Xinfo", #
"Presence ~ pH", #13
"Presence ~ Cdy", #
"Presence ~ Xinfo+Xinfo:MinDitchDist", #15
```

```

"Presence ~ Xinfo+pH",
"Presence ~ Xinfo+AREA",
"Presence ~ Xinfo+PERIMETER",#18
"Presence ~ Xinfo+MinElev",
"Presence ~ Xinfo+AveElev",
"Presence ~ Xinfo+MinEucWet",
"Presence ~ Xinfo+MyIsoIndex",#22
"Presence ~ Xinfo+Cdty",
"Presence ~ Xinfo*pH"

#no comma at end!
)

Cand.models<-list()
for (i in 1:length(ms)) {
Cand.models[[i]] <- glm(as.formula(ms[i]), family=binomial, data=subs)
}

Modnames<-paste("model", 1:length(Cand.models), sep="")

print(aictab(cand.set = Cand.models, modnames = ms, sort =
TRUE),digits = 2, LL = TRUE)

summary(Cand.models[[16]])

par(mfrow=c (1,1))

require(gridExtra)
Ace <- aictab(cand.set = Cand.models, modnames = ms, sort = TRUE)
boo <- data.frame ((Ace))

grid.table(format(boo, digits = 4),
  gpar.coretext= gpar(fontsize = 12),
  gpar.coltext = gpar(fontsize = 12),
  gpar.rowtext = gpar(fontsize = 12),
  gpar.corefill = gpar(fill = "white", alpha = 0.5, col = TRUE),
  gpar.colfil =gpar(fill = "grey90", alpha =0.5, col = NA),
  h.even.alpha = 0.5,
  equal.width = FALSE,
  show.rownames = FALSE,
  show.vlines = TRUE,
  padding.h = unit(6, "mm"),
  padding.v = unit(6, "mm")
)

m1 <- glm(Presence ~ Xinfo+pH , data=subs, family = binomial)
m2 <- glm(Presence ~ Xinfo*pH , data=subs, family = binomial)
m3 <- glm(Presence ~ Xinfo+MinEucWet+Xinfo*pH , data=subs, family = binomial)
m4 <- glm(Presence ~ Xinfo+Xinfo:MinDitchDist , data=subs, family = binomial)
m5 <- glm(Presence ~ Xinfo+Cdty , data=subs, family = binomial)
m6 <- glm(Presence ~ Xinfo , data=subs, family = binomial)

```



```

summary (m1)

##Output table with journal font goes to working directory or User documents folder
#install.packages("stargazer") #Use this to install it, do this only once
library(stargazer)
stargazer(m1, type="html",
          title="", dep.var.labels=c("Presence"),
          covariate.labels=c("pH","Surface Drainage","Intercept"),
          out="presence_pH_Xinflo.htm")

summary(Cand.models[[1]])

par(mfrow=c (1,1))
library(AICcmodavg)
library(ggplot2)
require(ggplot2)
require(reshape2)
require(lme4)
require(compiler)
require(parallel)
require(boot)

libs <- c('ggplot2', 'latticeExtra', 'gridExtra', 'MASS',
         'colorspace', 'plyr', 'Hmisc', 'scales')
lapply(libs, require, character.only = T)

#fitting of the logistic regression model
Model_best <- glm((Presence ~Xinflo+pH) ,data=subs,family=binomial )

null.model <-glm(Presence ~ 1,data=subs, family=binomial)
AIC(Model_best,null.model)
summary(Model_best)

#HERE should be GLM! glm because of logistic regression
# Does not produce R square
m <- summary(glm(subs$Presence ~subs$Xinflo+subs$pH, family=binomial))

#predicting probability of snails where ditch and ph5.5 example
blah= predict(glm(Model_best,data.frame(Xinflo =1, pH =5.25),type="response", se.fit=TRUE)
blah

##pretty R plot of mixed model
par(bg='black', fg='white', col='white', col.axis='white',
    col.lab='white', col.main='blue', col.sub='cyan')

#individual creation of xand y axes to reflect 0 and 1 only
plot(subs$pH,subs$Presence, xlab="Wetland pH", ylab="Presence", col = 'white', ylim=c(0.0,1), axes = FALSE)
axis(side=2, at=c(0:1))
axis(side=1)
box()

```

```
points(subs$pH[sub$Xinfo==1], subs$Presence[sub$Xinfo==1],cex =2, cex.axis = 1.8, pch = 17,col = "blue")
points(subs$pH[sub$Xinfo==0], subs$Presence[sub$Xinfo==0],cex =2, cex.axis = 1.8,pch = 18,col = "gold")
```

```
plot (subs$Xinfo+subs$pH,predict(Model_best),pch=18,cex=1.8,xlab="ModelBest", ylab="presence",
col="grey")
```

```
prdt<-predict(glm(Presence ~Xinfo+pH ,family=binomial, data=subs),type = "response")
prdt
prdt<-predict(mod1,type = "response")
plot(subs$pH, prdt)
par(mfrow=c(1,1))
```

```
Ditch <- as.factor(subs$Xinfo)
```

```
snaildistr <- ggplot(subs,aes(pH,prdt, color=Ditch, shape = Ditch))+
  scale_color_manual( values = c("red","blue"))+ geom_point(size = 8, position = position_jitter(w = 0, h = 0.0))
snaildistr <-snaildistr + labs(x="pH", y="Predicted probability of presence")
snaildistr
```

```
snaildistr <- snaildistr + theme(panel.background = element_rect(fill= 'black'),panel.grid.major =
element_blank(), panel.grid.minor = element_line(colour = "grey15")) +
  theme(legend.text = element_text(size = 26), legend.title = element_text(size = 26)) +
scale_y_continuous(breaks=pretty_breaks(n=4))+
  theme(axis.title.y=element_text(size=26, vjust=0.2, face = 'bold'), axis.title.x=element_text(size=32,
vjust=0.2, face = 'bold'))+
  theme(axis.text.y=element_text(size=26, vjust=0.5, face = 'bold', color ="black")) + ylim(c(0,1.0))+
  theme(axis.text.x=element_text(size=26, vjust=0.5, face = 'bold', color ="black")) +
scale_x_continuous(breaks=pretty_breaks(n=6))
snaildistr
```

```
snaildistr <- snaildistr + geom_point(aes(pH,prdt), size =4, color = "black")
snaildistr
```

```
##black and white
```

```
Ditch <- as.factor(subs$Xinfo)
snaildistr <- ggplot(subs,aes(pH,prdt,shape = Ditch, color = Ditch)) + scale_color_manual( values =
c("red","blue"))+ scale_shape_manual( values = c(17,16), labels = c("Yes","No"))+
  geom_point(size = 8, position = position_jitter(w = 0, h = 0.0))
snaildistr <-snaildistr +
  theme(plot.title = element_text(size = 18, face='bold', vjust=3))+
  labs(x="pH", y="Predicted probability of presence")
snaildistr
```

```
snaildistr <- snaildistr + theme(panel.background = element_rect(fill= 'white'),panel.grid.major =
element_blank(), panel.grid.minor = element_blank()) +
  theme(legend.text = element_text(size = 24), legend.title = element_text(size = 22)) +
scale_y_continuous(breaks=pretty_breaks(n=4))+
  theme(axis.title.y=element_text(size=22, vjust=0.2, face = 'bold'), axis.title.x=element_text(size=22,
vjust=0.2, face = 'bold'))+
  theme(axis.text.y=element_text(size=26, vjust=0.5, face = 'bold', color ="black")) +
```

```

  theme(axis.text.x=element_text(size=26, vjust=0.5, face = 'bold', color ="black")) +
scale_x_continuous(breaks=pretty_breaks(n=6))+
  theme(panel.background = element_rect(colour = "black", size=2, fill=NA))
snaildistr

##colour and shape
Ditch <- as.factor(subs$Xinfo)
snaildistr <- ggplot(subs,aes(pH,prdt,shape = Ditch, color = Ditch)) + scale_shape_manual( values = c(16,17))+
scale_color_manual( values = c("red","blue"))+
  geom_point(size = 8, fill = NA, position = position_jitter(w = 0, h = 0.0))
snaildistr <-snaildistr + theme(plot.title = element_text(size = 18, face='bold', vjust=3))+ +
scale_shape_manual( values = c(16,17),labels = c("Yes","No"))
  labs(x="pH", y="Predicted probability of presence")
snaildistr

snaildistr <- snaildistr + theme(panel.background = element_rect(fill= 'black'),panel.grid.major =
element_blank(), panel.grid.minor = element_blank()) +
  theme(legend.text = element_text(size = 24), legend.title = element_text(size = 22)) +
scale_y_continuous(breaks=pretty_breaks(n=4))+
  theme(axis.title.y=element_text(size=22, vjust=0.2, face = 'bold'), axis.title.x=element_text(size=22,
vjust=0.2, face = 'bold'))+
  theme(axis.text.y=element_text(size=26, vjust=0.5, face = 'bold', color ="black")) +
  theme(axis.text.x=element_text(size=26, vjust=0.5, face = 'bold', color ="black")) +
scale_x_continuous(breaks=pretty_breaks(n=6))+
  theme(panel.background = element_rect(colour = "black", size=2, fill=NA))
snaildistr

#spatial autocorrelation
library(nlme)
require(geoRglm)

```

REFERENCES

- Andreotta, H., M. Chimney, T. DeBusk, B. Garrett, L. Gerry, J. Henry, D. Ivanoff, M. Jerauld, M. Kharbanda, M. Kirkland, N. Larson, S. Miao, T. Piccone, K. Pietro, L. Schwartz, D. Sierer-Finn, L. Toth, S.K. Xue, Y. Yan, M. Zamorano, and H. Zhao. 2015. "Chapter 5B : Performance of the Everglades Stormwater Treatment Areas." *SFWMD 2015 South Florida Environmental Report 5B* (In M. Chimney (Ed.)): 83.
- Bates, Douglas, Martin Maechler, and Ben Bolker. 2013. "lme4: Linear Mixed-Effects Models Using S4 Classes." *R Package Version 0.999999-2*: 999999. doi:citeulike-article-id:1080437.
- Bilton, DT, JR Freeland, and Beth Okamura. 2001. "Dispersal in Freshwater Invertebrates." *Annual Review of Ecology and ...* 32 (2001): 159–181.
- Blackburn, Tim M, Petr Pyšek, Sven Bacher, James T Carlton, Richard P Duncan, Vojtěch Jarošík, John R U Wilson, and David M Richardson. 2011. "A Proposed Unified Framework for Biological Invasions." *Trends in Ecology & Evolution* 26 (7) (July): 333–9. doi:10.1016/j.tree.2011.03.023.
- Bliese, P. D. 2005. "Multilevel Modeling in R: A Brief Introduction to R, the Multilevel Package, and the NLME Package." *Downloadbar von Http://cran. Es. Rproject. org/doc/contrib/Bliese_Multilevel. Pdf. Abgerufen Am* 15: 2006. doi:http://cran.r-project.org/web/packages/multilevel/index.html.
- Bohlen, Patrick J., Sarah Lynch, Leonard Shabman, Mark Clark, Sanjay Shukla, and Hilary Swain. 2009. "Paying for Environmental Services from Agricultural Lands: An Example from the Northern Everglades." *Frontiers in Ecology and the Environment* 7 (1): 46–55. doi:10.1890/080107.
- Boughton, Elizabeth H., Pedro F. Quintana-Ascencio, Patrick J. Bohlen, David G. Jenkins, and Roberta Pickert. 2010. "Land-Use and Isolation Interact to Affect Wetland Plant Assemblages." *Ecography* (August 2009) (January): 461–470. doi:10.1111/j.1600-0587.2009.06010.x.
- Burks, Romi L., Sarah a. Hensley, and Colin H. Kyle. 2011. "Quite the Appetite: Juvenile Island Apple Snails (Pomacea Insularum) Survive Consuming Only Exotic Invasive Plants." *Journal of Molluscan Studies* 77 (4): 423–428. doi:10.1093/mollus/eyr022.
- Cáceres, Carla E., and Daniel a. Soluk. 2002. "Blowing in the Wind: A Field Test of Overland Dispersal and Colonization by Aquatic Invertebrates." *Oecologia* 131 (3): 402–408. doi:10.1007/s00442-002-0897-5.
- Carlsson, Nils. 2004. "INVADING HERBIVORY : THE GOLDEN APPLE SNAIL ALTERS." *Ecology* 85 (6): 1575–1580.
- Conner, S. L., C. M. Pomory, and P. C. Darby. 2008. "Density Effects of Native and Exotic Snails on Growth in Juvenile Apple Snails Pomacea Paludosa (Gastropoda: Ampullariidae): A Laboratory Experiment." *Journal of Molluscan Studies* 74 (4) (July 28): 355–362. doi:10.1093/mollus/eyn024.
- Cowie, R H. 2002. "Apple Snails (Ampullariide) as Agricultural Pests: Their Biology, Impacts and Management." In *Molluscs as Crop Pests*, edited by G M Barker, 576. CAB international.

doi:10.1079/9780851993201.0145 ER.

- Diamond, Jared M. 1975. "The Island Dilemma: Lessons of Modern Biogeographic Studies for the Design of Natural Reserves." *Biological Conservation* 7 (7): 129–146. doi:10.1016/0006-3207(75)90052-X.
- Glass, Nancy H., and Philip C. Darby. 2008. "The Effect of Calcium and pH on Florida Apple Snail, *Pomacea Paludosa* (Gastropoda: Ampullariidae), Shell Growth and Crush Weight." *Aquatic Ecology* 43 (4) (December 13): 1085–1093. doi:10.1007/s10452-008-9226-3.
- Havel, John E., Jonathan B. Shurin, and John R. Jones. 2002. "Estimating Dispersal from Patterns of Spread: Spatial and Local Control of Lake Invasions." *Ecology* 83 (12): 3306–3318. doi:10.1890/0012-9658(2002)083[3306:EDFPOS]2.0.CO;2.
- Hayes, Kenneth a., Robert H. Cowie, Silvana C. Thiengo, and Ellen E. Strong. 2012. "Comparing Apples with Apples: Clarifying the Identities of Two Highly Invasive Neotropical Ampullariidae (Caenogastropoda)." *Zoological Journal of the Linnean Society* 166 (4) (December 26): 723–753. doi:10.1111/j.1096-3642.2012.00867.x.
- Hunter, R Douglas. 1990. "Effects of Low pH and Low Calcium Concentration on the Pulmonate Snail *Planorbella Trivolvis*: A Laboratory Study." *Canadian Journal of Zoology* 68 (7) (July 1): 1578–1583. doi:10.1139/z90-233.
- Jenkins, David G., and Arthur L. Buikema. 1998. "Do Similar Communities Develop in Similar Sites? A Test with Zooplankton Structure and Function." *Ecological Monographs* 68 (3): 421–443. doi:10.1890/0012-9615(1998)068[0421:DSCDIS]2.0.CO;2.
- Kyle, CH, AW Kropf, and RL Burks. 2011. "Prime Waterfront Real Estate: Apple Snails Choose Wild Taro for Oviposition Sites." *Current Zoology* 57 (5).
- Lockwood, Julie L., Martha F. Hoopes, and Michael P. Marchetti. 2007. *Invasion Ecology*. 6th ed. Malden, MA: Blackwell Publishing.
- Lowe, S, M Browne, and S Boudjelas. 2004. "100 of the World's Worst Invasive Alien Species." *A Selection from the Global Invasive Species ...* (Aliens 10).
- MacArthur, Robert H, and Edward O Wilson. 1967. *The Theory of Island Biogeography / by Robert H. MacArthur and Edward O. Wilson. Monographs in Population Biology: 1*. Princeton, N. J., Princeton University Press, 1967, 1967.
- MacIsaac, H. J., and R. I. Colautti. 2004. "A Neutral Terminology to Define 'invasive' species." *Diversity & Distributions* 10: 135–141.
- Marc J. Mazerolle. 2015. "Package 'AICcmodavg.'" *R Environment*: 1–141.
- Morrison, Wendy E., and Mark E. Hay. 2010. "Feeding and Growth of Native, Invasive and Non-Invasive Alien Apple Snails (Ampullariidae) in the United States: Invasives Eat More and Grow More." *Biological Invasions* 13 (4) (September 30): 945–955. doi:10.1007/s10530-010-9881-x.

- Ostrom, April S, and Thomas C Chesnes. 2014. "An Assessment of Submersion as a Mechanical Control Technique of Pomacea Insularum Eggs in Southern Florida , USA" 2 (1): 6–10. doi:10.13189/nrc.2014.020102.
- Pimentel, David, Lori Lach, Rodolfo Zuniga, and Doug Morrison. 2000. "Environmental and Economic Costs of Nonindigenous Species in the United States." *BioScience* 50 (1): 53. doi:10.1641/0006-3568(2000)050[0053:EAECON]2.3.CO;2.
- Puth, LM, and DM Post. 2005. "Studying Invasion: Have We Missed the Boat?" *Ecology Letters*: 715–721. doi:10.1111/j.1461-0248.2005.00774.x.
- Rawlings, Timothy a, Kenneth a Hayes, Robert H Cowie, and Timothy M Collins. 2007a. "The Identity, Distribution, and Impacts of Non-Native Apple Snails in the Continental United States." *BMC Evolutionary Biology* 7 (January): 97. doi:10.1186/1471-2148-7-97.
- Rawlings, Timothy, Kenneth Hayes, Robert Cowie, and Timothy Collins. 2007b. "The Identity, Distribution, and Impacts of Non-Native Apple Snails in the Continental United States." *Bmc Evolutionary Biology* 7 (1): 97. doi:10.1186/1471-2148-7-97.
- Reiss, Kelly Chinners. 2006. "Florida Wetland Condition Index for Depressional Forested Wetlands." *Ecological Indicators* 6 (2): 337–352. doi:10.1016/j.ecolind.2005.03.013.
- Richardson, David M, Petr Pyšek, Marcel Rejmánek, Michael G Barbour, F Dane Panetta, and Carol J West. 2000. "Naturalization and Invasion of Alien Plants: Concepts and Definitions." *Diversity and Distributions* 6 (2): 93–107. doi:10.1046/j.1472-4642.2000.00083.x.
- Ricklefs, Robert E. 1987. "Community Diversity: Relative Roles of Local and Regional Processes." *Science* 235 (4785): 167–171.
- . 2004. "A Comprehensive Framework for Global Patterns in Biodiversity." *Ecology Letters* 7 (1): 1–15. doi:10.1046/j.1461-0248.2003.00554.x.
- Seuffert, María E, and Pablo R Martín. 2013. "Juvenile Growth and Survival of the Apple Snail Pomacea Canaliculata (Caenogastropoda: Ampullariidae) Reared at Different Constant Temperatures." *SpringerPlus* 2 (January): 312. doi:10.1186/2193-1801-2-312.
- Seuffert, María E., and Pablo R. Martín. 2009. "Dependence on Aerial Respiration and Its Influence on Microdistribution in the Invasive Freshwater Snail Pomacea Canaliculata (Caenogastropoda, Ampullariidae)." *Biological Invasions* 12 (6) (September 17): 1695–1708. doi:10.1007/s10530-009-9582-5.
- Simberloff, D. 2003. "Eradication - Preventing Invasions at the Outset." *Weed Science* 51 (2): 247–253. doi:10.1614/0043-1745(2003)051.
- Steinman, a. D., J. Conklin, P. J. Bohlen, and D. G. Uzarski. 2003. "Influence of Cattle Grazing and Pasture Land Use on Macroinvertebrate Communities in Freshwater Wetlands." *Wetlands* 23 (4): 877–889. doi:10.1672/0277-5212(2003)023[0877:IOCGAP]2.0.CO;2.

- Theoharides, K a, and J S Dukes. 2007. "Plant Invasion across Space and Time: Factors Affecting Nonindigenous Species Success during Four Stage of Invasion." *New Phytologist* 176 (2): 256–273.
- Václavík, Tomáš, and Ross K. Meentemeyer. 2012. "Equilibrium or Not? Modelling Potential Distribution of Invasive Species in Different Stages of Invasion." *Diversity and Distributions* 18 (1) (January 25): 73–83. doi:10.1111/j.1472-4642.2011.00854.x.
- Valéry, Loïc, Hervé Fritz, Jean-Claude Lefeuvre, and Daniel Simberloff. 2008. "In Search of a Real Definition of the Biological Invasion Phenomenon Itself." *Biological Invasions* 10 (8) (February 1): 1345–1351. doi:10.1007/s10530-007-9209-7.
- Van Leeuwen, Casper H a, Naomi Huig, Gerard Van Der Velde, Theo a Van Alen, Cornelis a M Wagemaker, Craig D H Sherman, Marcel Klaassen, and Jordi Figuerola. 2013. "How Did This Snail Get Here? Several Dispersal Vectors Inferred for an Aquatic Invasive Species." *Freshwater Biology* 58 (1): 88–99. doi:10.1111/fwb.12041.
- Vicente, Joana, Paulo Alves, Christophe Randin, Antoine Guisan, and João Honrado. 2010. "What Drives Invasibility? A Multi-Model Inference Test and Spatial Modelling of Alien Plant Species Richness Patterns in Northern Portugal." *Ecography* 33 (6): 1081–1092. doi:10.1111/j.1600-0587.2010.6380.x.
- Wada, Shinichiro, Kazuto Kawakami, and Satoshi Chiba. 2012. "Snails Can Survive Passage through a Bird's Digestive System." *Journal of Biogeography* 39 (1): 69–73. doi:10.1111/j.1365-2699.2011.02559.x.
- Wada, Takashi, Katsuya Ichinose, Yoichi Yusa, and Naoyuki Sugiura. 2004. "Decrease in Density of the Apple Snail *Pomacea Canaliculata* (Lamarck) (Gastropoda: Ampullariidae) in Paddy Fields after Crop Rotation with Soybean, and Its Population Growth during the Crop Season." *Applied Entomology and Zoology* 39 (3): 367–372. doi:10.1303/aez.2004.367.
- Wickham, H. 2008. "ggplot2: An Implementation of the Grammar of Graphics. R Package Version 0.7." ... 0.7, URL: <http://CRAN.R-Project.Org/package=ggplot2>.
- Xu, Ronghui. 2003. "Measuring Explained Variation in Linear Mixed Effects Models." *Statistics in Medicine* 22 (22): 3527–3541. doi:10.1002/sim.1572.
- Youens, Abigail K., and Romi L. Burks. 2008. "Comparing Applesnails with Oranges: The Need to Standardize Measuring Techniques When Studying *Pomacea*." *Aquatic Ecology* 42 (4): 679–684. doi:10.1007/s10452-007-9140-0.
- Meyer KD, Kent GM, Hart K, Fujisaki I. 2011 Seasonal movements and habitat use of snail kites (*Rostrhamus sociabilis*) in Florida: a comparative study of satellite and VHF tracking methodologies. (p. 44. Final Report for U.S. Fish and Wildlife Service, Vero Beach, Florida.