Species responses of colonising beetles to variation in patch quality, number, and context in experimental aquatic landscapes

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Abstract. 1. Increased diversity with increasing habitat area is a well-established ecological pattern. However, habitat selection theory suggests that patch quality rivals area in determining rates of colonisation and resulting community structure.

2. Colonisation by natural populations of aquatic beetles was quantified along gradients of increasing patch number and patch quality. Four circular experimental landscapes, each containing six unique locality types (combinations of number and type of patch), were established using 84 cattle tanks (volume 1000 litres) as patches. Patch quality varied in terms of the presence/absence and spatial proximity of predatory fish, and patch number varied from one to eight patches in each locality.

3. Patch quality significantly affected the colonisation rate of most aquatic beetle species in both major families (Dyticidae and Hydrophilidae), as species avoided patches containing fish and also showed spatial contagion of predation risk by avoiding fishless patches in close proximity to these predators. Effects of patch number were passive, resulting in linear increases in abundance, with rates highly dependent on patch quality.

4. Patch quality may equal or exceed landscape characteristics such as patch number in determining colonisation rate and abundance of colonising beetles, and in generating resulting patterns of species diversity.

Key words. Biodiversity, Coleoptera, colonisation, dispersal, Dytiscidae, habitat selection, Hydrophilidae, spatial contagion.

Introduction

Aquatic dytiscid and hydrophilid beetles are an important component of freshwater aquatic communities. Carnivorous (dytiscid) and omnivorous (hydrophilid) adults and predatory larvae of both families play very significant ecological roles, especially in smaller and less permanent habitats lacking fish (Wellborn *et al.*, 1996). These habitats dominate landscapes in terms of their number and support high levels of insect diversity (Weir, 1972; Matta, 1979; Healey, 1984; Schneider & Frost, 1996; Fairchild *et al.*, 2000, 2003), but are most vulnerable to disturbance, degradation, and habitat loss (Semlitsch & Bodie, 1998). They are almost entirely dependent on seasonal (re)colonisation by insects and other species

with complex life cycles. Many species of aquatic beetle are highly vagile and appear to be obligate, or highly facultative dispersers, as evidenced by rapid colonisation of new bodies of water (Layton & Voshell, 1991; Eyre *et al.*, 1992; Jeffries, 1994). Numerous studies have examined the distribution of aquatic beetles along habitat gradients, in particular hydroperiod and factors correlated with pond permanence, such as the presence of predatory fish and pond area (Eyre *et al.*, 1992; Schneider & Frost, 1996; Fairchild *et al.*, 2000, 2003; Lundkvist *et al.*, 2001). How dispersal interacts with these characteristics to determine beetle colonisation rates and their distribution, abundance and the structure of communities in which they play an important role is not well understood.

Passive colonisation rates are determined by patch size, patch number, and isolation (MacArthur & Wilson, 1967; Allen, 1987; Hanski & Gilpin, 1997; Leibold *et al.*, 2004), while active colonisation rates are determined by measures

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of patch quality and intraspecific density (Fretwell & Lucas, 1970). Early work suggested that beetle colonisation was driven largely by patch area rather than by habitat selection (Young, 1960; Galewski, 1971). Others suggested that biotic variables play little role in the colonisation and distribution of aquatic beetles, focusing on abiotic and landscape variables as primary drivers (Larson, 1985; Ranta, 1985; Friday, 1987; Layton & Voshell, 1991; Eyre *et al.*, 1992; Nilsson & Swenson, 1994; Gee *et al.*, 1997; Lundkvist *et al.*, 2001). Recent work, however, shows that biotic variables (presence of predators, community assembly, canopy coverage) strongly influence colonisation and distribution when patch area is held constant (Resetarits, 2001; Åbjörnsson *et al.*, 2002; Binckley & Resetarits, 2005, 2007, 2008, 2009; Brodin *et al.*, 2006; Resetarits & Binckley, 2009, 2013; Kraus & Vonesh, 2010; Vonesh *et al.*, 2009).

Larger permanent bodies of water are relatively stable in abiotic and biotic conditions compared with smaller, more ephemeral sites that are highly variable, both temporally and spatially, as a result of interannual variation in hydroperiod (Wellborn *et al.*, 1996). Thus, beetles colonising small or ephemeral water bodies should be especially sensitive to variation in characteristics that influence fitness. Patch size should influence colonisation, but aquatic beetles might also respond to local variation in patch number to provide insurance against deterioration of selected or encountered patches. Thus, habitat selection may reinforce passive capture probabilities to favour larger patches or more numerous sets of patches. Patch quality also affects colonisation rates (Resetarits *et al.*, 2005). Debates on the importance of patch quality, size, number, and connectivity in conservation planning, particularly in the context of climate change, emphasise the need to better understand the contribution of these factors to colonisation rates and resulting population, community, and metacommunity dynamics (e.g. Hodgson *et al.*, 2009, 2011; Mortelliti *et al.*, 2010; Nicol & Possingham, 2010; Doerr *et al.*, 2011).

Our experiment directly manipulated patch quality, number, and context (the number and quality of surrounding patches), allowing detailed examination of the role of these factors in determining the colonisation dynamics of the individual members of a diverse assemblage of aquatic beetles. Patterns of beetle abundance (total number) and species richness were discussed in a previous paper (Resetarits & Binckley, 2013). Here we focus in detail on individual species patterns of colonisation in order to better understand the autecology of the species colonising our experimental landscapes. While limited data exist on habitat associations of dytiscid and hydrophilid beetles, associations tell us little about actual habitat preferences. These preferences form a critical component of our ability to understand how aquatic beetles identify and select habitats, and how environmental variation impacts colonisation dynamics, distribution, and processes of community assembly.

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 initially disperse (fly) to new ponds from terrestrial pupation sites to feed and reproduce in water. Here we focus on the prospection and colonisation phase, where beetles determine where to settle for growth and reproduction. Little is known regarding their movement dynamics; however, dispersal is energetically costly and limited evidence suggests that once initial settlement is complete, beetles rarely undergo secondary dispersal unless conditions change dramatically (e.g. pond drying) (Zalom *et al.*, 1979; Layton & Voshell, 1991; Sheldon, 1992). This may result from individuals (especially females) of some species metabolising flight muscles to fuel reproduction and/or development of swimming muscles (Johnson, 1969), which limits vagility among sites.

Typical habitats in our study area are small, ranging from $\ll 1\,\text{m}^2$ to a few m^2, and number in the thousands due to low elevation ($\sim 3\,\text{m}$ above sea level) and little topography. Such habitats are important to a variety of species (Semlitsch & Bodie, 1998) and are capable of supporting a diverse array of aquatic organisms (e.g. beetles – Matta, 1979; Schneider & Frost, 1996). This results in a mosaic of habitat patches and patterns of potential interconnection that vary with rainfall.

Experimental landscapes were set up using cattle watering tanks (0.61 m deep $\times$ 1.52 m diameter, ~ 1000 litres total volume) as individual patches (Resetarits, 2001; Binckley & Resetarits, 2005). Four circular experimental landscapes were established, each containing six locality types (unique combinations of total number and types of patch). Each landscape comprised 21 tanks (patches) divided among six localities (clusters of patches) (Fig. 1a). Patch number was manipulated by varying the number of patches per locality, and quality was manipulated by varying the presence/absence of predatory fish and the spatial association of fish and fishless patches. This generated three types of patches ($n = 84$ total, 28 for each patch type): predator-free, predator-associated (predator-free patches spatially associated with predator patches), and predator-present (Fig. 1b). Analysis of set ($n = 36$ total, 12 for each category) had three quality categories – predator-free, predator-associated, and predator-present – each with one, two, and four patches (Fig. 1a,b). Locality ($n = 24$ total) had two quality categories, predator-free and mixed, comprising one, two, and four versus two, four, and eight patches, respectively (Fig. 1a,b). Six locality types were randomly assigned to positions in each landscape (Fig. 1a).

All landscapes were established within a large abandoned field adjacent to a remnant arm of the Great Dismal Swamp in Chesapeake, Virginia, USA. Fish were present in the permanent creeks and some permanent ponds, while fish presence/absence in most seasonal ponds varied interannually as a result of flooding and duration/amount of annual rainfall. The field was surrounded by second-growth forest dominated by red maple (*Acer rubrum*), sweetgum (*Liquidambar styraciflua*), and loblolly pine (*Pinus taeda*). Landscapes did not differ in distance to natural ponds and were in full sunlight to enhance beetle colonisation.

On 8 July all cattle tanks (patches) were covered with a tight-fitting fibreglass screen ($1.3 \times 1.13\,\text{mm}$ mesh) to

(a)

(b)

Patch

Response to
individual patches
of different habitat
type and spatial
context

Set

Response to sets of
patches of the
same habitat type
distributed across
the landscape

Locality

Response to
spatially grouped
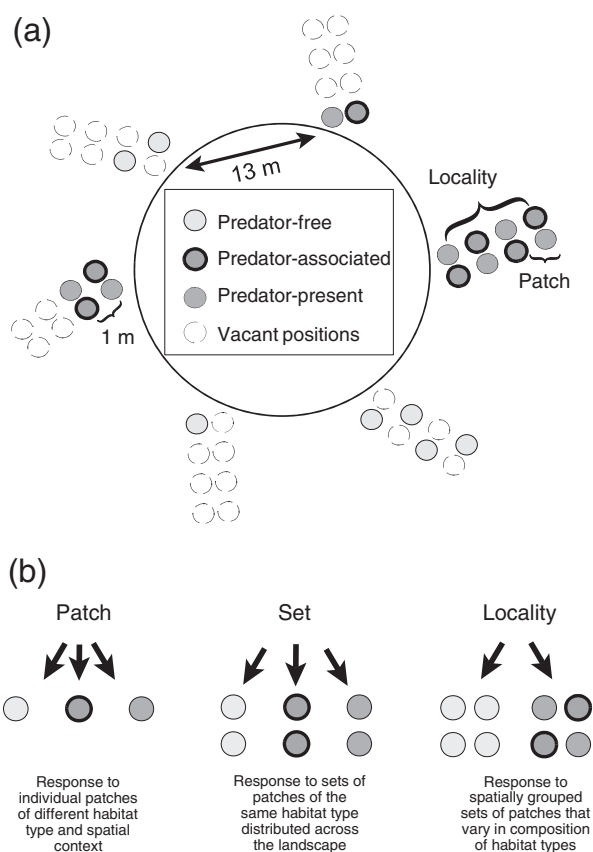sets of patches that
vary in composition
of habitat types

Fig. 1. (a) Diagram of an experimental landscape. Four such landscapes were placed in a large mowed oldfield surrounded by hardwood and pine forest. Localities (six) consisted of one, two, four, or eight patches, and patches were of three types: predator-free, predator-associated, and predator. 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 symmetrical 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 colonisation in response to variation in patch quality and patch number.

prevent premature colonisation and filled with water pumped (through finer mesh screen) from a nearby borrow pit. Two days later, randomised aliquots of 0.4 kg of dried leaf litter and 1.0 litre of zooplankton (primarily Cladocera, and Copepoda) and phytoplankton collected from nearby ponds were added and predators (five banded sunfish, *Enneacanthus obesus*, each ~4.5 g in mass) placed under screens. Screens were then pushed underwater in all tanks, thus allowing colonisation. This eliminated physical interactions between predators and colonising organisms, but allowed chemical communication and a complete inventory of all but the smallest colonising adult beetles. We did not assay beetle larvae. Pools were opened for colonisation on 10 July, and adult beetles were collected from pools on 27 July, preserved in ethanol, identified to species at the Smithsonian Institution using pre-existing vouchers from Chesapeake, Virginia, and counted.

Data analysis

Our design allowed the examination of responses to variation in patch number and quality (perceived predation risk) in three distinct ways: patch, which consisted of individual pools (84); set, which consisted of spatial clustered pools of the same patch type (36); and locality, which consisted of spatially clustered groups of pools (24). Analysis of variance (ANOVA) was performed on mean abundance for each species for patch, set, and locality (Table 1). Factors were landscape (block), number (number of patches per locality, or number of patches per type per locality), quality (two locality types, three patch types) and the number × quality interaction. The experiment comprised a randomised block design, incompletely crossing patch quality with patch number in locality and patch analyses, but completely crossing quality and number in set analyses.

Looking at individual beetle species abundance at the level of patch examines whether patch type and context (defined as the number and quality of neighbouring patches) were important in determining patch-specific colonisation rates, by examining whether colonisation rates are affected by individual patch quality and quality of neighbouring patches. For number, it addresses whether colonisation depends on number of adjacent habitat patches (Fig. 1b).

Looking at set examines whether sets of patches are differentially colonised relative to sets of patches of differing habitat type, holding patch number constant (Fig. 1b). Set thus examines how colonisation is parsed among sets of patches of a specific type across a landscape.

Finally, looking at locality, we examined whether variation among spatially discrete sets of patches of differing number and quality (as a result of spatial contagion of perceived predation risk, where characteristics of one habitat patch affect the perceived quality of nearby patches; Resetarits & Binckley, 2009) generates different rates of colonisation (Fig. 1b). Localities containing both fish and fishless patches should present greater habitat heterogeneity to colonising organisms compared with localities containing only fishless patches (Fig. 1).

Fisher's protected least significant difference test (for main effects with $P < 0.1$) was conducted to examine differences among discrete quality levels; multiple comparisons were not carried out for number because it represents continuous variation, and thus the main effects are of primary interest. In order to look for any evidence of interspecific avoidance, we generated a simple pairwise correlation matrix (Pearson) of the abundances for the eight most numerous species. We used SAS 9.2 (SAS Institute, 2008) with type III sums of squares and $\alpha = 0.05$ for all tests.

Results

A total of 7299 individuals of 34 species of aquatic beetles colonised our experiment: 4588 individuals of 20 species of Dytiscidae; 2696 individuals of 11 species of Hydrophilidae; and one species each of Noteridae (one individual), Haliplidae (two), and Hydraenidae (12) (Fig. 2, Table 2).

Table 1. ANOVA summary of the responses of the eight most abundant beetle species for patch, set, and locality. Because factors in patch and locality analyses are incompletely crossed, the interaction is based only on the completely crossed portion of the design, as reflected in the interaction degrees of freedom. Set is completely crossed and thus the interaction uses the full design.

	Patch			Set			Locality		
	Quality **d.f**. (2,72)	Number (3,72)	Quality × number (3,72)	Quality (2,24)	Number (2,24)	Quality × number (4,24)	Quality (1,15)	Number (3,15)	Quality × number (1,15)
Copelatus glyphicus	25.60	1.04	0.76	20.84	15.64	5.80	20.55	12.45	6.05
	<0.0001	0.3816	0.5199	**<0.0001**	**<0.0001**	**0.0021**	**<0.0004**	**<0.0002**	**0.0265**
Enochrus ochraceus	11.61	0.31	0.50	8.26	11.43	2.14	6.40	6.03	2.00
	<0.0001	0.8173	0.6818	**0.0019**	**0.0003**	0.1070	**0.0231**	**0.0066**	0.1774
Hydroporus ruficeps	32.89	0.34	0.22	41.29	31.52	7.66	18.12	20.46	2.76
	<0.0001	0.7979	0.8807	**<0.0001**	**<0.0001**	**0.0004**	**<0.0007**	**<0.0001**	0.1173
Uvarus granarius	14.71	0.61	0.42	15.71	6.56	2.26	12.52	3.89	3.37
	<0.0001	0.6083	0.7418	**<0.0001**	**0.0053**	0.0922	**0.0030**	**0.0307**	0.0863
Laccophilus proximus	4.18	0.63	0.67	3.70	12.64	1.13	0.6	5.61	1.05
	0.0192	0.5964	0.5745	**0.0398**	**0.0002**	0.3664	0.4488	**0.0088**	0.3215
Laccophilus rufus	9.45	0.29	0.45	10.59	11.11	2.49	10.58	7.99	3.54
	0.0002	0.833	0.7196	**0.0005**	**0.0004**	0.0701	**0.0054**	**0.0021**	0.0793
Heloporus lineatus	10.22	1.93	1.18	11.70	6.87	4.87	10.38	5.51	4.57
	0.0001	0.1318	0.3237	**0.0003**	**0.0044**	**0.0051**	**0.0057**	**0.0094**	**0.0494**
Enochrus perplexus	13.14	0.13	0.17	10.52	7.07	2.21	12.39	5.27	2.52
	< 0.0001	0.9493	0.9177	**0.0005**	**0.0039**	0.0987	**0.0031**	**0.0111**	0.1333

Species responses – patch

For patch, the pattern was very clear; quality was significant for the eight most numerous species (*Laccophilus proximus*, $P = 0.0192$; all others, $P < 0.0001$), and there were no significant effects of patch number or any quality × number interaction (Table 1, Figs 3a–d and 4a–d). The lack of significant effects of patch number or interactions indicates that variation in abundance/patch was driven by differences in quality, and variation in the number of patches/locality did not affect the colonisation rate of individual patches.

Predator-free and predator patches differed significantly for all species (Figs 3a–d and 4a–d), and six of the eight most numerous species showed significant risk contagion, with abundance in predator-associated sites intermediate between predator-present and predator-free patches(Figs 3a–d and 4a–d). Thus, predator-associated patches were affected by their proximity to patches containing predators. For the two remaining species, *Hydroporus ruficeps* and *L. proximus*, predator-free and predator-associated were equally preferred over predator patches (Figs 3c and 4a). The abundances of the eight most numerous beetle species were positively correlated across the 84 individual patches (18 of the 21 species pairs significantly positively correlated), suggesting congruent habitat preferences and no interspecific avoidance in the context of our three patch types (Table 3).

Species responses – set

For sets of patches characterised by patch type, both quality and number significantly affected the mean abundance for all eight species (Table 1), with three showing a significant

quality × number interaction, suggesting that the effects of number on colonisation varied with patch quality. For all species, predator-free and predator sets were significantly different in abundance (Figs 3e–g and 4e–g). Responses in predator-associated sets were species-specific, with three species intermediate between and significantly different from predator-free and predator types (Figs 3e,h and 4f); for three others, predator-associated and predator patch types were not significantly different, but differed significantly from predator-free (Figs 3f and 4g,h). For the remaining two species, predator-free and predator-associated were not significantly different but were significantly different from predator patches (Figs 3g and 4e). Thus, six of the eight species colonised predator-associated sets at a lower rate than predator-free sets, despite the former not actually containing predators.

Species responses – locality

Both quality and number significantly affected the mean abundance of the eight most numerous species (Table 1). Two of the eight species showed a significant quality × patch number interaction, with a steeper slope with increasing patch number for predator-free versus mixed localities (Figs 3i–l and 4i–l).

Discussion

Our data demonstrate that patch quality, number and context influence the colonisation rate of a variety of aquatic beetles, and affect the structure of the resulting communities. Beetles clearly respond to the presence of fish in individual patches,
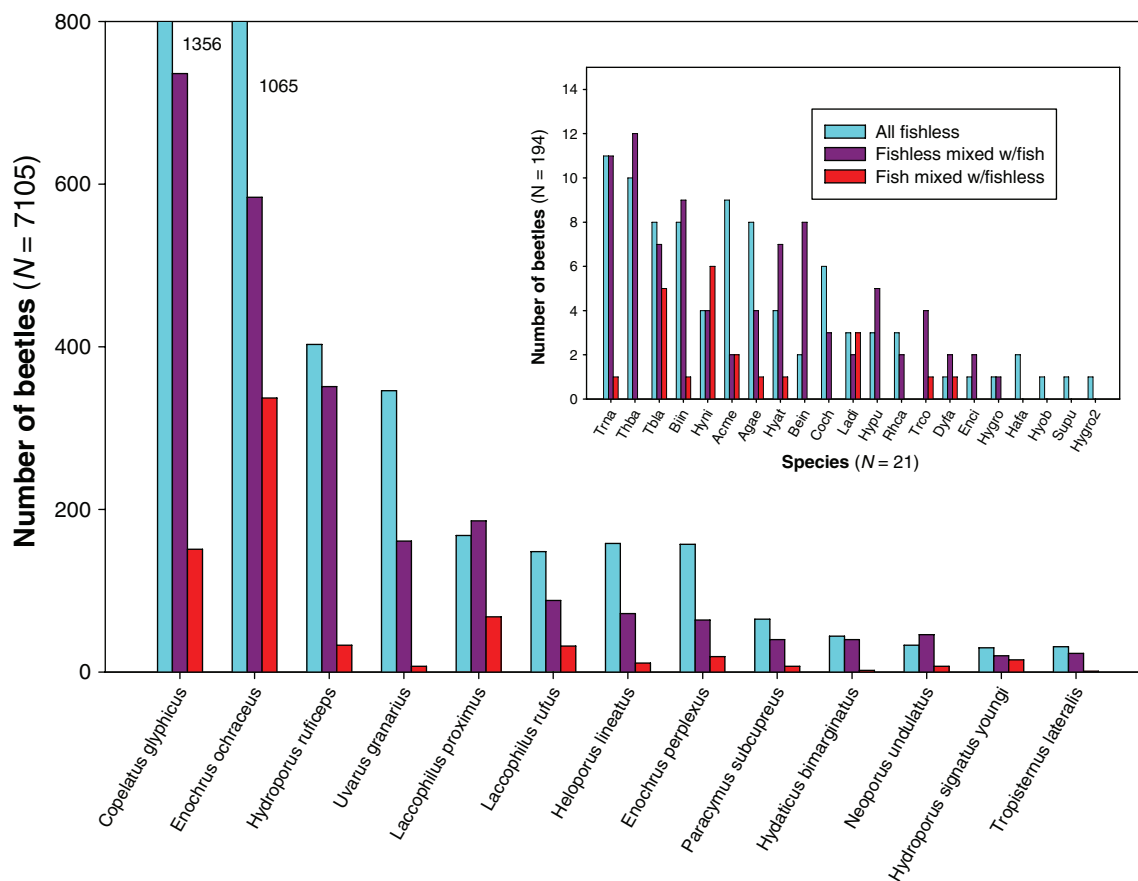
Fig. 2. Total number of colonists of the 13 most abundant beetles (main figure) and the remaining 21 species (inset) across the three patch types, showing the differences in colonisation rate for patches of the three types. Variation in patch number (not shown) affected colonisation in a strictly proportional fashion, with different slopes bases on patch type (Figs 3 and 4). The beetle assemblages generated by variation in colonisation of the three patch types are distinctly different. Abbreviations in inset (species, family): Acme, *Acilius mediatus*, Dytiscidae; Agae, *Agabus aeruginosus*, Dytiscidae; Bein, *Berosus infuscatus*, Hydrophilidae; Biin, *Bidessonotus inconspicuus*, Dytiscidae; Coch, *Copelatus chevrolati*, Dytiscidae; Dyfa, *Dytiscus fasciventris*, Dytiscidae; Enci, *Enochrus cinctus*, Hydrophilidae; Hafa, *Haliplus fasciatus*, Haliplidae; Hyat, *Hydrena atlantica*, Hydraenidae; Hyni, *Hydroporus niger*, Dytiscidae; Hyob, *Hydrochara obtusata*, Hydrophilidae; Hypu, *Hydrovatus pustulatus*, Dytiscidae; Hygro, *Hygrotus* sp., Dytiscidae; Hygro2, *Hygrotus* sp. 2, Dytiscidae; Ladi, *Laccornis difformis*, Dytiscidae; Rhca, *Rhantus calidus*, Dytiscidae; Supu, *Suphisellus puncticollis*, Noteridae; Thba, *Thermonectus basillaris*, Dytiscidae; Tbla, *Tropisternus blatchleyi*, Hydrophilidae; Trco, *Tropisternus collaris*, Hydrophilidae; Trla, *Tropisternus lateralis*, Hydrophilidae; Trna, *Tropisternus natator*, Hydrophilidae; Uvgr, *Uvarus granarius*, Dytiscidae.

and to the presence of fish in nearby patches, showing spatial contagion of predation risk. Thus, habitat decisions are made at multiple spatial scales, among individual patches, and among groups of spatially clustered patches. This significantly lowers expected colonisation rates of individual patches containing or associated with fish, and decreases species richness (Resetarits & Binckley, 2013), in localities with a mixture of fish and fishless patches. Thus, individual patch characteristics influence habitat selection, as does patch context related to predation risk, but the number of patches does not affect habitat decisions. Larger sets of patches do not attract a disproportionately larger number of beetles, as colonisation scales linearly with the number of patches. This is surprising as larger sets of patches should be more easily detected and might actually be preferred (Palmer *et al.*, 1997). Possibly, the spatial scale of our experimental landscapes is such that each

circular landscape forms the general attractant, and decisions are then made among localities and patches, obviating the passive effects of increasing patch number within localities.

Recent studies have documented the important role of habitat quality in colonisation rate and resulting community structure in aquatic insects (see review in Blaustein, 1999; Åbjörnsson *et al.*, 2002; Binckley & Resetarits, 2005; Resetarits & Binckley, 2009, 2013; Vonesh *et al.*, 2009; Hurst *et al.*, 2010; Kraus & Vonesh, 2010). However, these typically manipulate quality while holding patch size and density constant and were not designed to compare their relative importance. Thus, the relative importance of patch number versus quality and how quality interacts with area is not well understood. Quality frequently equals or exceeds size and distance when explaining population-level patterns of patch occupancy, turnover and abundance in terrestrial systems (Dennis & Eales, 1997;
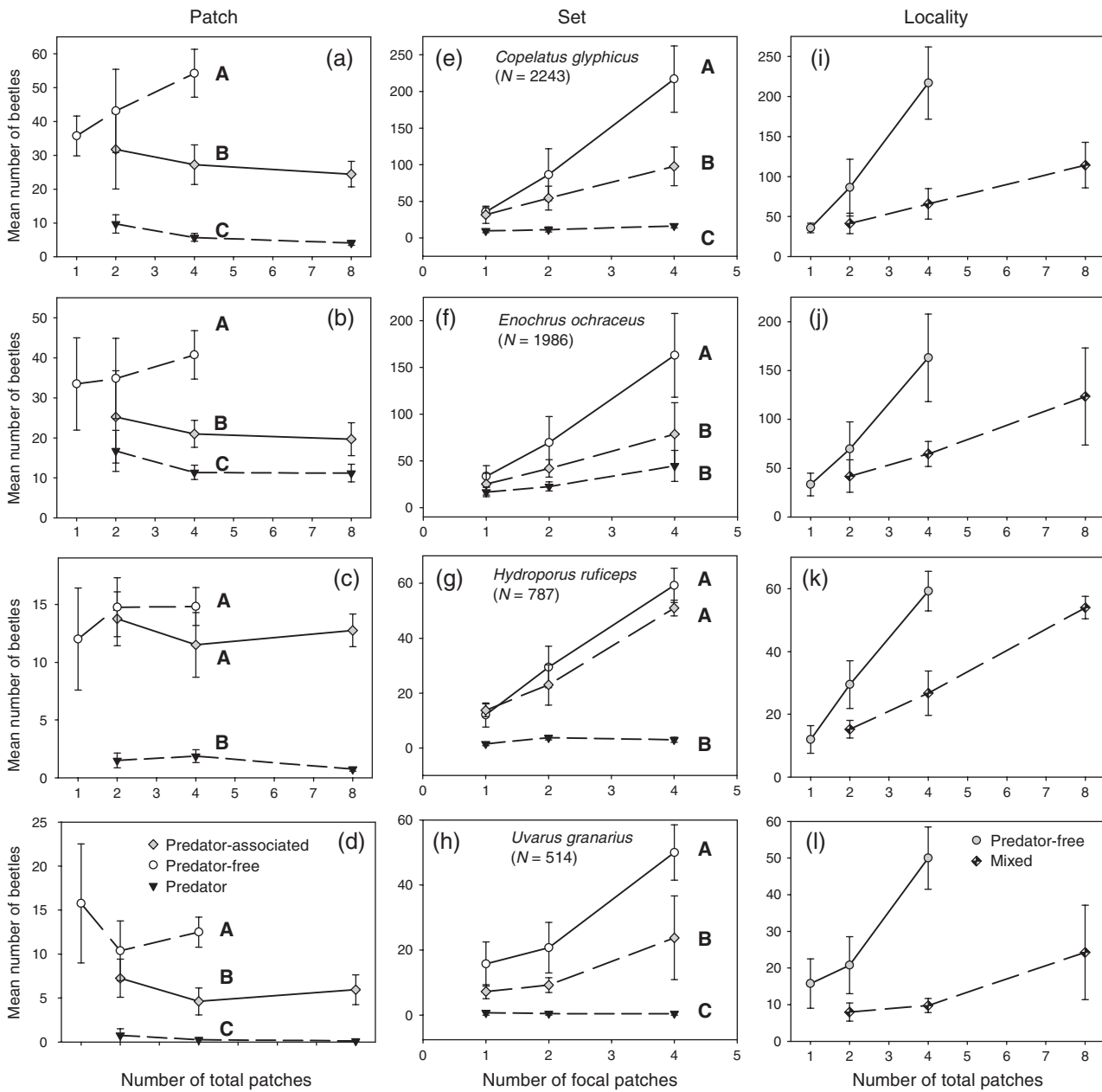
Fig. 3. Responses of the first through fourth most abundant beetles (all species with > 200 total colonists) to variation in patch (a–d), set (e–h), and locality (i–l) (mean ± 1 SEM) (see Table 3). The response variable was the number of individuals per patch. Different letters indicate significant differences among habitat types using Fisher's protected least significant difference test. See also Fig. 4.

Fleishman *et al.*, 2002; Collinge *et al.*, 2003; Summerville & Crist, 2004; Summerville *et al.*, 2005; but see Moilanen & Hanski, 1998). However, quantity and quality are often confounded when concentrations of limiting resources are correlated with habitat area (see review in Haynes & Cronin, 2004; Krauss *et al.*, 2005; Rabasa *et al.*, 2008), thus leaving open the question of which drives observed patterns. Our results should provide multiple hypotheses to be tested by those examining field abundance patterns in non-experimental settings by suggesting that patch quality, number and their

interaction determine colonisation rates but their importance varies by species and the scale at which analysis occurs (Table 1, Figs 2–4).

Looking for general patterns among the beetles, both dytiscids and hydrophilids demonstrated avoidance of predator and predator-associated patches, and individual species in both families demonstrated a pattern of risk contagion (Figs 3 and 4). Two congeneric species pairs were included among the eight most abundant species. We could anticipate congeners to be similar in habitat preferences or, conversely, to diverge
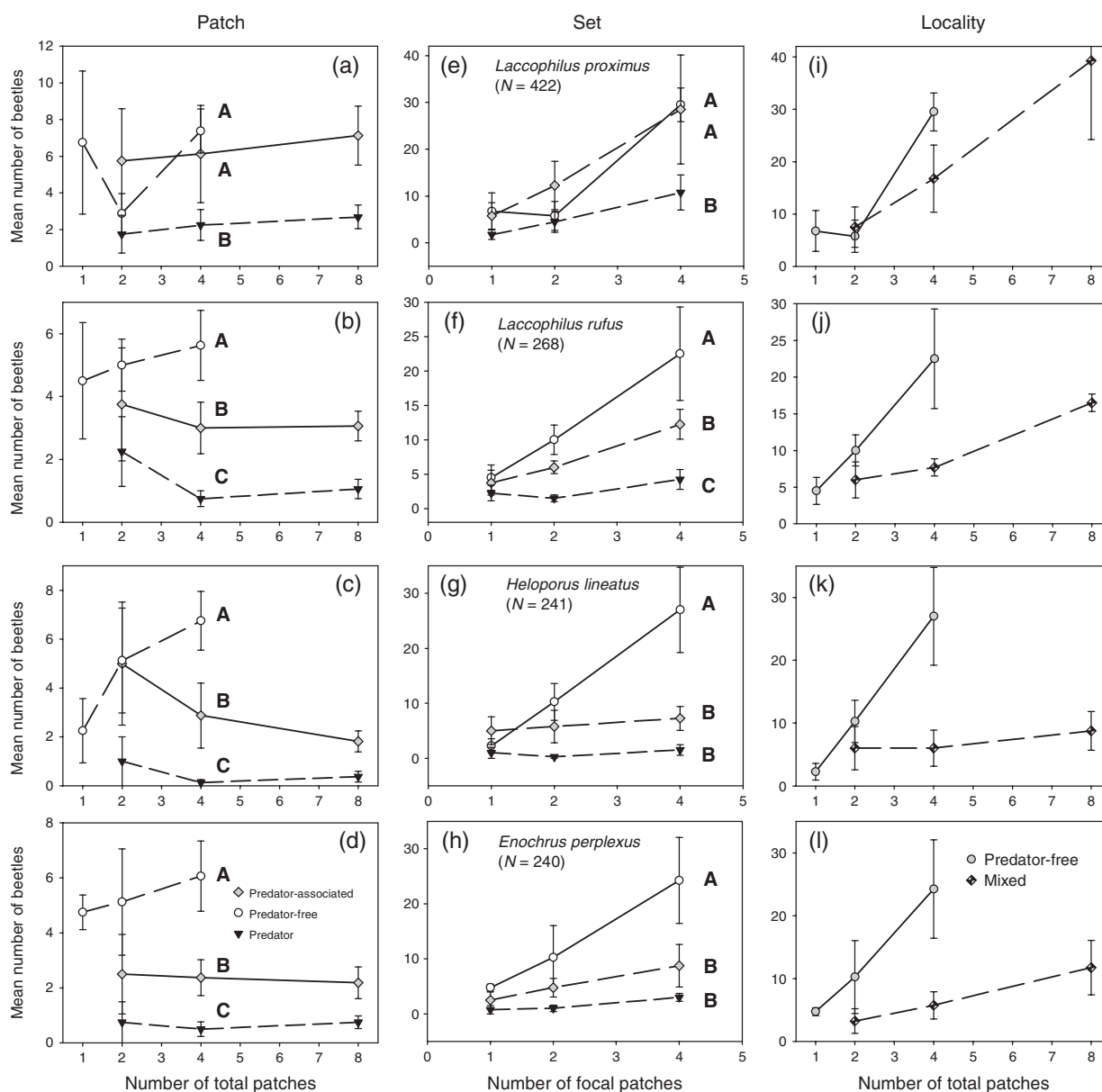
Fig. 4. Responses of the fifth through eighth most abundant beetles (all species with > 200 total colonists) to variation in a-d) Patch, e-h) Set, and i-l) Locality (mean ± 1 s.e.m) (see Table 3). Response variable was number of individuals/patch. Different letters indicate significant differences among habitat types using Fisher's Protected LSD. See also Fig. 3.

in preferences to provide some niche separation. *Enochrus ochraceus* and *Enochrus perplexus* (hydrophilids) showed similar patterns of response, with both demonstrating risk contagion (Figs 3b and 4h), while *L. proximus* and *Laccophilus rufus* (dytiscids) showed contrasting patterns; both strongly avoided predators, but only *L. rufus* showed contagion (Fig. 4a,b).

Beetle responses overall were very consistent. For the eight most abundant species, all but three species pairs were significantly positively correlated in their abundances at the patch level (Table 3). The three species pairs that were not significantly correlated all involved *L. proximus*, one of only

two species that did not demonstrate contagion. While these strong correlations may also suggest heterospecific attraction, competition theory suggests that they more likely reflect shared habitat preferences.

Locality data illustrate that groups of spatially associated fishless patches accumulate individuals at significantly faster rates as patch number increases. Rather than more diverse sets of patches increasing the accumulation of individuals and species, the association of risky with high-quality patches reduces colonisation (Figs 2–4). Interestingly, increasing the total number of fish patches does not decrease colonisation rate, indicating that perception of fish is a threshold effect (one fish

Table 2. Species list with family.

Species	Family
Acilius mediatus	Dytiscidae
Agabus aeruginosus	Dytiscidae
Berosus infuscatus	Hydrophilidae
Bidessonotus inconspicuus	Dytiscidae
Copelatus chevrolati	Dytiscidae
Copelatus glyphicus	Dytiscidae
Dytiscus fasciventris	Dytiscidae
Enochrus cinctus	Hydrophilidae
Enochrus ochraceus	Hydrophilidae
Enochrus perplexus	Hydrophilidae
Haliplus fasciatus	Haliplidae
Helophorus lineatus	Hydrophilidae
Hydaticus bimarginatus	Dytiscidae
Hydrena atlantica	Hydraenidae
Hydrochara obtusata	Hydrophilidae
Hydroporus niger	Dytiscidae
Hydroporus ruficeps	Dytiscidae
Hydroporus signatus youngi	Dytiscidae
Hydrovatus pustulatus	Dytiscidae
Hygrotus sp.	Dytiscidae
Hygrotus sp. 2	Dytiscidae
Laccophilus fasciatus rufus	Dytiscidae
Laccophilus proximus	Dytiscidae
Laccornis difformis	Dytiscidae
Neoporus undulatus	Dytiscidae
Paracymus subcupreus	Hydrophilidae
Rhantus calidus	Dytiscidae
Suphisellus puncticollis	Noteridae
Thermonectus basillaris	Dytiscidae
Tropisternus blatchleyi	Hydrophilidae
Tropisternus collaris	Hydrophilidae
Tropisternus lateralis	Hydrophilidae
Tropisternus natator	Hydrophilidae
Uvarus granarius	Dytiscidae

patch contaminates surrounding patches) or a frequency response, as all mixed localities had a 1 : 1 ratio of fish to fishless patches.

Larval hydrophilids and dytiscids, along with adult dytiscids, are important predators in temporary aquatic systems. Factors that affect colonisation will doubtless affect their prey and species with whom they compete. Variation in predation regime in aquatic systems can cascade into surrounding terrestrial systems as well, elevating the importance of species turnover across landscapes of aquatic habitats (Knight *et al.*, 2005; Burkle *et al.*, 2012). Avoidance of fish appears to be a predictably adaptive response, but individuals or species that avoid otherwise suitable habitats because of proximity to predators miss opportunities for themselves and open up opportunities for individuals/species that exercise a more precise assessment of habitat quality. For example, the two species of *Enochrus* show similar responses, with a resulting covariance in distribution and abundance, while our two species of *Laccophilus* show different responses, with a resulting reduction in covariance. Thus, in environments with increasing frequency of fish, behavioural habitat loss proceeds more rapidly for all species except *L. proximus* because of risk contagion.

Factors and processes that generate variation in patch-specific colonisation rates contribute to local and regional patterns of co-occurence and landscape-level variation in species distribution and community structure (Resetarits *et al.*, 2005; Abrams *et al.*, 2007). The beetle species colonising our experimental landscapes showed largely similar responses, especially to aspects of patch quality as determined by the distribution of predators. Most species were represented in all three patch types, with variation centred on the abundance of colonists, rather than variation among patch types in the identity of colonists. We saw little evidence of the type of species segregation suggestive of true habitat specialisation. Whether this represents variation among individuals in habitat

Table 3. Pearson correlation coefficients for the joint abundances in individual patches ($N = 84$) of the eight most abundant beetle species.

	Cogl	*Enoc**	*Hyru*	*Uvgr*	*Lapr*	*Laru*	*Heli**
*Enoc**[†]	0.7756						
	<0.0001						
Hyru	0.5500	0.5184					
	<0.0001	**<0.0001**					
Uvgr	0.5306	0.5506	0.5063				
	<0.0001	**<0.0001**	**<0.0001**				
Lapr	0.2482	0.2580	0.4083	0.2144			
	<0.0228	**<0.0178**	**<0.0001**	<0.0501			
Laru	0.4646	0.4369	0.4276	0.4204	0.1311		
	<0.0001	**<0.0001**	**<0.0001**	**<0.0001**	< 0.2343		
*Heli**	0.4895	0.4566	0.6124	0.2449	0.4281	0.3579	
	<0.0001	**<0.0001**	**<0.0001**	**<0.0247**	**<0.0001**	**<0.0001**	
*Enpe**	0.8240	0.8238	0.4819	0.4711	0.1628	0.3782	0.4453
	<0.0001	**<0.0001**	**<0.0001**	**<0.0001**	<0.1390	**<0.0001**	**<0.0001**

All but three species pairs were significantly positively correlated (in bold) and these involve *Laccophilus proximus*, indicating a general congruence of habitat choices and little interspecific avoidance.

*Indicate Hydrophilidae.

[†]Abbreviations (species, family): Cogl, *Copelatus glyphicus*, Dytiscidae; Enoc, *Enochrus ochraceus*, Hydrophilidae; Enpe, *Enochrus perplexus*, Hydrophilidae; Heli, *Helophorus lineatus*, Hydrophilidae; Hyru, *Hydroporus ruficeps*, Dytiscidae; Laru, *Laccophilus fasciatus rufus*, Dytiscidae; Lapr, *Laccophilus proximus*, Dytiscidae; Uvgr, *Uvarus granarius*, Dytiscidae.

preferences – as a result of genetic variation in sensory abilities or behavioural algorithms, imprinting on natal habitats, or ideal free processes of density compensation – is unknown and a subject for further enquiry. Certainly, the answer is likely to differ among species. Here we have, at the least, determined that a variety of aquatic beetles respond to variation in biotic conditions in specific patches, assess patch context in terms of perceived predation risk, and make colonisation decisions at multiple spatial scales. This reinforces a unique characteristic of habitat selection, in that it simultaneously affects the dynamics of both colonised and avoided habitats (Resetarits, 2005; Resetarits *et al.*, 2005) and emphasises the critical role of habitat selection in the distribution and abundance patterns of aquatic beetles.

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