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Investigation of Darwin's naturalization hypothesis in invaded macrophyte communities

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Abstract Although native macrophytes are beneficial in aquatic ecosystems, invasive macrophytes can cause significant ecological and economic harm. Numerous studies have attributed invasiveness to species' characteristics, whereas others attribute invasion to biotic and abiotic characteristics of the invaded community. It has been suggested that studying the link between invader and invaded community is key to understanding invasiveness, and that invasions can be understood through the framework of community ecology theory. Charles Darwin hypothesized that introduced species would be less likely to naturalize in areas containing closely related species [Darwin's naturalization hypothesis (DNH)], suggesting competition between closely related species could limit naturalization potential (phylogenetic repulsion). The goal of this research was to test DNH using two species of highly invasive aquatic plants, *Myriophyllum spicatum* L. and *Potamogeton crispus* L., and assess whether results were consistent at small and large scales. Twenty-nine lakes containing invasive macrophytes were surveyed between 1997 and 2011. Invasive *P. crispus* occurred in 15 lakes and *M. spicatum* occurred in 19 lakes. There were 15 native *Potamogeton* species and 4 *Myriophyllum*. We used generalized linear mixed models with congeneric species richness data to estimate probability of invasive *P. crispus* or *M. spicatum* occupying a given sampling location. Contrary to predictions of DNH, the relationship between congeneric richness and presence of *P. crispus* at point and lake scales was positive. Unlike models for *P. crispus*, native *Myriophyllum* genera richness was not a significant model parameter. These results do not support DNH (the expectation of a negative relationship); furthermore, models had relatively low determination coefficients indicating very little explained variation. Although this study found no evidence for DNH, there is still a need to investigate how community assembly processes influence species invasions.

Keywords Aquatic plants · Niche theory · Biodiversity · *Myriophyllum spicatum* · *Potamogeton crispus*

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Introduction

Species invasions are highly non-random in freshwater ecosystems (Strayer 2010), and although native macrophytes are beneficial, invasive aquatic plants can cause significant ecological and economic harm. High densities of invasive macrophytes such as *Myriophyllum spicatum* and *Hydrilla verticillata* interfere with foraging and spawning of some fish species (Valley and Bremigan 2002; Theel and Dibble 2008). Canopy forming invasive plants reduce light transmittance and oxygen diffusion into the water column which can lead to anoxic zones unsuitable for other aquatic organisms (Thomas and Room 1986; Caraco and Cole 2002). Because of physiological differences of introduced plants, nutrient cycles may be altered in some systems (Templer et al. 1998; Angeloni et al. 2006). They may also interfere with recreational opportunities and navigation, and can block water intakes (Madsen et al. 1991a). In addition, invasive aquatic plants may hybridize with native species, threatening native diversity (Boylan et al. 1999; Ailstock et al. 2001; Houlahan and Findlay 2004; Moody and Les 2007). Reservoirs and impoundments may facilitate invasion due to human-induced disturbances (Havel et al. 2005; Johnson et al. 2008); therefore, understanding the factors that lead to increased probability of invasion is of high importance to ecologists and aquatic resource managers.

Although the problems associated with invasive species are widely acknowledged and studied, there has been little predictive understanding of the mechanisms that lead to species invasion (Cadotte et al. 2006). There have been numerous studies attributing invasiveness to the characteristics of a species, whereas other studies link invasion to characteristics of the invaded community (including biotic and abiotic characteristics; Levine 2000; Kolar and Lodge 2001; Chadwell and Engelhardt 2008; Jacobs and MacIsaac 2009). Although there is theoretical support for these divergent claims, empirical evidence has not reconciled the differences, and it has been suggested that studying the match between invader and invaded community is key to understanding invasiveness (Ricciardi and Atkinson 2004).

It has been proposed that invasions can be understood through the framework of community ecology theory (Shea and Chesson 2002; Fargione et al. 2003). This may be an interesting approach but defining the framework requires an assumption of how communities are assembled. There are two general theories of community assembly that may be applied to the study of species invasions (Gravel et al. 2006). Niche theory of community development predicts that the community evolves as species interact and natural selection occurs (MacArthur and Levins 1967; Levine 2000). Competitive exclusion therefore would limit the ability of species with related traits to co-exist. The alternative is a neutral theory in which species are equivalent, co-occurrence patterns are simply treated as random, and competition between related species plays only a small role in the structure of the community (Hubbell 2001).

The usefulness of neutral theory of biodiversity may be simply to provide a null model to test patterns of species co-occurrence (i.e., to test if assembly rules exist; Dodds 2009). In the context of species invasions, if niche theory and species interaction are responsible for species co-occurrence patterns, interaction patterns should be evident among closely related species when niche conservatism is high within a group, and biogeographically disjunct populations are a result of vicariant or random dispersal events (i.e., evolutionary histories of species were not sympatric; Cavender-Bares et al. 2009).

The origin of these ideas goes back to the classical development of ecological theory. Charles Darwin hypothesized that introduced species would be less likely to naturalize (although his original hypothesis was opposite) in areas containing closely related species [Darwin's naturalization hypothesis (DNH); Darwin 1859; Daehler 2001]. The underlying assumption of this idea is based in niche theory and suggests that competition between closely related species could limit the naturalization potential from an introduced species (Fargione et al. 2003; MacDougall et al. 2009). Several studies have argued that phenotypic similarity between native communities and invaders reduces the success of invading species. This means that potential biotic resistance can be identified for a particular subset of species when gauging invasion risk, if assumptions are made that phenotypic similarity correlates with phylogenetic relatedness (Strauss et al. 2006; Proches et al. 2008). In addition to competition, closely related species may also share similar enemies which may provide another mechanism of community resistance to invasion (Strauss et al. 2006). Phylogenetic relatedness is implicitly expected to correlate with net ecological similarity (Strauss et al. 2006). The alternative interpretation of this potential mechanism is that more closely related species also may have similar resource requirements (and traits), which would facilitate co-existence. However, this would be expected where resources are not limiting (Shea and Chesson 2002).

Although community attributes may be an important determinant of invasion success, results of experimental and observational studies have been inconclusive and have differed across spatial scales (e.g., Kennedy et al. 2002; Stohlgren et al. 2003; Thomaz and Michelan 2011). Fridley et al. (2007) reviewed evidence for native-exotic richness relationships and found that, in general, small scale studies reported a negative relationship whereas large scale studies reported the opposite. This "invasion paradox" (sensu Fridley et al. 2007) opens new doors for inquiry into the causes of these seemingly scale dependent patterns and also provides opportunity to include community descriptors other than species diversity (e.g., congeneric richness) to predict invasion success.

Testing DNH may prove useful for studies of species invasion because it relates characteristics of a species to the characteristics of an invaded community (implied ecological similarity due to congeneric relatedness; Ricciardi and Atkinson 2004). In addition, species invasions provide an interesting opportunity to test hypotheses of community assembly by examining phylogenetic attraction versus phylogenetic repulsion (Cavender-Bares et al. 2004). The expectation would be that if phylogenetic repulsion is present, competition may indeed limit the absolute number of niches able to occupy a given area (e.g., niche saturation potential).

Two macrophyte species of special concern are Eurasian watermilfoil (*Myriophyllum spicatum*) and curlyleaf pondweed (*Potamogeton crispus*). *Myriophyllum spicatum* is an invasive vascular plant that has invaded freshwater lakes across the United States. The introduction of this species has likely resulted in the alteration of the complex interactions occurring in littoral habitats (Madsen 1997). *Myriophyllum spicatum* has been associated with declines in native plant species richness and diversity (Madsen et al. 2008, 1991b), reductions in habitat complexity resulting in reduced macroinvertebrate abundance or diversity (Keast 1984; Cheruvelil et al. 2002), and reductions in fish growth (Lillie and Budd 1992). *Myriophyllum spicatum* poses nuisance problems to humans by impeding navigation, limiting recreation opportunities, and increasing flood frequency and intensity (Madsen et al. 1991a). It is primarily spread by fragmentation and can be easily transported between water bodies by many vectors making it difficult to control after establishment. *Potamogeton crispus* also causes significant nuisance problems where it has become established (Catling and Dobson 1985; Bolduan et al. 1994; Woolf and Madsen 2003). It, like *M. spicatum*, is an influential invader that can accelerate internal nutrient loading and eutrophication (James et al. 2002). Management of this species is often more difficult due to its life history strategy (turion production) and the limited availability of effective management options. More information on the life histories of these species can be found in Nichols and Shaw (1986).

The goal of this research was to test Darwin's Naturalization Hypothesis using two species of highly invasive aquatic plants, *M. spicatum* and *P. crispus*, and assess whether results were consistent at small and large scales. Based on DNH, probability of occurrence of an invasive species should be less as number of congeneric species increases at a location (i.e., have a negative relationship). We also tested the alternative hypothesis that native species richness and/or distance to nearest known occurrence of these species were related to the probability of occurrence at the point scale and that native species richness and/or area were related to the probability of occurrence at the lake scale. To address these hypotheses we asked the following questions at a small (point) and large (lake) scale: (1) Is presence of invasive species related to number of congeneric species occurring at a sampling location? (2) Is presence of invasive species related to native species richness occurring at a sampling location? (3) At a point scale, is presence of invasive species related to distance to nearest known location of the species (indicating dispersal rather than community attributes might be responsible for probability of occurrence)? and (4) At the lake scale, is presence of invasive species related to lake area (indicating absolute areal scale vs. ecosystem level scale as contributing factors)? In addition, if significant relationships existed, we noted whether they were positive, negative, or non-linear and evaluated which hypothesis was best supported by the data.

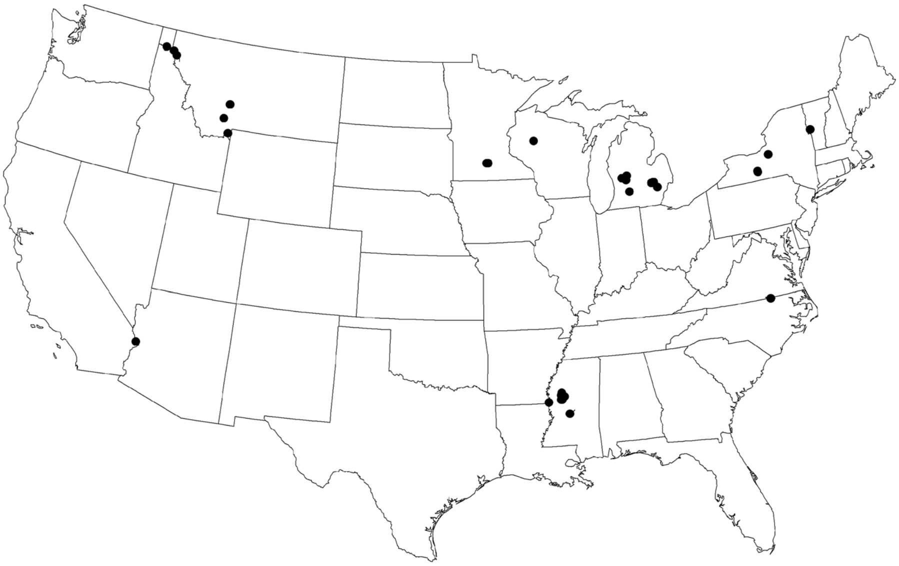

Fig. 1 Location of 29 lakes surveyed in the conterminous United States for aquatic invasive plants from 1997 to 2011

Methods

Study areas and design

The study area spanned the conterminous United States, where lakes and reservoirs (hereafter lakes; $n = 29$) were surveyed once at various times from 1997 to 2011 (Fig. 1). Lakes represented a variety of areas ranging from 7 to 36,000 ha and 9 freshwater ecoregions (Appalachain Piedmont 1, Chesapeake Bay 2, Colorado 1, Columbia Glaciated 3, Laurentian Great Lakes 8, Lower Mississippi 7, St. Lawrence 1, Upper Mississippi 3, Upper Missouri 3). Each lake was originally surveyed for a specific project goal to obtain a baseline of invasive and native species occurrence and distribution during peak growing season using the point-intercept method (Madsen 1999). Additional information on surveyed lakes can be found in Fleming (2012). For each lake, a grid of points was generated in a GIS and integrated with field GPS to navigate to each point by boat. Point spacing varied by lake area to ensure representative sampling in each lake. At each sample point, a rake was tossed and retrieved to collect plants occurring at that location. Rake tosses generally collect plants directly under the boat and are dragged 1–2 m along the bottom. This method allowed a large number of samples to be collected and insured that all plants occurring in an area were accounted for. Each plant collected was identified to species and recorded as present (1) or absent (0) at the location.

Additionally, distance (DIST) of each point to the nearest reported location of *P. crispus* and *M. spicatum* was calculated. Using data obtained from the USGS Nonindigenous Aquatic Species (NAS) database, points where each species was recorded were plotted in ArcGIS. Euclidian distances were then calculated for each point intercept survey location to the nearest recorded USGS NAS database location. Because random or auto-correlated dispersal may be responsible for presence of invasion and not specific characteristics of the community per se, this allowed us to test the alternative hypothesis that processes not related to a species' niche (i.e., neutral or random processes) may be more supported than niche based hypotheses.

All input variables [native congenerics (NC), native species richness (NSPP), and distance (DIST)] were centered and standardized to 2 standard deviations ($\text{Mean} = 0$, $\text{SD} = 0.5$) to improve model convergence because of differences in parameter value scales. This also allows more direct interpretation of the relative strength of parameter estimates for a given dataset.

We tallied numbers of native *Potamogeton* and *Myriophyllum* species for each survey location (native congenerics; NC). This allowed modeling presence of *P. crispus* and *M. spicatum* as a function of number of respective congenerics at a particular location. To test DNH at a larger scale, species and congeneric richness were aggregated, and total area was calculated for each lake.

Modeling and analysis

To estimate probability of invasive *P. crispus* or *M. spicatum* occupying a given sampling location, generalized linear mixed models with congeneric and native species richness data along with distances to nearest recorded location were used, and their performances were compared to select the best supported hypothesis. Models were developed using the lmer package in R (R Development Core Team 2012) and fit using the binomial family and logit link function with lake as a random effect.

For point scale analyses, model terms specific to the original hypotheses were selected. For presence of an invasive species, NC (native congenerics), NC^2 (quadratic native congenerics), DIST (distance to nearest recorded location), NSPP (native species richness), and $NSPP^2$ (quadratic native species richness) were used. Quadratic terms for congeneric and native species richness were included to test for potential non-linear effects on probability of occurrence of invasive species. Congeneric and native species richness were collinear for *Potamogeton* (Spearman correlation coefficient >0.4), and were not included in the same model in any model set, including those for *Myriophyllum* (for consistency). We also included global (excluding either NSPP or NC due to collinearity as noted above) and null models. All relevant combinations (i.e., avoiding collinearity) of these model terms were fit to separate models because we made no a priori assumptions that a particular subset of these model terms would provide more explanatory power than another.

For a test of DNH at the lake scale, the aggregated totals for NC, NC^2, NSPP, $NSPP^2$ and AREA (lake area) were used. These terms were centered and standardized to 2 standard deviations (Mean = 0, SD = 0.5). To estimate probability of invasive *P. crispus* or *M. spicatum* occupying a given lake, we fit a generalized linear model for binary data using the lake scale variables. The modeling approach was identical to the one used at the point scale; however, we did not include random effects because each lake represented the experimental unit of interest.

Ten models were created (including a null model) for each species (*P. crispus* and *M. spicatum*) at point and lake scales (i.e., four separate sets of 10 models). Performance of each model within a set (i.e., DNH and each alternative hypothesis) was evaluated using Akaike Information Criterion (AIC). At the point scale, sample sizes were sufficiently large relative to number of explanatory variables and therefore no adjustments were made to AIC scores. However, at the lake scale we used AIC corrected for small sample size (Burnham and Anderson 2002). Determination coefficients (pseudo-R^2 values) were also calculated to estimate amount of variation actually explained by each model.

Results

Twenty-nine lakes containing invasive macrophytes were surveyed between 1997 and 2011. Ninety-one species were identified including 11 species considered invasive; although *M. spicatum* and *P. crispus* were primarily the only species with multiple potential congenerics. A total of 10,547 points were surveyed. Of these, 4,113 (39 %) contained at least one plant and had a depth greater than zero. Total number of points surveyed averaged 363.7 (SD = 421.0) per lake, ranging from 55 to 1,623. Total number of points used in analyses (N = 4,113) averaged 141.8 (SD = 120.7) per lake ranging from 24 to 636. Invasive *P. crispus* occurred at 307 points and in 15 lakes and *M. spicatum* occurred at 1,130 points and 19 lakes. In total, there were 15 native species belonging in the *Potamogeton* genus and 4 in *Myriophyllum*.

For models testing competing hypotheses for *P. crispus* at the point scale, all models (n = 10) converged. Interestingly, native congeneric species richness (NC) and NC^2 were significant model terms when modeled separately from NSPP (Table 1). However, contrary to the predictions of DNH, the relationship between congeneric richness and presence of *P. crispus* was positive and non-linear. This evidence does not support DNH (the expectation of a negative relationship), except at extremely high values of native congeneric richness. Native species richness (NSPP) and $NSPP^2$ showed a positive, non-linear relationship with *P. crispus* occurrence. However,

Table 1 Model results for *P. crispus* at the point scale

Model terms[a]																		
Potamogeton NC	L	U	*Potamogeton* NC^2	L	U	NSPP	L	U	NSPP^2	L	U	DIST	L	U	AIC[b]	ΔAIC[c]	w_i^d	Psuedo-R^2
						1.72 (0.22)	1.29	2.15	**−0.28 (0.15)**	−0.57	0.01				**1,471.54**	**0.00**	**0.522**	0.06
						1.41 (0.15)	1.12	1.70							**1,473.43**	**1.89**	**0.203**	0.06
						1.72 (0.22)	1.29	2.15	**−0.28 (0.15)**	−0.57	0.01	−0.26 (1.04)	−2.30	1.78	**1,473.48**	**1.94**	**0.198**	0.06
						1.41 (0.15)	1.12	1.70				−0.25 (1.03)	−2.27	1.77	1,475.37	3.83	0.077	0.06
1.20 (0.22)	0.77	1.63	**−0.34 (0.16)**	−0.65	−0.03										1,524.76	53.23	0.000	0.02
1.20 (0.23)	0.75	1.65	**−0.34 (0.16)**	−0.65	−0.03							−0.41 (0.98)	−2.33	1.51	1,526.59	55.05	0.000	0.02
0.85 (0.14)	0.58	1.12													1,527.54	56.00	0.000	0.02
0.84 (0.14)	0.57	1.11										−0.41 (0.98)	−2.33	1.51	1,529.37	57.83	0.000	0.02
															1,558.64	87.10	0.000	Null
												−0.54 (0.99)	−2.48	1.40	1,560.33	88.80	0.000	0

Where parameters estimates have been omitted in the table, those parameters were not fit in the model. Models are listed in order of performance (best to worst). Data were collected from 29 lakes in the United States from 1997 to 2011

Bold parameter estimates are significant at $p < 0.1$

[a] Model terms are native congenerics (NC), native species richness (NSPP), and distance to nearest recorded location (DIST). Non-binary input variables were all standardized to 2 SD

[b] Akaike's Information Criterion Score

[c] ΔAIC = the difference between the AIC value of the best supported model and successive models

[d] W_i = Akaike model weight

Table 2 Model results for *P. crispus* at the lake scale

Model terms[a]																		
Potamogeton NC	L	U	*Potamogeton* NC^2	L	U	NSPP	L	U	NSPP^2	L	U	AREA	L	U	AIC$_c^b$	ΔAIC[c]	w_i^d	Psuedo-R^2
2.48 (1.03)	**0.46**	**4.50**													36.88	0.00	0.432	0.19
2.48 (1.1)	**0.32**	**4.64**	1.24 (2.82)	−4.29	6.77										39.16	2.28	0.139	0.2
						2.04 (0.99)	**0.10**	**3.98**							39.19	2.30	0.137	0.14
2.46 (1.05)	**0.40**	**4.52**										0.28 (1.48)	−2.62	3.18	39.34	2.46	0.126	0.19
						2.02 (1.01)	**0.04**	**4.00**	0.21 (1.83)	−3.38	3.80				41.67	4.79	0.039	0.14
						2.02 (1.02)	**0.04**	**4.04**				0.01 (1.21)	−2.36	2.38	41.68	4.79	0.039	0.14
2.49 (1.12)	**0.29**	**4.69**	1.3 (3.01)	−4.60	7.20							0.32 (1.80)	−3.21	3.85	41.83	4.95	0.036	0.2
															42.32	5.43	0.029	Null
												0.65 (0.95)	−1.21	2.51	44.05	7.17	0.012	0.1
						2.01 (1.03)	**−0.01**	**4.03**	0.19 (1.87)	−3.48	3.86	0.08 (1.25)	−2.37	2.53	44.38	7.49	0.010	0.14

Where parameters estimates have been omitted in the table, those parameters were not fit in the model. Models are listed in order of performance (best to worst). Data were collected from 29 lakes in the United States from 1997 to 2011

Bold parameter estimates are significant at $p < 0.1$

[a] Model terms are native congenerics (NC), native species richness (NSPP), and variables were all standardized to 2 SD

[b] Corrected Akaike's Information Criterion Score

[c] ΔAIC = the difference between the AIC value of the best supported model and successive models

[d] w_i = Akaike model weight

when comparing performances of NSPP and NC models, NSPP models performed better (i.e., had a lower AIC score and greater determination coefficient; Table 1). Also interestingly, NSPP and NC have non-linear effects. Although the relationship is initially positive, at large values of native species or congeneric richness, the influence changes to negative. Distance to nearest recorded location (DIST) was not a significant variable in any *P. crispus* model where it was included as a term. This indicates that non-random processes are likely influencing prescence of *P. crispus*.

Models testing DNH for *P. crispus* at the lake scale indicated a significant positive relationship between probability of occurrence and NC, providing no evidence to support DNH at this scale (Table 2), but indicates that co-occurrence may be facilitated by similar non-limited resource requirements. Other competing hypotheses (e.g., lake area) did not indicate significant support although NSPP was significant when it was included by itself in the model. The model containing only NC performed best in the set.

For models testing DNH for *M. spicatum*, only eight of the ten models converged. Models containing NC^2 (for *Myriophyllum*) did not converge. Although there were 4 native *Myriophyllum* species located in the study, there was never more than one native *Myriophyllum* at a sample point. This is likely responsible for model convergence failure because this causes the terms NC and NC^2 to be perfectly collinear. Unlike models for *P. crispus*, native *Myriophyllum* species richness (NC) was not a significant model term when modeled separately from NSPP, providing no evidence to support DNH (Table 3). However, NSPP, $NSPP^2$, and DIST were all significant, and the model containing all three terms outperformed all other models. Unlike the patterns for *P. crispus*, patterns of native species richness for *M. spicatum* were negative and non-linear providing some evidence to support biotic interaction with native species other than congenerics. DIST was significantly negatively correlated with *M. spicatum* presence, and models containing NSPP, $NSPP^2$, and DIST performed better than the models containing only the individual terms, indicating that dispersal events also play an important role in determining which areas may be invaded by this species. This also may indicate that specific reproductive or dispersal techniques are important to probability of occurrence across different scales. However, the relatively low determination coefficient indicated very little variation is actually explained by the model.

Models testing DNH for *M. spicatum* at the lake scale indicated a significant positive relationship between probability of occurrence and native species richness (Table 4). However, the relationship between occurrence and NC was not significant, providing no evidence to support DNH at this scale. Only native species richness was significant in the whole set of models and the model containing only native species richness performed best (lowest AIC and greatest determination coefficient). There was no evidence that lake area influenced presence of *M. spicatum*.

Discussion

Studying invasions in the context of community ecology theory has been suggested as a way to rectify some problems encountered by invasion ecologists who have struggled to identify consistent theories of species invasion (Shea and Chesson 2002). One way to investigate patterns of species invasions accounting for characteristics of a species and the invaded community is by testing DNH (MacDougall et al. 2009; Thomaz and Michelan 2011). This hypothesis is also useful for testing niche based theories that form the foundation of community assembly rules by assuming that related (congeneric) species share similar traits, and by extension resource requirements, making them less likely to co-exist in the event that one species is introduced into a community with limited resources that already contains a congeneric species (Fargione et al. 2003; Cavender-Bares et al. 2009). DNH has been tested rarely (Ricciardi and Atkinson 2004), but has made a recent resurgence in the ecological literature (e.g., Daehler 2001; Lambdon and Hulme 2006; Jiang et al. 2010). However, there are still limited data from only a few ecosystem types, a deficiency which necessitates further inquiry.

We found no evidence to support DNH, and where congeneric richness provided a significant contribution to prediction (which only occurred with *P. crispus*), the relationship was positive (the opposite of DNH predictions). Similar results have been reported on studies of plants inhabiting Mediterranean islands (Lambdon and Hulme 2006). At the point scale, native species richness outperformed

Table 3 Model results for *M. spicatum* at the point scale

Model terms[a]																
Myriophyllum NC	L	U	*Myriophyllum* NC^2	NSPP	L	U	NSPP^2	L	U	DIST	L	U	AIC[b]	ΔAIC[c]	w_i^d	Psuedo-R^2
				−0.24 (0.14)	**−0.51**	**0.03**	**0.73 (0.13)**	**−0.98**	**−0.48**	**−6.82 (1.73)**	**−10.21**	**−3.43**	**2,761.40**	**0.00**	**1.000**	0.03
				0.31 (0.11)	**0.09**	**0.53**				**−6.87 (1.72)**	**−10.24**	**−3.50**	2,794.85	33.45	0.000	0.02
				−0.25 (0.14)	**−0.52**	**0.02**	**0.75 (0.13)**	**−1.00**	**−0.50**				2,796.36	34.95	0.000	0.02
										−6.84 (1.71)	**−10.19**	**−3.49**	**2,801.05**	39.65	0.000	0.01
0.14 (0.19)	−0.23	0.51								**−6.83 (1.70)**	**−10.16**	**−3.50**	2,802.50	41.10	0.000	0.01
				0.31 (0.11)	**0.09**	**0.53**							2,830.92	69.52	0.000	0
													2,837.12	75.72	0.000	Null
0.15 (0.19)	−0.22	0.52											2,838.53	77.13	0.000	0
NA			NA							NA			NA	NA		NA
NA			NA										NA	NA		NA

Where parameters estimates have been omitted in the table, those parameters were not fit in the model. Models are listed in order of performance (best to worst). Data were collected from 29 lakes in the United States from 1997 to 2011

Bold parameter estimates are significant at $p < 0.1$

[a] Model terms are native congenerics (NC), native species richness (NSPP), and distance to nearest recorded location (DIST). Non-binary input variables were all standardized to 2 SD

[b] Akaike's Information Criterion Score

[c] ΔAIC = the difference between the AIC value of the best supported model and successive models

[d] w_i = Akaike model weight

Table 4 Model results for *M. spicatum* at the lake scale

Model terms[a]																		
Myriophyllum NC	L	U	*Myriophyllum* NC^2	L	U	NSPP	L	U	NSPP^2	L	U	AREA	L	U	AIC$_c$[b]	ΔAIC[c]	W_i[d]	*Psuedo*-R^2
						3.28 (1.38)	**0.58**	**5.98**							32.77	0.00	0.475	0.24
						3.30 (1.25)	**0.85**	**5.75**	−2.41 (1.93)	−6.19	1.37				33.98	1.21	0.259	0.28
						3.34 (1.41)	**0.58**	**6.10**				−0.41 (1.57)	−3.49	2.67	35.21	2.44	0.140	0.24
						3.33 (1.30)	**0.78**	**5.88**	−2.37 (1.97)	−6.23	1.49	−0.12 (1.20)	−2.47	2.23	36.68	3.91	0.067	0.28
1.56 (1.05)	−0.50	3.62													39.05	6.28	0.021	0.07
															39.51	6.74	0.016	Null
0.30 (182.8)	−357.99	358.59	12.2 (2,232.4)	−4,363.30	4,387.70										41.23	8.45	0.007	0.08
												0.55 (1.06)	−1.53	2.63	41.48	8.71	0.006	0
1.54 (1.08)	−0.58	3.66										0.17 (1.38)	−2.53	2.87	41.53	8.76	0.006	0.07
0.27 (181.9)	−356.25	356.79	12.4 (2,221.7)	−4,342.13	4,366.93							−0.21 (1.87)	−3.74	3.32	43.92	11.15	0.002	0.08

Where parameters estimates have been omitted in the table, those parameters were not fit in the model. Models are listed in order of performance (best to worst). Data were collected from 29 lakes in the United States from 1997 to 2011

Bold parameter estimates are significant at $p < 0.1$

[a] Model terms are native congenerics (NC), native species richness (NSPP), and lake area (AREA). Non-binary input variables were all standardized to 2 SD

[b] Corrected Akaike's Information Criterion Score

[c] ΔAIC = the difference between the AIC value of the best supported model and successive models

[d] w_i = Akaike model weight

congeneric richness, indicating species relatedness may be less important than number of native species occupying an area. Models for *P. crispus* showed the relationship was positive and non-linear for total native species and congenerics indicating that resources only become limiting when richness is high, or that *P. crispus* has a competitive advantage over a small subset of the species pool which only disappears with greater species richness. Theoretically this is plausible because as species richness increases, accumulation of niches occurs which potentially increases interspecific interaction (Proches et al. 2008). This could also indicate that in many sampling locations community assembly has not reached equilibrium (i.e., is not yet mature), assuming assembly is based on niche theory (Shea and Chesson 2002; Wilson 2007). At the lake scale, DNH was similarly unsupported but there was a significant positive relationship between probability of occurrence and native congeneric richness for *P. crispus*. Probability of occurrence of *P. crispus* also had a marginally significant positive relationship with native species richness, but at the lake scale, congeneric richness performed best. The latter of these results supports previous work that has found a positive relationship between invasive species and native species richness at large scales (Fridley et al. 2007). The former may be an indication that mechanisms contributing the “invasion paradox” may also act on congeneric species at large scales (i.e., positive relationships manifest at large scales due to increases environmental heterogeneity). However, it may also provide evidence that an introduced species closely related to species in a native community can naturalize more easily because of shared resource requirements and/or traits. If this is the case, interspecific interaction would be weak between introduced species and those in the native community, and it is likely that resource competition would not provide a biotic resistance to invasion. Careful consideration should be made when inferring from these patterns because studying these organisms at scales irrelevant to the mechanisms being tested is meaningless (Proches et al. 2008).

Although these results did not support DNH, there is still a great need to investigate how community level factors influence species invasions. This could be useful in reconciling patterns revealed by the “invasion paradox” which notes species diversity is negatively related to invasion at small scales but positively related at larger scales (Fridley et al. 2007). This is generally explained by strong interspecific interaction at small scales and greater environmental heterogeneity at large scales (Fridley et al. 2007). One of the major issues contributing to this paradox may be a limitation of using species diversity as a community descriptor. Using species diversity as a contributing factor to species invasions assumes that more resources are sequestered (used by a particular dimension of niche space) with increasing numbers of species. This, however, does not account for any functional diversity or evolutionary history of the community other than how many species currently occupy an area, and does not reveal any patterns of community assembly (Proches et al. 2008); the diversity observed in a community could still be based on random dispersal events, not the accumulation of niches resulting in a decrease in available space within particular niche dimensions. Phylogenetic diversity (based on relatedness), however, may be better at elucidating patterns of community assembly because it explicitly considers evolutionary history and assumes that related species share similar functional traits (an assumption that is lost altogether with species diversity calculations; Cavender-Bares et al. 2009). Phylogenetic relatedness is also expected to be more important at a small scale where interspecific interaction potential is greatest.

Unfortunately, phylogenetic information isn’t always available or easy to interpret (Cavender-Bares et al. 2009). This may be why species diversity has so far been more widely applied as a community descriptor. However, if the assumption is made that congeneric species are more related, and that they share similar functional traits, DNH may provide a way to gain insight into how invasions are related to community assembly processes in other ecosystems and allow better risk assessments for potential invaders.

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