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ORIGINAL PAPER

Dispersal and local environment affect the spread of an invasive apple snail (*Pomacea maculata*) in Florida, USA

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Abstract Dispersal and local environmental factors are major determinants of invasive species distribution. We examined how both dispersal-related geospatial characteristics and environmental factors influence an ongoing invasion of wetlands in a south-central Florida ranchland by non-native apple snails (*Pomacea maculata*, Ampullariidae). We found *P. maculata* in 73 (43%) of a random set of 171 wetlands in 2014. We used model selection to evaluate multiple hypotheses of predictors of *P. maculata* occurrence in 95 wetlands with standing water, including spatially-explicit distances in ditches from wetlands to the presumed entry point, Euclidean (overland) distances, presence/absence of ditches in wetlands, and environmental variables (e.g. pH). We also performed a 5-month field experiment in 20 wetlands to evaluate if snail absence was associated with conditions that limit survival and growth (i.e. unfavorable habitats). Snail occurrence was primarily associated with presence of ditches in wetlands and more neutral wetland pH. These variables more plausibly explained snail occurrence than did Euclidean (overland) distance and minimum ditch travel (rectilinear) distance from propagule sources (a major waterway). Wetland pH best explained survival and growth under the experimental conditions. We found no evidence that prior occupancy by conspecifics affected survival and growth, suggesting that dispersal limitation may contribute to lack of occupancy of wetlands, despite suitable pH. Our study supports man-made conduits as facilitators of dispersal by non-native species, where environmental characteristics (here pH) then also affect colonization within habitats. An understanding of both dispersal mechanisms and local environmental factors is necessary to better predict invasive species distribution.

Keywords Invasion · *Pomacea maculata* · Dispersal · Ditches · Wetlands · Colonization · pH

Introduction

Biological invasions generally occur where there is a reduction or removal of natural barriers, resulting in significant population growth and range expansion (Valéry et al. 2008). Invasions often arise from the introduction of a non-native species into novel environments, where the species may have an advantage in the ecologically naïve recipient habitat (Valéry et al. 2008). However the introduced species does not enter an ecological vacuum, but must overcome a suite of

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constraining ecological filters that reflect a complex local legacy of biogeography, evolution and stochastic events (Ricklefs 1987, 2004). Therefore, a biological invasion is a complex interplay of dispersal opportunities to new habitats (i.e. introduction), and overcoming ecological filters to establish a local population (colonization), presumably with effects on native populations in those habitats (Francis 2012).

Despite the inherent necessity of dispersal for biological invasion and the role of local environment for successful colonization, relatively few studies analyze both aspects simultaneously. For example, Puth and Post (2005) reviewed biological invasions literature and found only 27% of studies examined dispersal at *any* stage of invasion and only 10% were focused on initial dispersal. As highlighted by Puth and Post (2005), this lack of focus on dispersal was somewhat surprising given that the efficacy of control is highest during initial introduction (Pimentel et al. 2000; Simberloff 2003). Furthermore, if the species is dispersal-limited, the full environmental niche cannot be properly defined and used to predict invasive distribution (Václavík and Meentemeyer 2012). Although examples of the importance of dispersal for invasion have increased in the last decade, the concurrent evaluation of importance of dispersal and colonization remains limited. To more fully understand invasion success, factors that affect *both* dispersal to habitats and colonization of those habitats should be studied simultaneously (Gurevitch et al. 2011).

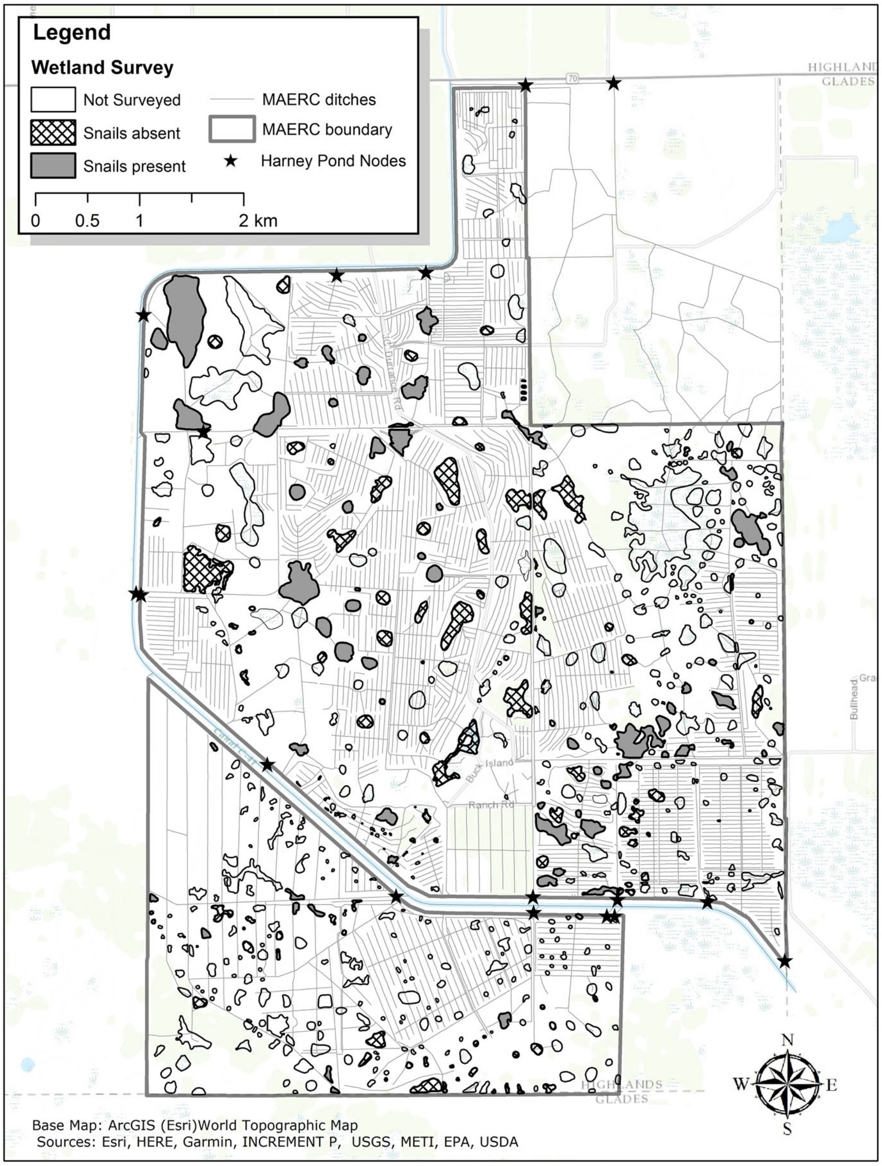
Human activity complicates the interaction between dispersal and colonization for invasive species. Landscape modification reduces and fragments “natural” habitat while introducing evolutionarily “novel” habitat that may vary widely as conduits for species movement and physiological suitability (Diamond 1975; Bilton et al. 2001; Bissonette and Adair 2008). While the probability of a species dispersing into a habitat patch increases with patch area and decreases with increasing patch isolation (Goodall 1968), anthropogenic landscapes may also introduce novel barriers or channels that modify effective dispersal distances between created patches. For example, within pastoral landscapes, large ditches installed to facilitate irrigation and drainage may impede movement of terrestrial organisms and serve as natural breaks to fires, potentially fragmenting contiguous pasture. Simultaneously the linearization of water flow across the landscape may accelerate the movement of dispersing aquatic organisms between isolated wetland systems (Mazerolle 2005; Herzon and Helenius 2008). Where appropriate, these modified dispersal pathways should be considered when calculating the functional isolation or connectivity of fragmented habitat (Mazerolle 2005; Herzon and Helenius 2008).

We examined how landscape factors affect dispersal (as inferred from presence/absence records) and local habitat variables influence an ongoing invasion by the non-native apple snail, *Pomacea maculata*, into a landscape of geographically isolated, seasonal wetlands. We estimated the spatial distribution of *P. maculata* in a random set of 171 wetlands (of ca. 600 wetlands total within the study site) to evaluate the relative importance of geospatial parameters and local habitat variables on *P. maculata* occurrence. We also conducted a translocation experiment in 20 wetlands to test the prediction that *P. maculata* absence indicates dispersal limitation.

Methods

Study system

The MacArthur Agro-Ecology Research Center (MAERC) in Lake Placid, Florida (lat 27°09″N; long 81°12″W) is a 4170-ha working cattle ranch that encompasses ca. 600 wetlands (0.01–41.9 ha) with varying levels of disturbance, spatial isolation and interconnectivity via a ditch network and irrigation structures (Fig. 1). The ranch is within the Northern Everglades watershed, and like much of South Florida, has relatively flat topography and distinct wet/dry seasons in a subtropical climate (Noss 2011). We hypothesized that the point sources of invasive *P. maculata* into MAERC are nodes of connection between MAERC ditches and Harney Pond Canal (Fig. 1) which flows slowly from Lake Istokpoga to Lake Okeechobee. The MAERC wetlands are embedded in 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 managed pastures are seeded with Bahia grass (*Paspalum notatum*), periodically limed and fertilized, and are extensively ditched to facilitate drainage (0.15 km of ditch per hectare)



Base Map: ArcGIS (Esri)World Topographic Map
Sources: Esri, HERE, Garmin, INCREMENT P, USGS, METI, EPA, USDA

Fig. 1 Map of MacArthur Agro-ecology Research Center (MAERC). MAERC has more than 600 wetlands (*dark outline*). Presence survey included 171 wetlands. *Pomacea maculata* presence was documented in ~43% (73/171) of surveyed wetlands (*solid grey fill*). Harney Pond nodes (*stars*) show the presumed entry points of *P. maculata* into the canal network at MAERC

whereas the semi-natural pastures are managed only to prevent tree encroachment (prescribed burning and occasional roller chopping) and far less ditched (0.08 km per hectare). Please refer to Boughton et al. (2010) for further information on MAERC and wetland floral assemblages.

Study organism: *Pomacea maculata*

Pomacea maculata (Perry) (Caenogastropoda:Ampullariidae) is a large-bodied dioecious but sexually monomorphic snail with a broad native range throughout South America (Rawlings et al. 2007; Hayes et al. 2012). Although anecdotal reports of *P. maculata* occurrence in Florida date back to the 1990s, molecular phylogenetic data infers multiple introductions from populations stemming from Brazil and Argentina respectively (Hayes et al. 2008), most likely due to aquaria release. These snails are particularly damaging to freshwater environments with aquatic macrophytes as they are generalist feeders on a wide variety of macrophytes. These snails are particularly successful in naïve habitats as they can reach high densities due to the high fecundity and iteroparity (Seuffert and Martín 2009; Morrison and Hay 2010; Kyle et al. 2011). However, the snails also require sufficient 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). Although no overland dispersal has been documented, these snails are quite mobile within water bodies (Seuffert and Martín 2009). These snails can also disperse passively as buoyant, free-floating individuals or attached to floating vegetative material (Cowie 2002) allowing them to easily disperse in flow. Established populations of non-native *Pomacea* apple snails can completely denude rice crops in Southeast Asia and are considered a significant threat to freshwater ecosystems (Wada et al. 2004; Carlsson 2004; Rawlings et al. 2007). Given their prodigious capacity for reproduction and their potential to modify novel aquatic habitats, *P. maculata* is ranked among the world's most invasive species (Lowe et al. 2000). We observed *P. maculata* snails in wetlands peripheral to our study site within the last 5 years, and expected the invasion to be ongoing there. We studied *P. maculata* in wetlands of a well-described agricultural landscape, where wetlands provide important foraging and water resources for cattle as well as hydrological and nutrient ecosystem services (Swain et al. 2007; Bohlen et al. 2009).

Pomacea maculata distribution

We evaluated plausible factors influencing the presence of snails in the wetlands (Table 5, 6 and 7 in "Appendix"). We included wetland level variables such as pH, conductivity, elevation, wetland area and perimeter, and presence of and number of ditches that connect with the Harney Pond Canal (inferred original source of snails). We also evaluated regional spatially explicit variables. We used intersections of the Harney Pond Canal and MAERC ditches as origination points (source points) and calculated rectilinear and Euclidean distances to all wetlands (recipient habitat). We define "rectilinear distance" as the distance between two points in the network of ditches, when measurement is constrained along the network of ditches. Euclidean distance refers to the straight-line overland distance between two points. We also evaluated wetland aggregation based on Euclidean distance and using the method described by Hanski and Thomas (1994). This equation describes the relationship of all other patches to a focal patch including effects of patch distance and patch size summarizing the effects of habitat configuration.

We predicted that minimum ditch network rectilinear distances may be strongly related to *P. maculata* presence in MAERC wetlands as these ditches provide habitat and dispersal corridors when water levels are sufficiently high. Alternatively, Euclidean (straight line) distances from source populations into MAERC wetlands would be plausible only if (a) flood conditions during the wet season connect otherwise separated wetlands for enough time for snails to crawl to another site, or (b) snails are vectored efficiently between wetlands as neonate passengers on visiting waterfowl or as mishandled/dropped prey items by limpkins (*Aramus guarana*) and Everglades snail kites (*Rostrhamus sociabilis plumbeus*) (Van Leeuwen et al. 2013; Cattau et al. 2016). In fact, flooding during the wet season is typically a matter of only days or weeks, and phoretic dispersal by birds is most common for other taxa with smaller propagules adapted to extended dormant phases (e.g., Cladocera, Figuerola and Green 2002).

Two hundred wetlands were chosen via a stratified random design to encompass variation in environmental conditions and spatial coverage of MAERC. All wetlands within MAERC were stratified independently according to (1) Euclidean distances and (2) wetland ditch distances (i.e., minimum rectilinear distances) from the connections of MAERC ditches to the Harney Pond canal (Fig. 1). Fifty wetlands per quartile were randomly selected.

Pomacea maculata occurrence

Each selected wetland was surveyed twice for snail presence, first in June–July 2014, and then again in August–September of the same year. *Pomacea maculata* presence was determined by surveying wetlands for adult snails, remnant shells and/or egg clusters (bright pink) which are oviposited on emergent structures (Posch et al. 2013). To qualify as a presence indicator, a minimum of 5 relatively intact predated (perforated) shells had to be found, at least 10 m apart within the surveyed wetland (to avoid predation middens that may transferred from other locations). The only visually-similar mollusk found in the region, the native Florida apple snail (*P. paludosa*), is not documented to occur within MAERC waterways, and its egg clusters are markedly different in egg diameter, density and color from those of *P. maculata*. During surveys, 29 of the 200 wetlands were excluded due to ambiguous wetland boundaries, ambiguous ditch connectivity or excessive cattle disturbance that prohibited reliable aquatic parameter measurement due to bioturbation. Thus, presence/absence data were collected for 171 wetlands.

Pomacea maculata colonization: suitable habitat conditions

During survey visits wetland physicochemical parameters (pH, conductivity and temperature) were measured using a YSI Professional Series Probe. Water samples (~200 ml, preserved with 2 ml HNO_3 per sample, maintained on ice) were also taken when standing water exceeded 30 cm (to avoid sediment disturbance for reliable readings with the probe), yielding physicochemical data for 95 of the seasonal wetlands. These grab samples were analyzed in the lab for water hardness (combined calcium and magnesium content) using an YSI 9500 EcoSense photometer and Palintest Water Hardness Test (Hardicol) reagents.

Pomacea maculata colonization: survival and growth

To differentiate potentially unsuitable wetland habitat from inaccessible (or un-accessed) wetland habitat, we experimentally tested *P. maculata* survival and growth in wetlands both with and without snails. Snails were first reared from seven egg clusters in laboratory conditions for eight months to approach sexual maturity and sufficient size for retention in wire mesh enclosures, and then reared in enclosures in wetlands. All snails selected for the experiment were approximately the same age, as neonate emergence from all clusters occurred within a period of two weeks. Introduced snails were naïve to wetland vegetation prior to placement in enclosures.

There was no standardized size-maturity class assignment for *P. maculata* (Burks et al. 2011). However in accordance with the morphometric work of Youens and Burks (2008) all snails used were late juveniles (~21 mm shell width). Reared snails were measured for initial size and experimental effects on growth, using standardized metrics (Youens and Burks 2008). Operculum width (Burks et al. 2011) and length were measured using a digital micrometer and snail mass (blotted wet live weight; in g) was recorded using a digital balance. Individual snails were marked on their shells with identifying codes using a non-toxic liquid correction pen (“White out”) and cyanoacrylate sealant. Snails were stratified into 3 weight classes and selected at random from classes (1 snail from each class) to ensure equitable mass in each enclosure.

Previously surveyed wetlands were sorted into (4) treatments according to *P. maculata* presence (present or absent) and pasture type (semi-natural or intensively managed). Six wetlands within each of those four treatment (n = 24) were randomly selected from a stratification of pH values measured during surveys. Completely enclosed, wire mesh enclosures (1.0 × 0.5 × 0.5 m, 12.7 mm mesh) were then placed into each of these 24 wetlands during October 2014, after the seasonal wetlands filled in. The wire mesh retained snails to prevent introduction of *P. maculata* to previously unoccupied wetlands and excluded large predators. Wetland vegetation displaced by enclosure placement (or a representative sample of neighboring vegetation) was placed into the enclosure.

A maximum density of one *Pomacea* snail per 8 l volume is recommended in captive breeding repopulation programs of the native congener to avoid significant density dependent growth effects (Conner et al. 2008), equivalent to $\leq$30 snails in the submerged enclosures. We placed only three snails (mean total mass = 43.6 g (+8.43 g SD) in each enclosure to avoid potential density dependent effects on survival and growth.

Enclosures were checked biweekly for egg mass deposition and to ensure the enclosures remained intact and upright. Egg cluster deposition, while entirely possible because snails at the experimental size can be sexually mature, was not a desired outcome as we did not want to create a population of snails in previously unoccupied wetlands. Snail growth and survival in the wetland enclosures were assessed after 5 months. Enclosures were removed and opened in February 2015, immediately after the coldest weather (frost) of the 2014–2015 South Florida winter season. Vegetation and soil contents were sifted through until snails were located. Closing or further withdrawal of closed operculum by extracted snails indicated survival. All previous growth measurements (including blotted wet weight, where possible) were repeated with collected snails. Change in measurement from individual initial values was used to indicate growth.

Statistical analyses

Pomacea maculata occurrence

We evaluated the probability of *P. maculata* presence/absence as a function of regional and wetland-specific variables in the surveyed wetlands. All models evaluating presence/absence were generalized linear models with binomial errors and a logit link. Thirty alternative models (including a null model; see "Appendix") were compared using information-theoretic model selection based on the corrected Akaike Information Criterion (AICc), utilizing the AICcmodavg package in R (Mazerolle 2013). Correlation plots were examined to ensure no collinearity of independent variables. All statistical analyses were performed using the R software package (R Development Core Team 2014, v2.15.1) and all plots were generated using the ggplot2 R package (Wickham 2008).

Pomacea maculata survival and growth experiment

We evaluated survival probability of *P. maculata* as function of experimental variables with logistic regressions and AICc-based model selection (as above). We evaluated ten generalized mixed models with wetland as the random effect (including a null model and all based on binomial errors and a logit link) using the nlme R package (Bliese 2012). Given the expected importance of pH and calcium, additive effects were considered between pH, calcium, and the remaining local variables—prior snail occupancy, soil type and pasture type.

We used linear mixed models (with wetlands as a random effect) to evaluate the effect of pH, water hardness, pasture type (i.e., semi-natural or intensively-managed) and soil type on snail growth. Again, a model selection framework (as above) was used, and a null model was included as an option. To estimate model fit, we used the lme4 R package (Bates et al. 2013) and R^2 for generalized linear mixed models (Nakagawa and Schielzeth 2013).

Results

P. maculata distribution

Our presence survey of wetlands encompassed roughly 25% of all MAERC wetlands. Of the 171 wetlands included in the presence survey, 43% (73) wetlands indicated presence of *Pomacea maculata*. Of those 171 wetlands, 95 were measured for physicochemical conditions. All physicochemical measurements were within the ranges found in other South Florida wetlands (Reiss 2006) and long term MAERC water quality datasets.

We found that a third of all MAERC wetlands (32.7%) were isolated from the ditch network (i.e. no ditches running to or from wetlands). The measured wetlands also approximate this ratio; 67 (out of 95) wetlands were extensively ditched, and 28 (29.4%) wetlands were disconnected from the ditch network. Four of the 28 wetlands (14.2%) without direct ditch connectivity showed evidence of *P. maculata* presence. In contrast, 44 of the 67 (67%) wetlands with direct ditch connectivity showed evidence of *P. maculata* presence.

The most plausible model (AICc weight = 0.68) for *P. maculata* presence included additive effects of ditch presence and pH (Table 1 and Table 8 in "Appendix"). The next most plausible model (AICc = 0.30) represented an interaction between ditch presence and pH (Table 1). We infer that ditch presence and pH affected *P. maculata* presence and represented 98% of AICc weight; for simplicity we focus on the most plausible additive model. Wetlands with ditches had a greater likelihood of snail presence than wetlands without ditches and probability of snail presence increased with pH (Fig. 2). There was evidence that probability of *P. maculata* presence increased with wetland aggregation (Hanski and Thomas index) and decreased with greater rectilinear and Euclidean distance to the main canal but these models were less plausible and support for these variables was trivial when in the same model as ditch presence (AICc weight < 0.001; Table 8 in "Appendix").

Survival and growth experiment

We deployed caged snails into 24 wetlands, and recovered 20 cages without damage (4 cages were

Table 1 Abbreviated table of AIC model selection for *P. maculata* presence

Model names	K	AICc	Delta_AICc	AICc Weight
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	<0.001
Presence ~ ditch	2	113.28	10.73	<0.001
Presence ~ ditch + ditch: minimum ditch distance	3	113.98	11.42	<0.001
Presence ~ 1	1	133.73	31.17	<0.001

Ditch = ditch presence/absence and minimum ditch distance = rectilinear nearest neighbor. Models including Euclidean distance and wetland aggregation (Hanksi index) were not included in the top models (for all models see Table 8 in "Appendix")

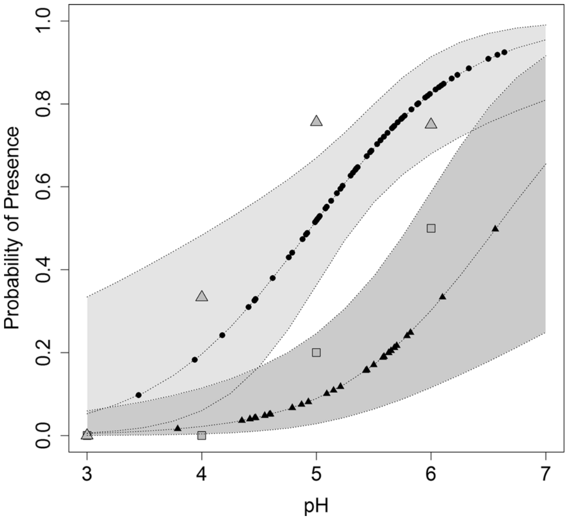


Fig. 2 Predicted probability of *P. maculata* presence as a function of ditch presence across measured values of wetland pH (95% CI as *shaded gray areas* around the model). Wetlands without ditches (*filled triangles*) had a lower likelihood of snail presence than wetlands with ditches (*filled circles*). The probability of snail presence also increases with wetland pH. Observed probabilities of snail presence (calculated with arbitrary binned proportions to maximize sample size) are shown as *gray characters*: *open gray triangles* wetlands with ditches; *open gray squares* wetlands without ditches

damaged by cattle). No egg clusters were observed during the course of this study. Of those 60 snails (3 per cage), 41 (68%) were alive at the end of the enclosure experiment. We found evidence (dead snails or empty shells) to confirm the death of 16 snails. Three snails were not present in intact enclosures and were also presumed to be dead. We did not find evidence of differences in pH and Hardness between pasture types or intended translocation sites (Table 2).

Models including wetland pH and the combination of wetland pH and water hardness were almost equally plausible predictors for *P. maculata* survival (Table 3). Evaluation of the coefficients for plausible models for survival (i.e., those with ΔAICc < 2) indicated that pH was the only plausibly important variable. Model averages indicated that pH was 12 times more important than hardness and 4 times more important than previous snail presence. There was increased probability of survival in wetlands with a more neutral wetland pH, with pH explaining 74% (mixed model R^2; 34% for fixed effects and 40% for random effects) of survival (Fig. 3). Five-month growth (i.e., shell width increase and mass increase; $n = 41$) was best predicted by wetland pH (Table 4). We found no evidence of an effect of prior presence/absence on *P. maculata* growth (Fig. 4). Estimates of variance accounted by (mixed model R^2) wetland pH were 69% (11% for fixed effects and 58% for random effects) for increase in shell width and 57% (15% for fixed effects and 42% for random effects) for increase in mass (Fig. 3).

Discussion

Both dispersal and niche requirements influence the spatial distribution of an invasive species (Sakai et al. 2001). Consistent with this expectation, the presence of the invasive *P. maculata* on MAERC was associated with dispersal-aiding spatial features, (e.g. the presence of ditches), and local wetland characteristics, primarily pH. Our results show wetlands connected to the ditch network have a higher probability of snail presence than unconnected wetlands. However, suitable habitat conditions, primarily pH, also dictate if

Table 2 Mean (and standard deviation; SD) of pH and hardness among wetlands in the survival and growth experiment

Recipient site (Pasture type, snail presence[a])	Mean pH (SD)	Mean hardness (SD)
Improved, present	5.40 (0.8)	11.8 (5.3)
Improved, absent	5.5 (0.8)	12.2 (5.3)
Semi-native, present	5.7 (0.5)	16.9 (10.2)
Semi-native, absent	5.1 (1.1)	13.1 (0.63)

Note that all wetlands used in the experiment have relatively low pH and hardness

[a] Snail presence refers to whether snails were present or absent in wetlands as determined by survey, prior to enclosure introduction

Table 3 Abbreviated table of AIC model selection for *P. maculata* survival (with random effect of wetland)

Model names	K	AICc	Delta_AICc	AICc weight
Survival ~ pH + random	3	65.9	0.00	0.30
Survival ~ pH + hardness + random	4	66.0	0.13	0.28
Survival ~ pH + previous snails + random	4	67.4	1.47	0.14
Survival ~ pH + pasture type + random	4	67.8	1.90	0.12
Survival ~ pH + pasture type + hardness + random	5	67.9	2.04	0.11

See Tables 5 and 6 in "Appendix" for additional, relatively implausible models

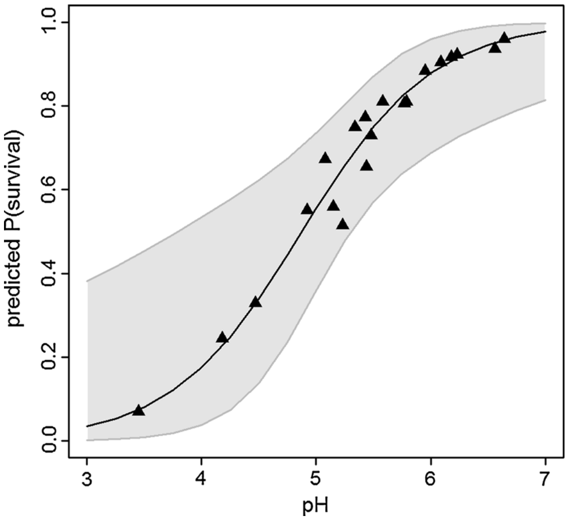


Fig. 3 Predicted probability of *P. maculata* survival after translocation as function of pH. Fixed effects are the *continuous line* (95% CI as *shaded area* around this model). Model predictions with both effects as *black triangles*. Probability of survival was increased at more neutral wetland pH. Pseudo-R^2 for pH within the mixed model for survival was 0.74 (0.34 for the fixed effects)

establishment can occur. Importantly, the absence of the invader did not reliably indicate unsuitable habitat; experimentally-transplanted snails survived and grew equally well in both previously occupied and non-occupied wetlands, depending on pH. This result suggests dispersal limitation may have prevented the invasive snail from occupying many wetlands during the study period, consistent with an ongoing invasion.

We speculate that snail dispersal initially occurred as pulses with the seasonal inundation of shallow ditches connecting primary propagule sources (Harney Pond Canal nodes) to recipient wetlands within MAERC. Because we sampled only a portion of the regional wetlands we could not evaluate the role of occupied wetlands to advance the invasion. A metapopulation patch dynamics model that includes dispersal distances between occupied wetlands as a predictor of *P. maculata* occurrence may improve subsequent research. However this would require an exhaustive presence survey of hundreds of wetlands.

pH predicted snail occurrence and explained variation in survival and growth, consistent with pH and dissolved calcium requirements for growth (Glass and Darby 2008). The probability of *P. maculata* presence decreased with lower pH, with snails found only in wetlands with pH > 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 south Florida wetland pH studies

Table 4 Generalized mixed model coefficients (and SE) for *P. maculata* survival, shell width increase and change in live mass as explained by pH

	Survival	Shell width	Live mass
Fixed effects			
Intercept	−8.6 (1.05)**	−0.43 (0.49)	−2.30 (1.43)
pH	1.76 (0.58)**	0.16 (0.09)*	0.56 (0.25)**
Random effects by wetland			
Intercept	0.37	0.19	0.44
Residual	0.61	0.08	0.65
N	60	41	41

All models include wetland level variation as a random intercept

* $p < 0.1$; ** $p < 0.05$

(Reiss 2006). Given the calcareous nature of their shells, low pH can result in thin, easily-eroded shells, increased demand for calcium to perform shell repair and can arrest growth even with high calcium availability (Hunter 1990; Glass and Darby 2008).

The ditches provide a conduit for snails coming from Harney Pond Canal sources, and presence of those ditches was best associated with *P. maculata* presence. Euclidean or rectilinear distance from the source population and the spatial configuration of wetlands (as described by the Hanski and Thomas isolation index) were associated with snail presence but these variables were less plausible drivers of dispersal into wetlands, suggesting the importance of having a connection with the putative source of invaders.

In tandem, the importance of both ditch presence and pH suggests that the ditches increase the probability of snail introduction to wetlands and pH then affects snail persistence. The fact that snails survived and grew equally well in wetlands with suitable pH (regardless of prior occupancy) suggested dispersal limitation in the ongoing invasion. The fact that rectilinear ditch and Euclidean distances were less plausible predictors of snail presence than ditch presence suggests that the ditches within the ranch serve both as conduits and snail habitat, and therefore proximity of a wetland to a ditch is a better predictor of snail access to wetlands.

Pasture intensification can influence invertebrates in wetlands (Steinman et al. 2003; Medley et al. 2015), but we did not find evidence that pasture type was an important predictor of snail performance in this study. Beyond management differences between pasture types (fertilizer application, cattle rotation, and prescribed burning) that could affect snails (Glass and Darby 2008), we expected prior lime application to intensively managed pastures to affect snail distribution, survival and growth. However, lime was applied to intensively-managed pastures in years earlier (2011) and it is possible that timing of a study relative to timing of lime application or other events (e.g., a major prescribed burn) would yield different results. The timing of management events (e.g., pasture liming) and *P. maculata* population dynamics may prove important to understand *P. maculata* population growth and potential environmental impacts.

Dispersal and dispersal limitation is widely expected to be important to understanding invasion, but is less often empirically tested in natural systems (Puth and Post 2005). When dispersal is evaluated relative to local habitat conditions, it is typically correlative, after extensive invasion has occurred (e.g., Havel et al. 2002). Our study combined correlative proxies for dispersal with measures of local habitat conditions and experimental transplants to evaluate the relative roles of dispersal limitation and local habitat suitability as controls of an ongoing invasion (Havel et al. 2002). Our results indicate that man-made conduits (i.e. ditches) can increase permeability of the landscape, facilitating the dispersal and introduction of nonnative, invasive species in complex ways not fully represented here by our distance measures. Colonization success was also affected by pH. Thus dispersal conduits (ditches) and pond habitat

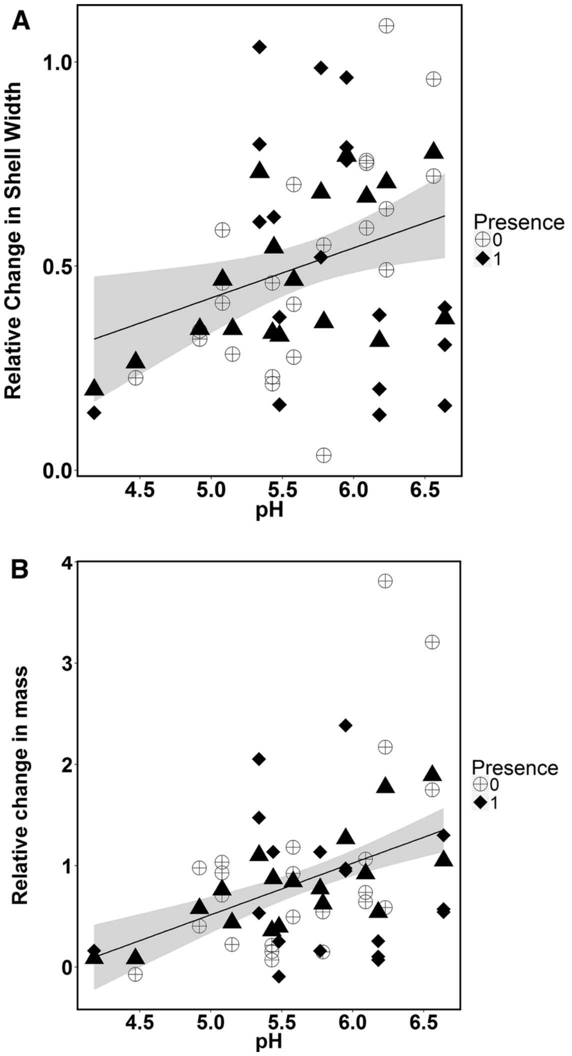


Fig. 4 Relative change in *P. maculata* mass (**a**) and shell width (**b**) across wetland pH. *Black triangles* indicate the predicted relative increase (with fixed and random effects) for recorded wetland pH values. The model based on fixed effects is represented by the *black line* and the random effect of the wetland is displayed as the deviation of the *black triangles* from the *line*. The *crosshair symbols* indicate observed relative change in wetlands where snails were not present. The *diamond symbols* indicate relative observed change in wetlands where snails were present. Pseudo-R^2 for relative change in mass with pH was 0.57 (0.15 for fixed effects). Pseudo-R^2 for relative change in shell width was 0.69 (0.11 for fixed effects)

conditions acted together to affect invasion success of these snails in this system. This result is consistent with the main point of other analyses for non-native species invasions, where human-mediated dispersal enhances spread into novel habitats (e.g., Medley 2010).

Without active and labor-intensive control efforts, *P. maculata* will likely invade most suitable wetlands at MAERC and other suitable habitats in Florida. Given sufficient expanded range and density, *P. maculata* could modify wetland vegetation and wetland ecosystem function because they are voracious consumers of most macrophytes. Submerged aquatic vegetation in storm water treatment areas (STAs) downstream of the MAERC recently experienced unprecedented defoliation due to increasing *P. maculata* populations, leading to a nearly four-fold increase in outflowing sediment and nutrient load (Cattau et al. 2016). Therefore, the unchecked proliferation of these snails increases sediment and nutrient loading into the Everglades and estuaries, which in turn reduces water quality and threatens costly restoration efforts for the historically oligotrophic Everglades and its native biota. In the Northern Everglades watershed, *P. maculata* may compete with cattle for high-quality forage in the numerous wetlands. Based on these results of this study, we recommend research on mechanisms of propagule movement and suitable habitat needed for colonization to prevent invasion success in other habitats.

Coupled with increasingly anthropogenic landscapes and globalized trade markets, long distance dispersal of potentially invasive propagules seems almost inevitable (Heger et al. 2013). Research on the effects of those introductions on habitats, and in turn habitat's influences on invader persistence and colonization, will remain crucial. Because the process of biological invasion is also contingent on propagule movement, we argue that invasion science will be better informed by also incorporating measures of species dispersal, using either direct measurements or through geospatial (Gurevitch et al. 2011).

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Appendix

See Tables 5, 6, 7, 8, 9, 10 and 11.

Table 5 Rationale for variables used to assess *P. maculata Presence*—wetland level variables

Variable description	Rationale for inclusion	Variable name[a]
Minimum and Average 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 SD for 10 points = 0.3 m)	MinElev AveElev
Conductivity	A measure of ions in solution. An indicator of nutrient load in water body	Cdty
pH	From literature re, pH is ecologically important to freshwater organism, especially those with calcareous shells	
Count of ditch entry points into wetland	The number of potential connections to sources of propagules influences propagule pressure	WetInfloCount
Wetland ditch presence	The presence of a direct ditch connection influences the probability of snail arrival and propagule pressure	Xinflo

[a] Variable name column included to facilitate understanding of R script used for analysis

Table 6 Rationale for variables used to assess snail presence—spatially explicit variables

Variable description	Rationale for inclusion	Variable name[a]
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 and Average ditch distance from point source to wetland ("rectilinear" nearest neighbor)	Distances via ditch network between the originating point source and the recipient wetland. Wetlands at closer distance to point source should be more likely to receive propagules 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	MinDitchDist AveDitchDist
Wetland area in hectares	Area available for plant growth and snail occupation	AreaHA
Isolation Index (Hanski and Thomas 1994)	Measurement of Euclidean inter-wetland distances which is a commonly used metric for the effects of wetland proximity on wetland composition	Hanski Index

[a] Variable name column included to facilitate understanding of R script used for analysis

Table 7 Rationale for selected local variable and *P. maculata* response metrics

Description of response metric/ Variable	Rationale for use	Variable name[a]
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
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 *P. maculata*. 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

[a] Variable name column included to facilitate understanding of R script used for analysis

Table 8 AICc model selection table for *P. maculata* presence

Model names	K	AICc	Delta_AICc	AICc weight	Cumulative weight
Presence ~ ditch presence + pH	3	102.56	0.000	0.68	0.68
Presence ~ ditch presence × pH	4	104.16	1.60	0.30	0.98
Presence ~ ditch presence + conductivity	3	113.06	10.5	0.00	0.99
Presence ~ ditch presence	2	113.28	10.73	0.00	0.99
Presence ~ ditch presence + ditch presence: min. ditch distance[a]	3	113.98	11.42	0.00	0.99
Presence ~ ditch presence + area	3	115.24	12.69	0.00	0.99
Presence ~ ditch presence + min. elevation	3	115.3	12.75	0.00	1.00
Presence ~ ditch presence + ave. elevation	3	115.33	12.77	0.00	1.00
Presence ~ ditch presence + min. Euclidean dist	3	115.41	12.85	0.00	1.00
Presence ~ ditch presence + perimeter	3	115.41	12.86	0.00	1.00
Presence ~ pH	2	118.87	16.32	0.00	1.00
Presence ~ conductivity	2	129.84	27.29	0.00	1.00
Presence ~ Hanski index	2	130.24	27.68	0.00	1.00
Presence ~ Wetland ID	2	131.03	28.47	0.00	1.00
Presence ~ perimeter	2	132.52	29.96	0.00	1.00
Presence ~ area	2	132.72	30.16	0.00	1.00
Presence ~ 1	1	133.73	31.17	0.00	1.00
Presence ~ average elevation	2	135.12	32.56	0.00	1.00
Presence ~ minimum elevation	2	135.44	32.88	0.00	1.00
Presence ~ min. Euclidean distance	2	135.81	33.25	0.00	1.00

[a] Not all wetlands have ditches. Ditch presence + minimum ditch distance is specified as ditch presence + ditch presence: minimum ditch distance

Table 9 AICc model selection table for *P. maculata* survival

Model names	K	AICc	Delta_AICc	AICc weight	Cumulative weight
Survival $\sim$ pH + (1|wetland)	3	65.9000	0.0000	0.2981	0.2981
Survival $\sim$ pH + calcium + (1|wetland)	4	66.0278	0.1278	0.2796	0.5777
Survival $\sim$ pH + conspecific snails + (1|wetland)	4	67.3742	1.4742	0.1426	0.7204
Survival $\sim$ pH + pasture type (1|wetland)	4	67.8022	1.9022	0.1152	0.8355
Survival $\sim$ pH + pasture type +calcium + (1|wetland)	5	67.9431	2.0431	0.1073	0.9429
Survival $\sim$ pH + pasture type + conspecific snails + (1|wetland)	5	69.5079	3.6079	0.0491	0.9919
Survival $\sim$ 1 + (1|wetland)	2	75.1148	9.2148	0.0030	0.9949
Survival $\sim$ calcium + (1|wetland)	3	75.1527	9.2527	0.0029	0.9978
Survival $\sim$ pasture type + (1|wetland)	3	76.9775	11.0775	0.0012	0.9990
Survival $\sim$ conspecific snails + (1|wetland)	3	77.2947	11.3947	0.0010	1.0000

Table 10 AICc model selection table for *P. maculata* growth: change in shell width (Δ_{width})

Model names	K	AICc	Delta_AICc	AICc weight	Cumulative weight
$\Delta_{width} \sim$ pH	4	7.6684	0	0.2428	0.2428
$\Delta_{width} \sim$ 1	3	8.4537	0.7852	0.1639	0.4067
$\Delta_{width} \sim$ pH + pasture type	5	9.5839	1.9154	0.0932	0.4999
$\Delta_{width} \sim$ pH + soil	5	9.6945	2.0261	0.0881	0.5880
$\Delta_{width} \sim$ pasture type	4	9.8478	2.1793	0.0816	0.6696
$\Delta_{width} \sim$ pH + calcium	5	10.2664	2.598	0.0662	0.7359
$\Delta_{width} \sim$ pH + conspecific snails	5	10.2696	2.6012	0.0661	0.8020
$\Delta_{width} \sim$ calcium	4	10.8278	3.1594	0.0500	0.8520
$\Delta_{width} \sim$ conspecific snails	4	10.8689	3.2005	0.0490	0.9010
$\Delta_{width} \sim$ soil type	4	10.9063	3.2378	0.0481	0.9491
$\Delta_{width} \sim$ calcium + pasture type	5	12.3769	4.7085	0.0231	0.9722
$\Delta_{width} \sim$ calcium + conspecific snails	5	13.3763	5.7078	0.0140	0.9861
$\Delta_{width} \sim$ calcium + soil type	5	13.3959	5.7275	0.0139	1.0000

Table 11 AICc model selection table for *P. maculata* growth: change in mass (Δ_{mass})

Model names	K	AICc	Delta_AICc	AICc weight	Cumulative weight
$\Delta_{mass} \sim$ pH	4	102.9065	0.0000	0.2856	0.2856
$\Delta_{mass} \sim$ pH + pasture type	5	104.6568	1.7503	0.119	0.4046
$\Delta_{mass} \sim$ pH + conspecific snails	5	104.781	1.8745	0.1119	0.5165
$\Delta_{mass} \sim$ pH +soil	5	105.0417	2.1353	0.0982	0.6147
$\Delta_{mass} \sim$ 1	3	105.1639	2.2575	0.0924	0.7070
$\Delta_{mass} \sim$ pH + calcium	5	105.5096	2.6032	0.0777	0.7847
$\Delta_{mass} \sim$ soil	4	105.9744	3.068	0.0616	0.8463
$\Delta_{mass} \sim$ pasture type	4	106.3232	3.4167	0.0517	0.8981
$\Delta_{mass} \sim$ conspecific snails	4	107.3602	4.4537	0.0308	0.9289
$\Delta_{mass} \sim$ calcium	4	107.4296	4.5231	0.0298	0.9586
$\Delta_{mass} \sim$ calcium + soil	5	108.5654	5.6589	0.0169	0.9755
$\Delta_{mass} \sim$ calcium + pasture type	5	108.7517	5.8452	0.0154	0.9908
$\Delta_{mass} \sim$ calcium + conspecific snails	5	109.786	6.8795	0.0092	1.0000

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