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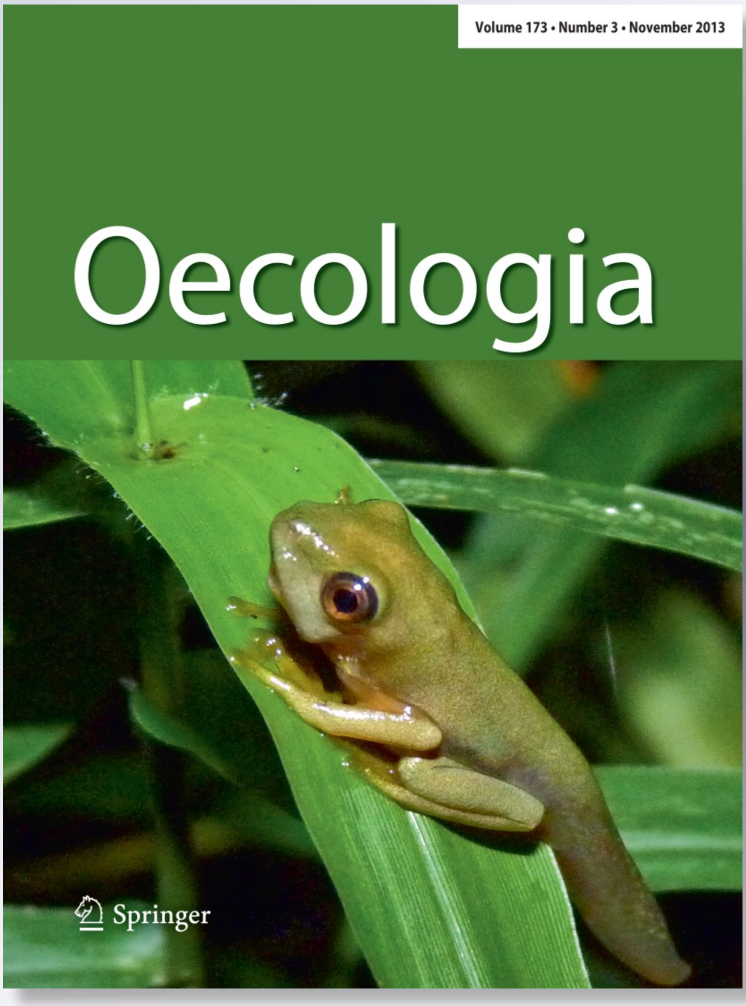

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COMMUNITY ECOLOGY - ORIGINAL RESEARCH

Patch quality and context, but not patch number, drive multi-scale colonization dynamics in experimental aquatic landscapes

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Abstract Colonization and extinction are primary drivers of local population dynamics, community structure, and spatial patterns of biological diversity. Existing paradigms of island biogeography, metapopulation biology, and metacommunity ecology, as well as habitat management and conservation biology based on those paradigms, emphasize patch size, number, and isolation as primary characteristics influencing colonization and extinction. Habitat selection theory suggests that patch quality could rival size, number, and isolation in determining rates of colonization and resulting community structure. We used naturally colonized experimental landscapes to address four issues: (a) how do colonizing aquatic beetles respond to variation in patch number, (b) how do they respond to variation in patch quality, (c) does patch context affect colonization dynamics, and (d) at what spatial scales do beetles respond to habitat variation? Increasing patch number had no effect on per patch colonization rates, while patch quality and context were critical in determining colonization rates and resulting patterns of abundance and species richness at multiple spatial scales. We graphically illustrate how variation in immigration rates driven by perceived predation risk (habitat quality) can further modify dynamics of the equilibrium theory of island biogeography beyond predator-driven effects on extinction rates. Our data support the importance of patch quality and context as primary determinants of colonization rate, occupancy, abundance, and resulting patterns of species richness, and reinforce the idea that management of metapopulations for species preservation, and metacommunities for local and regional diversity, should incorporate habitat quality into the predictive equation.

Keywords Field-of-dreams hypothesis · Habitat selection · Island biogeography · Metacommunities · Propagule redirection

Introduction

Differential rates of colonization (immigration, settlement) and extinction drive local population dynamics, community structure, and spatial patterns of biological diversity. Existing paradigms of island biogeography, metapopulation biology, and metacommunity ecology emphasize patch size, number, and isolation as the primary characteristics influencing these processes (MacArthur and Wilson 1967; Hanski and Gilpin 1997; McIntyre and Wiens 1999; Shurin 2001; Kneitel and Miller 2003; Leibold et al. 2004). Under all three theoretical frameworks, patch specific colonization rates are a function of number, size, and distance to target patches. These habitat characteristics interact with varying dispersal (emigration) tendencies of a regional species pool to determine colonization (immigration) rates. Under this scenario, colonization can be described as "blind" to variation in habitat quality. Effects of variation in local conditions (predators, competitors, abiotic

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variables, etc.) manifest themselves via post-colonization mortality.

In contrast, habitat selection theory emphasizes habitat quality as a primary determinant of patch-specific colonization rates (Fretwell and Lucas 1970; Wiens 1976; Pulliam and Danielson 1991; Rosenzweig 1995; Morris 2003; Resetarits et al. 2005). The behavioral filter imposed by habitat selection can obviate post-colonization processes, or at least co-determine (with post-colonization processes) patterns of local diversity (Binckley and Resetarits 2005, 2007; Resetarits and Binckley 2009; Vonesh et al. 2009). Underscoring the importance of landscape-level variables in colonization dynamics, recent work illustrates that not only inherent patch characteristics, but also patch context, are important in determining perceived habitat quality (Resetarits 2005; Resetarits and Binckley 2009). Thus, patch quality could be expected to both rival and strongly interact with patch size, number, and isolation in determining colonization rates and community structure. Given the emphasis on dispersal, conservation biology has begun to focus on habitat quality, particularly in the context of climate change, and the need to better understand its role in population, community, and metacommunity dynamics (e.g., Hodgson et al. 2009, 2011; Nicol and Possingham 2010; Mortelliti et al. 2010; Doerr et al. 2011; Schooley and Branch 2011).

For passively dispersed or non-selective colonists (e.g., plants, planktonic organisms, bacteria) a "quality blind" approach may adequately capture the relevant dynamics of dispersal and colonization. However, even passively dispersed larvae of many organisms exhibit some control over settlement [e.g., sand dollars (Highsmith 1982); corals (Harrington et al. 2004); oysters (Tamburri et al. 2007)]; and many motile species are capable of precisely directing their movements in complex landscapes. The prevalence of habitat selection, which specifically links colonization to some indicator of perceived patch quality, suggests that a quality blind approach might fail to capture essential processes determining patch specific rates of colonization and the resulting dynamics and spatial structure of species distributions within communities and metacommunities (Armsworth and Roughgarden 2005; Resetarits 2005; Kadmon and Allouche 2007; Schooley and Branch 2011). Whereas spatial characteristics are relatively immutable, habitat quality, especially if affected by species composition and intraspecific density, is dynamic; spatial and temporal species turnover enhance the complexity of the colonization landscape and spatial variation in quality should interact with physical habitat characteristics, making decision processes more complex (Resetarits and Wilbur 1989; Wellborn et al. 1996; Leibold et al. 1997; Blaustein 1999; Abrams 2007; Abrams et al. 2007; Schooley and Branch 2011). Species capable of assessing relative quality of patches can effectively respond to the shifting mosaic nature of such complex landscapes by directing colonization to high-quality patches (Resetarits and Wilbur 1989; Resetarits 1996).

Despite considerable interest in the role of patch number in both theory (e.g., Allen 1987; Ylikarjula et al. 2000; Hein et al. 2004) and conservation planning (Stasek et al. 2008; Hodgson et al. 2009, 2011; Nicol and Possingham 2010) we know very little of its role in colonization dynamics, patch size and isolation having dominated the discussion. Under random dispersal and colonization, greater size increases the probability that a patch will be colonized (target area hypothesis) (MacArthur and Wilson 1967; Connor and McCoy 1979; Rosenzweig 1995; Hanski 1999), but is this also true of a greater number or density of patches? Under the field-of-dreams hypothesis (Palmer et al. 1997), increases in habitat availability should lead to proportional increase in the number of colonists, while the propagule redirection hypothesis (Carr and Hixon 1997; Osenberg et al. 2002) proposes that colonists will be redirected away from existing patches to colonize new patches, resulting in lower per patch colonization rates (Stier and Osenberg 2010). Invoking habitat selection, larger or more densely concentrated sets of habitat patches may also be more easily detected—cues are more apparent—or may actually be preferred, resulting in proportional increases in per patch colonization rate. For aquatic systems, cues indicating presence of water, such as reflectance and chemosensory cues, are clearly related to both patch area and patch number. Thus, random capture probabilities and active habitat selection may interact; larger "targets" may be proportionally or disproportionately more perceptible to colonizing species and habitat quantity, manifested as either size or number, may drive colonization dynamics.

We experimentally examined the relative importance of patch quality, patch number, and patch context on colonization dynamics (and resulting community structure) of an assemblage of highly vagile organisms: aquatic beetles of the families Dytiscidae and Hydrophilidae. A previous paper (Resetarits and Binckley 2009), based on the same experiment, presented a limited analysis focused specifically on spatial contagion of predation risk as an example of the importance of patch context in determining patch quality, colonization rate, and resulting community structure. Here we expand both our analyses and discussion to examine four issues addressed by our experimental design:

(a) How do colonizing beetles respond to variation in number of habitat patches?
(b) How do colonizing beetles respond to variation in patch quality?
(c) Does patch context affect colonization dynamics?
(d) At what spatial scales do beetles assess and respond to habitat variation?

Materials and methods

Most species at our study site are predaceous diving beetles (Dytiscidae), with carnivorous adults and larvae, or water scavenger beetles (Hydrophilidae), with primarily omnivorous or herbivorous adults (grazer/scavengers) and carnivorous larvae. They feed and reproduce in water, but initially disperse (fly) to new ponds from terrestrial pupation sites. There are several distinct components to the process of dispersal and colonization; here we focus on the prospecting and colonization phase, wherein beetles determine where to settle for growth and reproduction. Relatively little is known regarding movement dynamics of aquatic beetles; however, the dispersal phase is energetically costly and limited evidence suggests that once the initial settlement phase is complete, beetles rarely undergo secondary dispersal unless conditions change dramatically (e.g., pond drying) (Zalom et al. 1979; Layton and Voshell 1991; Sheldon 1992). This may partly result from the fact that individuals (especially females) of some species metabolize flight muscles to fuel reproduction and/or development of swimming muscles (Johnson 1969), which limits subsequent vagility among sites.

Typical aquatic habitats in our study area are quite small, ranging from <<1 m^2 to a few square meters, and number in the thousands as a result of low elevation (≈3 m above sea level) and little topography. Such habitats are important to a variety of species (Semlitsch and Bodie 1998) and are capable of supporting a diverse array of aquatic organisms [e.g., beetles (Matta 1979; Schneider and Frost 1996)]. However, limited topographic variation does not necessarily translate into interconnection. Topography of a few centimeters can isolate habitat patches resulting in mosaic patterns of habitat types and patterns of interconnection that vary with amount and timing of rainfall. Certain patches reliably connect during wet conditions, while others remain reliably isolated, even at distances of <1 m.

Experimental landscapes were set up using cattle watering tanks (0.61 m deep × 1.52 m diameter, ≈1,000 L total volume) as individual patches. These can be varied in spatial arrangement and habitat conditions [predators, competitors, canopy cover, nutrients, etc. (e.g., Resetarits 2005; Binckley and Resetarits 2005, 2007, 2008)]. We established four circular experimental landscapes, each containing six locality types (unique combinations of total number and types of patch). Each landscape comprised 21 tanks (patches) divided among six localities (groups of patches) (Fig. 1a). Patch number was manipulated by varying number of habitat patches per locality, and habitat quality by varying presence/absence of predatory fish and the spatial association of fish and fishless patches. This generated three Patch types ($n = 84$): predator-free, predator-present, and predator-associated (predator-free patches spatially associated with predator patches) (Fig. 1b). Set, which consists of patches of a given type in a locality ($n = 36$) also had the same three quality categories, each with one, two, and four patches (Fig. 1b). Locality ($n = 24$) had two quality categories, predator-free and mixed, comprising one, two, and four versus two, four, and eight patches, respectively (Fig. 1b). The six locality types were randomly assigned to positions around each circle (Fig. 1a). Patches within localities were separated by 1 m, localities were separated by 13 m.

The experimental landscapes were established within a large abandoned field adjacent to a remnant arm of the Great Dismal Swamp in Chesapeake, Virginia, USA. The field was surrounded by second-growth forest dominated by red maple (*Acer rubrum*), sweetgum (*Liquidambar*

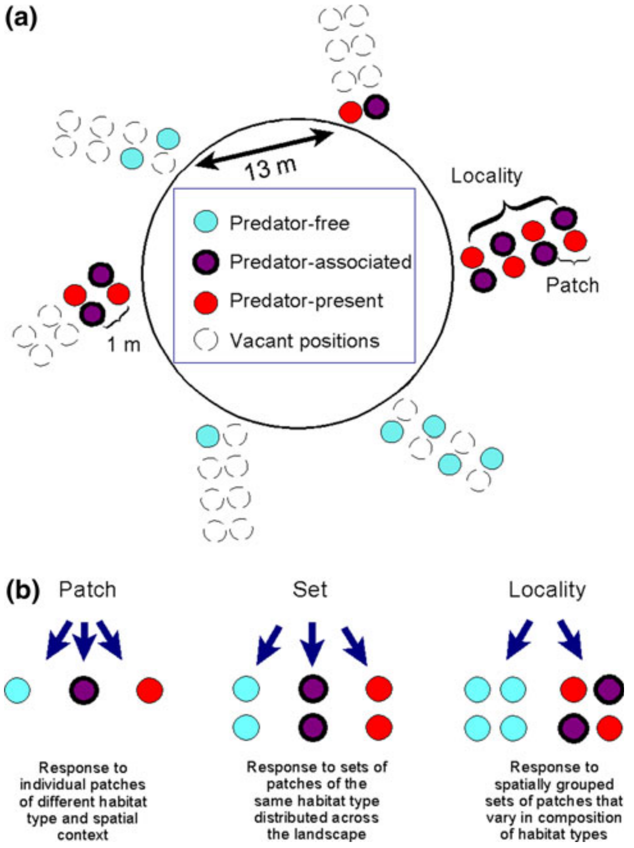

Fig. 1 **a** Diagram of an experimental landscape. Four such landscapes were placed in a large, mowed old field surrounded by hardwood and pine forest. Six localities consisted of one, two, four, or eight patches, and patches were of three types: predator-free, predator-associated, and predator-present. Each locality consisted of either all predator-free patches or predator-present and predator-free patches in a 50/50 ratio. Vacant positions illustrate the symmetric layout of the experimental array and tank positions. **b** Conceptual design of the analysis at three different levels, which allows us to tease apart the dynamics of colonization in response to variation in patch quality and patch number

styraciflua), and loblolly pine (*Pinus taeda*). Landscapes did not differ in their distance to natural aquatic patches containing beetles and all were in full sunlight to enhance colonization (Binckley and Resetarits 2009). On 8 July pools were covered with tight-fitting fiberglass screen (2 mm^2) to prevent premature colonization and filled with water pumped (through fine-mesh screen) from a nearby borrow pit. Two days later, randomized aliquots of 0.4 kg of dried leaf litter and 1.0 L of a zooplankton and phytoplankton mixture collected from nearby ponds were added and predators (five ≈ 4.5-g banded sunfish, *Enneacanthus obesus*) placed under screens. Screens were then pushed underwater allowing colonization. This procedure eliminates physical interactions between predators and colonizing organisms, but allows chemical communication and a complete inventory of all but the smallest colonizing beetles (Binckley and Resetarits 2005). Beetles were collected from pools on 27 July, preserved in ethanol and identified to species at the Smithsonian Institution using pre-existing vouchers from Chesapeake, Virginia, and counted.

Data analysis

Our design and analysis allow us to examine responses to landscape-level variation in patch number and patch quality (perceived predation risk) in three distinct ways, rather than simply extrapolating from patch specific colonization rates. Looking at abundance and richness at Patch level addresses variation in alpha diversity, asking whether patch type and patch context were important in determining patch-specific colonization rates and resulting community structure. For patch quality, this addresses whether colonization rate and resulting community structure are affected by individual patch quality and quality of neighbouring patches. For patch number, it addresses whether colonization rate and community assembly are influenced by number of adjacent habitat patches (Fig. 1b).

Set examines how colonization is parsed among collections of patches of a specific type within a landscape. Thus, looking at Set asks whether collections of patches of the same type/quality are differentially colonized relative to sets of patches of differing habitat type, and thus more closely linked by processes operating at the metacommunity level (Fig. 1b).

Finally, looking at Locality, we ask whether variation among discrete groups of patches that are spatially linked, but differing in patch number and quality, generate different rates of colonization. Localities containing both fish and fishless patches should present greater habitat heterogeneity to colonizing organisms versus localities containing only fishless patches (Fig. 1). Conversely, spatial context may affect the perceived quality of patches in mixed localities.

The experiment comprised a randomized block design, incompletely crossing habitat quality with patch number in Patch and Locality analyses, but completely crossing quality and number in Set analyses. ANOVA was performed on number of beetles and multivariate ANOVA (MANOVA) on species richness and evenness for Patch, Set, and Locality (Table 1). Factors were landscape (block), patch number (number of patches/locality, or number of patches/set/locality), quality (two locality types, three patch and set types) and the patch number × quality interaction. The same analyses were performed using abundance as a covariate (ANCOVA/MANCOVA) to control for effects of abundance on species richness and evenness (Table 1; Online Resource 1). Fisher's protected least significant difference (LSD) (for main effects with $P < 0.1$) was conducted to examine differences among discrete quality levels; multiple comparisons were not carried out for patch number, which represents continuous variation, thus main effects are of primary interest. We used SAS 9.2 (SAS Institute 2006) with type III sums of squares and $\alpha = 0.05$ for all tests.

Results

Our experiment was colonized by 7,299 individuals of 34 species of aquatic beetles: 4,588 individuals of 20 species of Dytiscidae, 2,696 individuals of 11 species of Hydrophilidae, and one species each of Noteridae (one individual), Haliplidae (two), and Hydraenidae (12).

Patch

Beetle abundance/patch was significantly affected by variation in patch quality, but was not affected by variation in patch number, and there was no quality × number interaction (Table 1; Fig. 2a). All three patch types were significantly different in mean abundance (Fig. 2a), with the most beetles in predator-free patches. Predator-associated patches were intermediate, indicating they had different perceived quality despite absence of predators. Thus, quality was important in determining patch-specific colonization rates, but whether a patch occurred in a locality with more total patches did not affect per patch colonization rate and this relationship did not vary among levels of quality.

Quality also generated significant variation in patch-specific species richness, with the perceived higher quality treatments [predator-free and predator-associated (Resetarits 2005; Resetarits and Binckley 2009)] containing significantly higher richness than predator patches but not

Table 1 ANOVA/MANOVA results for abundance, species richness, and evenness of beetles by Patch (predator-free, predator-associated, predator), Set (predator-free, predator-associated, predator), and Locality (predator-free, mixed)

Patch

Abundance

Source	*df*	SS	MS	*F*	*P*
Landscape	3	44,749.8	14,916.6	10.15	<0.0001
Quality (Q)	2	113,742.6	56,871.3	38.72	<0.0001
Number (N)	3	2,139.3	713.1	0.49	0.6934
$Q \times N$	3	5,450.4	1,816.8	1.24	0.3027

MANOVA—species richness and evenness

Source	Num. *df*	Den. *df*	Wilk's λ	*F*	P (P_N)
Landscape	6	142	0.567	7.76	<0.0001 (<0.0001)
Quality	4	142	0.549	16.14	<0.0001 (0.0015)
Number	6	142	0.982	0.22	0.9708 (0.7809)
$Q \times N$	6	142	0.906	1.20	0.3077 (0.2950)

Species richness

Source	*df*	SS	MS	*F*	P (P_N)
Landscape	3	14.33	4.78	1.39	0.4896 (0.0155)
Quality	2	432.74	216.37	53.11	<0.0001 (0.0004)
Number	3	3.17	1.06	0.37	0.9096 (0.5440)
$Q \times N$	3	41.67	13.89	3.23	0.0776 (0.0666)
Evenness					
Landscape	3	0.2245	0.0748	16.23	<0.0001 (<0.0001)
Quality	2	0.0234	0.0117	2.54	0.0862 (0.4306)
Number	3	0.0039	0.0013	0.28	0.8365 (0.7391)
$Q \times N$	3	0.0032	0.0011	0.23	0.8728 (0.9671)

Set

Abundance

Source	*df*	SS	MS	*F*	*P*
Landscape	3	104,416	34,805	4.18	0.0163
Quality	2	476,508	238,254	28.62	<0.0001
Number	2	460,220	230,110	27.64	<0.0001
$Q \times N$	4	223,404	55,851	6.71	0.0009

MANOVA—species richness and evenness

Source	Num. *df*	Den. *df*	Wilk's λ	*F*	P (P_N)
Landscape	6	46	0.382	4.75	0.0008 (0.0017)
Quality	4	46	0.233	12.32	<0.0001 (0.0071)
Number	4	46	0.305	9.32	<0.0001 (0.1818)
$Q \times N$	8	46	0.717	1.04	0.4188 (0.2838)

Species richness

Source	*df*	SS	MS	*F*	P (P_N)
Landscape	3	24.00	8.00	1.34	0.2840 (0.0657)
Quality	2	413.17	206.58	34.67	<0.0001 (0.0017)
Number	2	236.17	118.08	19.82	<0.0001 (0.2648)
$Q \times N$	4	51.67	12.92	2.17	0.1033 (0.0463)

Table 1 continued

Species richness

Source	*df*	SS	MS	*F*	P (P_N)
Evenness					
Landscape	3	0.1063	0.0354	9.97	0.0002 (0.0020)
Quality	2	0.0120	0.0060	1.69	0.2049 (0.4475)
Number	2	0.0594	0.0297	8.35	<.0018 (0.1159)
$Q \times N$	4	0.0022	0.0006	0.16	0.9586 (0.9798)

Locality

Abundance

Source	*df*	SS	MS	*F*	*P*
Landscape	3	156,624	52,208	4.08	0.0264
Quality	1	281,961	281,961	22.05	0.0003
Number	3	652,839	217,613	17.02	<0.0001
$Q \times N$	1	87,320	87,320	6.83	0.0196

MANOVA—species richness and evenness

Source	Num. *df*	Den. *df*	Wilk's λ	*F*	P (P_N)
Landscape	6	28	0.294	3.94	0.0056 (0.0160)
Quality	2	14	0.526	6.31	0.0111 (0.8425)
Number	6	28	0.276	4.21	0.0038 (0.4388)
$Q \times N$	2	14	0.928	0.54	0.5917 (0.7025)

Species richness

Source	*df*	SS	MS	*F*	P (P_N)
Landscape	3	18.46	6.15	0.89	0.4692 (0.0652)
Quality	1	60.06	60.06	8.68	0.0100 (0.9167)
Number	3	212.44	70.81	10.23	0.0006 (0.2070)
$Q \times N$	1	7.56	7.56	1.09	0.3124 (0.4911)
Evenness					
Landscape	3	0.0510	0.0170	9.06	0.0011 (0.0208)
Quality	1	0.0141	0.0141	7.54	0.0150 (0.5524)
Number	3	0.0289	0.0096	5.13	0.0122 (0.6731)
$Q \times N$	1	0.0004	0.0004	0.23	0.6400 (0.6438)

Because factors in Patch and Locality analyses are incompletely crossed, interaction terms are based only on the completely crossed portion of the design, as reflected in the interaction *df*. Set is completely crossed and thus the interaction uses the full design. *P*-values *in parentheses* are from the equivalent ANCOVA and MANCOVA analyses using abundance (N) as a covariate (detailed analysis in Online Resource 1)

Num. Numerator, *Den.* denominator

differing from each other in the uncorrected analysis (Table 1; Fig. 2d). Effects of quality were robust to inclusion of abundance as a covariate and Fisher's LSD following ANCOVA showed all three treatments significantly different from one another, indicating that species richness was driven directly by variation in quality independent of effects on abundance. Patch number did not significantly affect richness in either analysis, nor was there a significant interaction between quality and number; patch-specific species richness was largely determined by variation in patch quality.

Evenness (Table 1; Fig. 2g) was not significantly affected by quality or number, nor was there a significant interaction. These results were unaffected by inclusion of abundance as a covariate. The species abundance relationship for Patch saturated, with each patch type largely occupying a different portion of this classic curve (Fig. 2j).

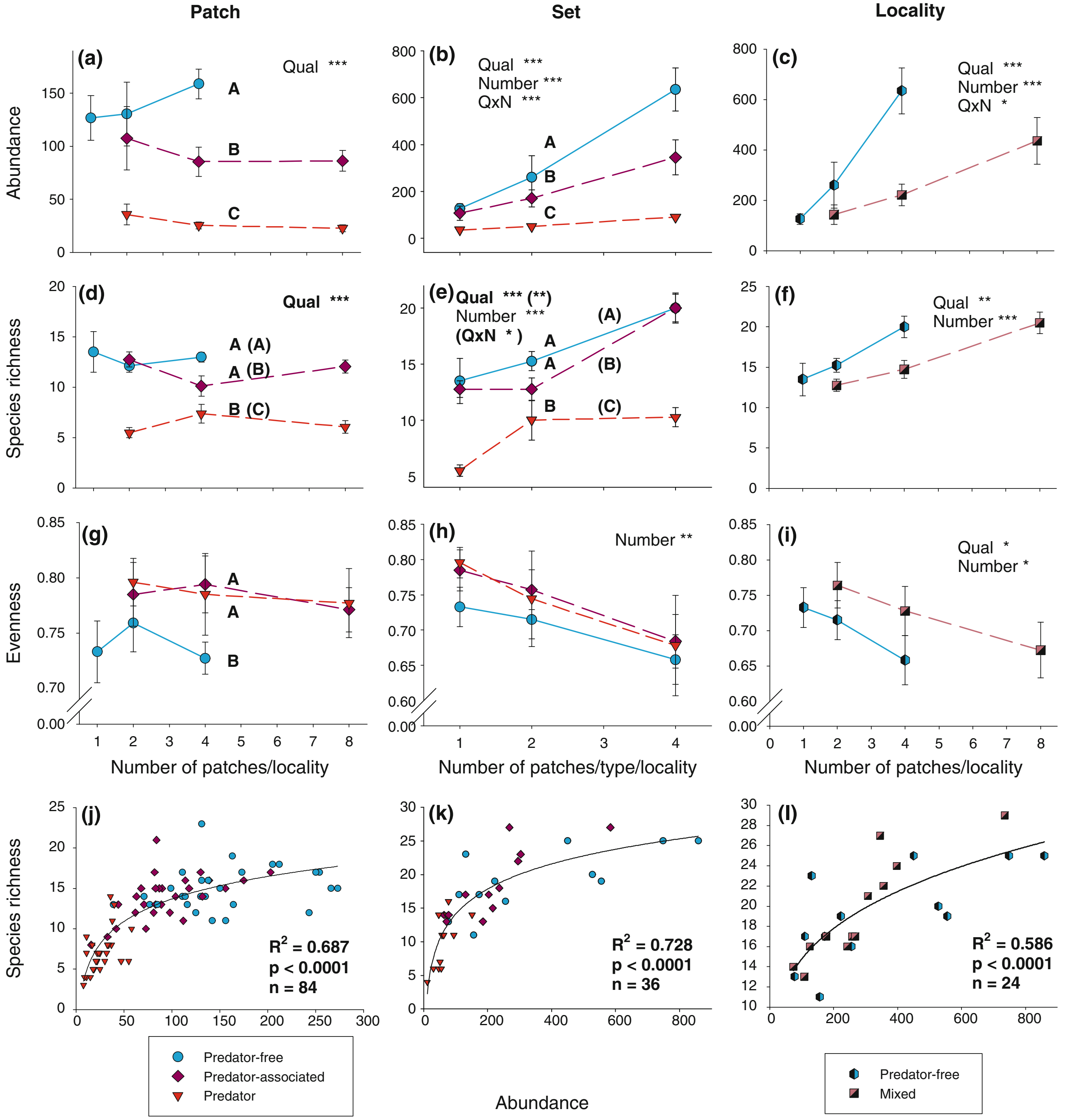

Fig. 2 Responses of colonizing beetles (mean ± 1 SEM) to patch quality (*Qual*; *Q*), patch number (*Number*; *N*) and the interaction ($Q \times N$) for mean **a–c** abundance, **d–f** species richness, and **g–i** evenness, and **j–l** resultant species saturation curves by Patch, Set, and Locality. **a**, **b**, **d**, **e**, **g**, **h**, **j**, **k** Legend *lower left*; **c**, **f**, **i**, **l** legend *lower right*. Main effects and interactions appear only if significant (* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$). Effects *in bold* for species richness and evenness indicate effects remaining significant after correction using abundance as a covariate; effects *in parentheses* represent effects that achieve significance only after correction. *Different letters* indicate significant differences ($P < 0.05$) in habitat quality using Fisher's protected ($\alpha = 0.1$) least significant difference; those *in parentheses* indicate significant differences after correction (Table 1; Online Resource 1). Note data in **a** and **d** are also in Resetarits and Binckley (2009) and are presented and analyzed slightly differently because of the differing nature of the questions addressed and the more extensive analyses presented in this paper

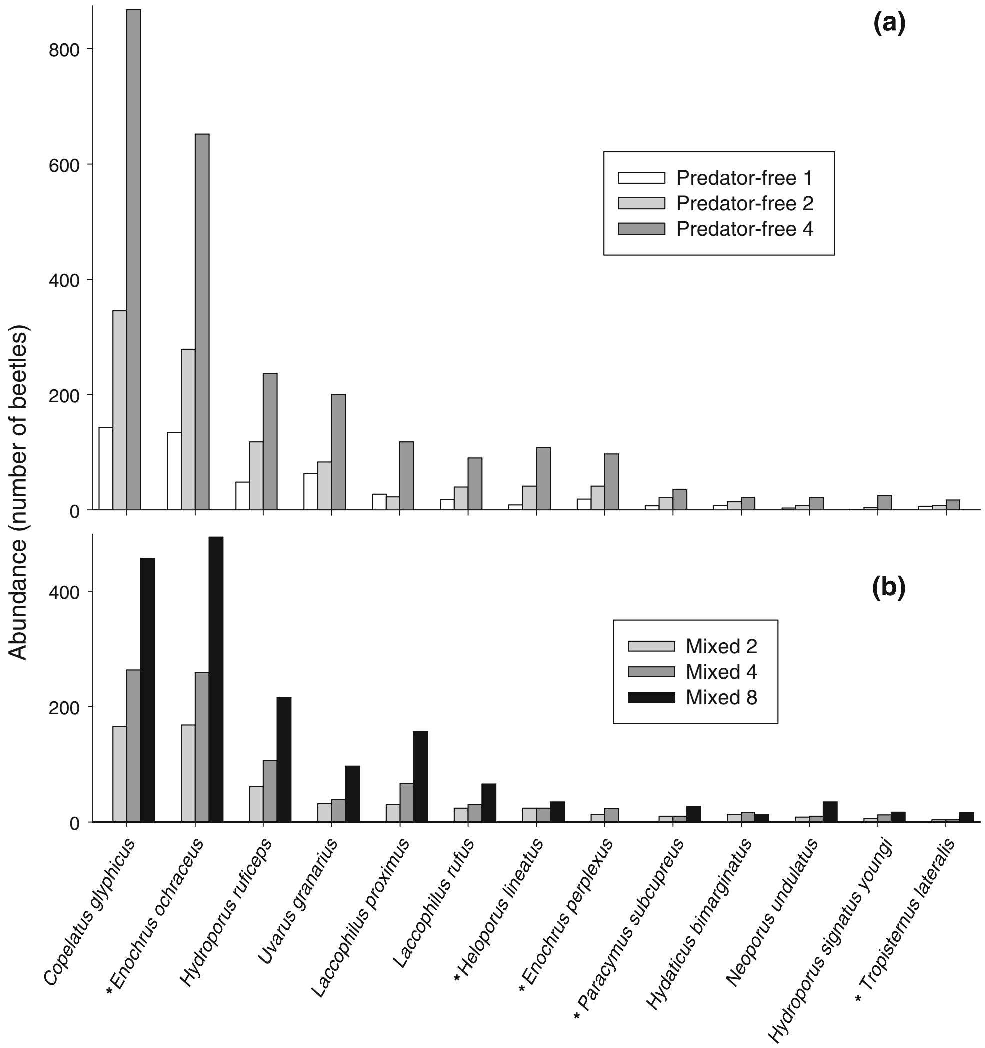

Fig. 3 Abundance of the 13 most numerous beetles ($n = 7{,}105$; *asterisks* indicate Hydrophilidae) by locality type, **a** Predator-free or **b** Mixed, and number of patches (*shading*), illustrating consistency of responses among colonizing beetles to variation in patch number and quality. *Bars of the same shade* represent localities with the same number of patches. Predator-free localities have a greater number of beetles than mixed localities of the same patch number for all 13 species

Set

Abundance varied significantly among Sets of patches of different type (predator-free, predator-associated, and predator) as a result of variation in quality, number, and their interaction. All three quality levels were significantly different (Table 1; Fig. 2b) and mean abundance per Set increased in a linear fashion with number of patches/set. Thus, within Set type increasing patch number did not generate increasing colonization rates; however, the effect of increasing patch number differed for each of the three quality treatments, generating different slopes and the highly significant quality × patch number interaction (Table 1; Fig. 2b). Thus, both patch quality and number strongly affected beetle colonization rates, and the quality × number interaction generated three habitat-specific abundance-area curves characterized by increasing steepness of slope with increasing quality.

Quality and number also generated significant variation in species richness. Predator-free and predator-associated Sets had significantly higher richness than predator Sets, but did not differ from each other in the uncorrected analysis (Table 1; Fig. 2e). Species richness significantly increased with increasing number of patches, but there was no difference in the slopes of the respective lines (no quality × number interaction). Including abundance as a covariate eliminated the effect of patch number, but not quality, and revealed a significant quality × number interaction. All three quality levels were significantly different, indicating that while patch number effects on species richness were driven by variation in abundance (colonization rates), the significant quality effects were robust to inclusion of the covariate, were parsed more finely among levels, and a quality × number interaction was specifically revealed by correction for abundance.

Evenness significantly decreased with increasing number, indicating that as number of patches increased, variation in per species abundance increased (Table 1; Fig. 2h). There was no effect of quality and no quality × number interaction. The effect of number on evenness was not robust to correction for abundance, indicating that variation in abundance/patch drove variation in evenness. The species abundance relationship for Set also saturated, with each set type occupying a different, but overlapping, portion of the curve (Fig. 2k).

Locality

Mean beetle abundance per Locality also varied significantly with quality (predator-free vs mixed), number, and their interaction (Table 1; Fig. 2c). Predator-free and mixed localities differed significantly in abundance, and mean total abundance increased linearly with number of patches/locality, but the relationship differed for the two locality types, as reflected in the highly significant quality × number interaction (Table 1; Fig. 2c). Predator-free localities had a steeper positive relationship with increasing patch number than mixed localities, generating two distinct abundance by area curves. The 13 most abundant species showed very consistent responses to variation in quality and number at the Locality level (Fig. 3); for all 13 species, Predator-free localities have more beetles than mixed localities with the same number of patches.

Predator-free localities also had significantly higher species richness than mixed localities (Table 1; Fig. 2f), and there was a significant positive relationship with number; however, there was no significant interaction, indicating that the relationships differed in magnitude but not in slope. Neither the effects of quality nor number on richness were robust to inclusion of abundance as a covariate, indicating that differences in richness among localities were driven by variation in colonization rates (abundance).

As seen previously for Set, evenness showed a significant negative relationship with number, and additionally there was a significant effect of quality, with higher quality Localities being less even; there was no interaction (Table 1; Fig. 2i). These effects disappeared with inclusion of the covariate, indicating that greater abundance resulted in more skewed distribution among species. The species abundance relationship for Locality, unlike previous curves, shows a less clear delineation of treatment (Fig. 2l), but Mixed localities range from two to eight tanks while Predator-free range from one to four (see Fig. 3).

Discussion

Viability of local populations can be enhanced, or diversity maintained, within local communities either by decreasing the extinction rate or increasing the colonization rate. This is the essence of conservation of both individual species of concern and local and regional species diversity. Ongoing debates related to patch size versus patch number, as well as the role of connectivity and spatial synchrony/asynchrony on regional extinction rates, reflect this understanding (e.g., Hodgson et al. 2009, 2011; Nicol and Possingham 2010; Mortelliti et al. 2010; Doerr et al. 2011; Schooley and Branch 2011). We manipulated both number and quality of available patches to examine the colonization dynamics of aquatic beetles. We were interested in two sets of questions. First, how do variation in patch quality, patch number, and patch context affect habitat selection decisions and colonization dynamics, and second, at what spatial scales do aquatic beetles make habitat choices? Our experiment provides a snapshot of the early colonization dynamics of this assemblage of beetles, allowing us to examine how colonization plays out in a complex landscape. Beetles located our experimental array, and by chance or choice colonized a Landscape (one of four), a specific Locality (one of six) within that Landscape, and a specific Patch within that Locality. Clearly 17 days is sufficiently long for post-colonization processes to also play a role, but this early stage of community assembly is the most active in terms of colonization and is critically important because priority effects can strongly influence the community trajectory (Chase 2003, 2010; Kraus and Vonesh 2010), and effects of variation in early colonization can carry over into long-term population dynamics and community structure (Vonesh et al. 2009; Stier and Osenberg 2010).

Patch quality, patch number, and spatial scale

Habitat quality was of critical importance in determining colonization rate and community structure, and strongly influenced how patch number affected both colonization rate and patterns of abundance and species richness. Stier and Osenberg (2010) found that per patch colonization rates of reef fish declined with increasing patch number and a sixfold increase in patch number resulted in only a 1.3-fold increase in total colonization. In contrast, our expectation was that larger sets of patches would at least be more easily detected, and might also be preferred relative to isolated patches (Palmer et al. 1997). Interestingly, our observed per patch colonization rates were neither higher or lower in larger sets of patches; total colonization rates scaled linearly with increasing patch number, albeit with very different slopes driven by variation in quality. Thus, effects of patch number on colonization are strictly passive, as in most island biogeography, metapopulation, and metacommunity models (e.g., MacArthur and Wilson 1967; Hanski and Gilpin 1997; Shurin 2001; Kneitel and Miller 2003; Leibold et al. 2004), while showing no evidence of propagule redirection (Stier and Osenberg 2010) (except between patches of different quality), or enhanced colonization (Palmer et al. 1997). Whether this is also true for patch size remains to be determined. The relative effectiveness of increasing patch size or patch number on colonization depends on the size of the colonist pool, dispersal abilities, and how a given species or set of species perceive the habitat landscape, including patch context and matrix effects (Stasek et al. 2008). How this affects subsequent recruitment and population dynamics depends on in situ biological processes, such as density dependence and predation (Stier and Osenberg 2010).

In contrast to results for patch number, increasing patch quality had a dramatic effect on colonization rate, and patch quality was affected by both inherent patch characteristics and spatial context in terms of the perceived quality of neighboring patches. Patch quality drives variation in abundance as well as species richness, and the trajectory of increasing patch number depends on habitat quality (quality × patch number interactions).

Theory and empirical work suggest that local and regional diversity are served by a spatial mosaic of habitat types. We expect greater species turnover between patches of different type and our mixed Localities should perhaps have greater species richness per patch than predator-free Localities. Instead, sets of predator-free patches (Localities) accumulate individuals at 3.5 times the rate of those with both predator and predator-free patches, and have greater species richness for the same number of patches. Predator-associated patches are affected by spatial contagion (Resetarits and Binckley 2009); colonization rates are below that expected for Predator-free patches and overall abundance and species richness in mixed Localities is reduced. Predator-associated patches constitute "repulsive sources" (high-quality habitats colonized at lower than expected rates [Resetarits and Binckley 2009]), which are the converse of "attractive sinks" sensu Delibes et al. (2001).

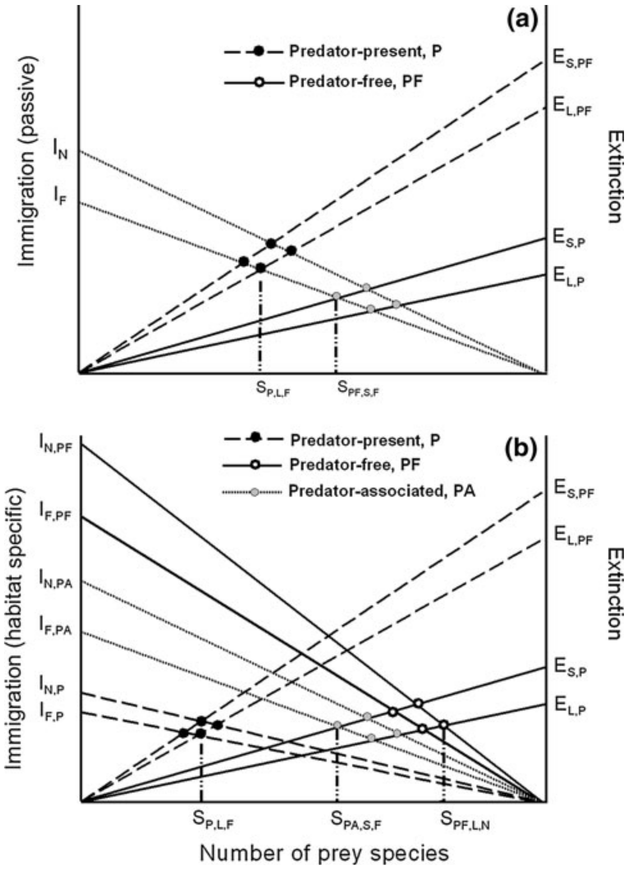

Fig. 4 **a** Island biogeographic model incorporating variation in habitat-specific extinction rates (*E*) as a result of predation regime [predator-present (*P*) or predator-free (*PF*)] coupled with passive immigration (*I*) for large (*L*) or small (*S*), and near (*N*) or far (*F*) habitat patches (after Ryberg and Chase 2007). **b** Island biogeographic model incorporating both habitat-specific extinction rates based on predation, and habitat-specific immigration rates (*I*) based on perceived predation risk. Predation-dependent extinction generates two different rates, one for those patches containing predators and one for those without, while predation-risk-dependent colonization generates three distinct rates in our example, because predator-associated patches differ from predator-free patches in immigration rate even though neither contain predators. Not all points where rates cross actually occur; predator immigration rate only couples with predator extinction rates, while both predator-free and predator-associated rates apply only to predator-free patches. Equilibrium species numbers (*S*) are illustrated for representative patch types: $S_{P,L,F}$ predator, large, far, $S_{PF,S,F}$ predator-free, small, far, $S_{PA,S,F}$ predator-associated, small, far, and $S_{PF,L,N}$ predator-free, large, near. Twelve distinct equilibrium points are specified by the interaction of habitat-specific extinction and immigration rates. Actual equilibrium points would integrate both passive immigration and habitat selection, coupled with predator-dependent extinction rates

Though the spatial scale of our experimental landscapes was limited, e.g., beetles can cover greater distances than those encompassed by our array, beetles colonizing our experiment clearly make habitat decisions at multiple spatial scales. Variation among Landscapes may simply reflect spatial encounter probabilities; however, habitat selection clearly plays a role for Patches and Localities. Beetles distinguish among patches varying in quality at very small spatial scales, but are also affected by larger scale processes, particularly patch context. This parallels results from ovipositing tree frogs (Resetarits 2005) and reinforces the idea that habitat-selection behavior links multiple spatial scales. Both the scale at which species detect and respond to variation in habitat quality, and how spatial variation in passive processes (e.g., capture probabilities) influence colonization rates, affect the dynamics of spatial processes and how we manage habitats.

Habitat selection, predation, and habitat-specific species-area relationships

Ryberg and Chase (2007) have suggested that variation in factors related to habitat quality (e.g., predation regime) can alter species-area relationships and the dynamics of island biogeographic models by generating patch-specific extinction rates. Considering predation regime [or other habitat heterogeneity—see Kadmon and Allouche (2007)] in defining extinction rates and species-area relationships increases our predictive power with respect to both existing communities and potential anthropogenic changes (Ryberg and Chase 2007). Similarly, variation in immigration rates driven by perceived predation risk generates patch-specific colonization rates that could also profoundly affect the equilibrium dynamics of habitat patches, and affect both community and metacommunity structure. In our experiment immigration rates for beetles take two alternative forms among Localities depending on fish presence (Fig. 2c, f). For both Patches and Sets of patches of the same type, we observed three, habitat-specific immigration rates (Fig. 2a, d, b, e). Immigration rates may alter richness of incoming colonists directly, or increase the probability of successful establishment or persistence by increasing colonists per species. Figure 4a illustrates the scenario generated by two sets of extinction curves, one for predator-free and one for predator habitats, for two patch sizes (large and small), and two levels of isolation (near and far)(after Ryberg and Chase 2007). We can match three sets of habitat-specific colonization rates (predator, predator-associated, and predator-free; Fig. 4b) to these habitat-specific extinction rates, generating 12 alternative equilibrium points based on the presence-absence of predators. The equilibrium points depend upon specific relationships, but there are substantial differences between habitats affected only by behavioral effects on colonization rate (those on the right) and those affected both by behavior and predator-driven increases in extinction rate. Colonization rates of predator habitats can also be zero for certain species, producing local behavioral extinction.

The species-area relationship is based on the idea that number of species increases with area sampled. We can envision variation in habitat-specific immigration rates, as best illustrated in Fig. 2b, resulting in variation in both abundance-area relationships that potentially affect local species richness, and species-area relationships analogous to those observed by Ryberg and Chase (2007). Both colonization and extinction rates are potentially implicated in variation in habitat-specific species-area relationships. The distinction is important because of the differences in community and metacommunity dynamics resulting from domination by pre-colonization or post-colonization filters, or from a combination of the two processes.

Habitat quality, community/metacommunity dynamics and conservation

Distribution and abundance patterns at the landscape level are driven not simply by variation in survival and performance in different habitats (differential mortality), but by habitat selection behavior based on expected survival and performance (Resetarits 2001, 2005; Kiflawi et al. 2003; Binckley and Resetarits 2005, 2007, 2008; Vonesh and Buck 2007; Resetarits and Binckley 2009; Vonesh et al. 2009; Silberbush and Blaustein 2011). Even species that do not actively select their habitats interact with species that do choose habitat patches based on perceived quality. Variation in colonization driven by quality makes landscapes more dynamic, because habitat quality has a greater capacity for temporal variation than size, number, or isolation.

Aquatic landscapes are linked to each other and the surrounding terrestrial matrix by species with complex life cycles, which re-colonize in each new generation. Habitat selection by such species directly links the dynamics of multiple patches within a landscape. Quality of a given habitat patch directly affects the number of colonists received by other patches, while also indirectly affecting them via effects on the total colonist pool (Binckley and Resetarits 2008). This is a critical distinction for metacommunity theory, which is defined by the strength and extent of linkages among communities (Leibold et al. 2004), and also crucial for management of systems where colonization plays a critical role in local and regional species diversity.

Patterns of connectivity among discrete habitat patches that link them into larger metacommunities are distinctly different when patch quality is the defining factor in species- and habitat-specific colonization rates; connectivity is not simply a function of distance (Resetarits 2005; Resetarits et al. 2005; Schooley and Branch 2009, 2011). Similar habitats are strongly linked by shared species and their population dynamics, while quite different habitats may be linked by *processes* of colonization via phantom interactions, whereby a species' presence in a given patch affects population densities and species diversity in other patches (Resetarits 2005; Orrock et al. 2010). Random immigration into habitats varying in size and isolation generates random patterns of species composition, which may then converge as a result of post-colonization sorting. In contrast, habitat selection generates assortative patterns of colonization driven by shared or divergent habitat preferences. Shared habitat preferences lead to positive covariation among species, as in our beetles, and an intensification of specific competitive and predatory interactions, while divergent habitat preferences lead to negative covariances, with both processes producing species sorting at the colonization stage. Likewise, presence and frequency of predator habitats directly affect the colonization rate of nearby predator-free habitats in a variety of ways, including spatial contagion (Resetarits 2005; Resetarits et al. 2005; Resetarits and Binckley 2009; Hughey et al. 2012). Thus, events in one habitat patch influence events in others, which is the definition of linkage. This leads to the broader definition of metacommunities as discrete communities linked by *processes* of dispersal, rather than by dispersal (i.e., exchange of individuals) per se. This is a critical distinction, as communities can be linked without sharing individuals or even sharing species in common, depending upon the processes that determine how individuals arrive in new habitats.

Habitat quality and how quality interacts with size, number, and isolation have a variety of ramifications for how communities are assembled, as well as how they are potentially linked into metacommunities. Non-random patterns of species colonization (and resulting patterns of co-occurrence or assortment), distinct abundance–area and species-area relationships, metacommunity substructure, and complex linkages among habitat patches are all specific effects of quality-driven colonization (habitat selection). We can add to this strong priority effects on community assembly when distributions of predators, competitors, or prey contribute to determining habitat quality (Chase 2003; Vonesh et al. 2009; Kraus and Vonesh 2010). Our experimental data build on recent suggestions that habitat quality may equal or surpass landscape characteristics such as size, number, and isolation as determinants of colonization rate, patch occupancy, and resulting patterns of species richness (Dennis and Eales 1997; Summerville and Crist 2001; Fleishmann et al. 2002; Mortelliti et al. 2010), as well as forming a critical component of habitat management strategies (Hodgson et al. 2009; Schooley and Branch 2009, 2011). Failing to incorporate habitat quality as a source of variation in patch-specific colonization rates misses essential dynamics of the process of community assembly. Explicit consideration of species responses to variation in patch quality (habitat selection) alters our view of the dynamics of how communities are assembled (Resetarits 2005; Abrams et al. 2007) and should modify how we incorporate dispersal and colonization into models of populations, metapopulations, communities and metacommunities, as well as how we manage systems for biological diversity.

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