2009

Spatial and Temporal Dynamics of Habitat Selection Across Canopy Gradients Generates Patterns of Species Richness and Composition in Aquatic Beetles

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Spatial and temporal dynamics of habitat selection across canopy gradients generates patterns of species richness and composition in aquatic beetles

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Abstract. 1. Colonisation is a critical ecological process influencing both population and community level dynamics by connecting spatially discrete habitat patches. How communities respond to both natural and anthropogenic disturbances, furthermore, requires a basic understanding of how any environmental change modifies colonisation rates. For example, disturbance-induced shifts in the quantity of forest cover surrounding aquatic habitats have been associated with the distribution and abundance of numerous aquatic taxa. However, the mechanisms generating these broad and repeatable field patterns are unclear.

2. Such patterns of diversity could result from differential spatial mortality post colonisation, or from colonisation alone if species select sites non-randomly along canopy coverage gradients. We examined the colonisation/oviposition dynamics of aquatic beetles in experimental ponds placed under both open and closed forest canopies.

3. Canopy coverage imposed a substantial behavioural filter on the colonisation and reproduction of aquatic beetles representing multiple trophic levels, and resulted in significantly higher abundance, richness, and oviposition activity in open canopy ponds. These patterns strengthened overtime; although early in the experiment, the most abundant beetle had similar abundance in open and closed ponds. However, its abundance subsequently declined and then most other species heavily colonised open canopy ponds.

4. The primary response of many aquatic species to disturbances that generate canopy coverage gradients surrounding aquatic ecosystems is behavioural. The magnitude of the colonisation responses reported here rivals, if not exceeds, those produced by predators, suggesting that aquatic landscapes are behaviourally assessed and partitioned across multiple environmental gradients. The community level structure produced solely by selective colonisation, is predicted to strongly modify how patch area and isolation affect colonisation rates and the degree to which communities are linked by the flux of individuals and species.

Key words. Colonisation, connectivity, dispersal, diversity, oviposition site selection, metacommunity.

Introduction

Mechanisms generating spatial and temporal variation in colonisation rates are integral to the concepts of island biogeography, metapopulation, and metacommunity ecology (MacArthur & Wilson, 1967; Hanski, 1999; Holyoak *et al.*, 2005). Different dispersal 'strategies' (non-selective, philopatry, habitat selection) used by species to sample and move through landscapes generate vastly dissimilar rates and patterns of colonisation that differentially affect population and community level dynamics (Sutherland, 1996; Hanski & Singer, 2001; Bohonak & Jenkins, 2003; Resetarits *et al.*, 2005; Amarasekare, 2007).

Thus, predicting the responses of species and communities to both natural and anthropogenic environmental change requires an understanding of how different dispersal strategies are distributed among sets of species, and how these interact with environmental heterogeneity to affect patch-specific colonisation rates (Binckley & Resetarits, 2002, 2008).

Aquatic communities are embedded within a terrestrial matrix, and linked strongly to this matrix by the movement of multiple species across aquatic-terrestrial boundaries (Wilbur, 1997). Disturbances such as fire, timber harvest, etc. generate gradients of canopy coverage surrounding freshwater habitats that correlate with variation in numerous abiotic and biotic factors in the underlying waters (Werner & Glennemeier, 1999; Skelly *et al.*, 2002; Batzer *et al.*, 2004; Schiesari, 2006). Arranging aquatic habitats along canopy coverage gradients, from open canopies receiving high levels of solar radiation to those with closed canopies and lower productivity, has been useful for predicting the distribution and performance of numerous aquatic taxa (Skelly *et al.*, 1999; Werner *et al.*, 2007). The general, but not exclusive, pattern has been reduced performance, abundance, and diversity of aquatic taxa in closed canopy sites (Nilsson & Svensson, 1995; Skelly *et al.*, 1999; Batzer *et al.*, 2000; Hill *et al.*, 2001; Palik *et al.*, 2001; Halverson *et al.*, 2003, Burne & Griffin, 2005; McCauley, 2005; Werner *et al.*, 2007). How modifications to the terrestrial matrix (forest loss or re-growth see Caspersen *et al.*, 2000; Chen *et al.*, 2006) affect aquatic ecosystems (Skelly *et al.*, 1999; Rubbo & Kiesecker, 2004) depends critically on how such changes affect colonisation dynamics.

These patterns of distribution and abundance along canopy gradients could be produced by differential mortality when (1) species non-selectively colonise all sites and experience increased mortality in closed canopy areas, or (2) when philopatric populations that continually return to natal waters for reproduction, suffer extinction after repeated reproductive failure in sites whose canopy coverage has changed over time (Resetarits *et al.*, 2005). Such mechanisms are implicitly tested in experiments measuring the performance of species placed in aquatic habitats under differing degrees of canopy coverage, or experiments manipulating characteristics typically correlated with canopy (Rubbo & Kiesecker, 2004; Williams *et al.*, 2007). However, an equally plausible alternative is that these patterns are produced by colonisation itself, as species detect and respond to site-specific canopy conditions (e.g. open or closed, see Binckley & Resetarits, 2007; Hocking & Semlitsch, 2007).

The effect of habitat selection on species distributions have been documented in a variety of aquatic taxa in response to both biotic and abiotic factors (Resetarits & Wilbur, 1989; Blaustein, 1999; Binckley & Resetarits, 2003, 2005; Vonesh & Buck, 2007). Recent work has documented selective colonisation of open canopy ponds (Binckley & Resetarits 2007; Hocking & Semlitsch, 2007). However, our understanding of the extent of species responses to variation in canopy cover is still limited by various factors that co-vary with canopy in the field. For example, aquatic diversity (including most beetles) at our study site is concentrated in numerous ephemeral open canopy ponds compared with the fewer but larger closed canopy ponds that often contain fish predators (C. Binckley, unpubl. data). These multiple

confounding factors correlated with canopy coverage require experimentation to quantify how canopy alone affects colonisation dynamics. In addition, responses to canopy are potentially complex, because actual canopy cover, and potential cues used to assess it, change seasonally in a predictable manner, as well as over larger time scales in response to natural and anthropogenic disturbance and succession (Hill *et al.*, 2001; Rubbo & Kiesecker, 2004; Schiesari, 2006). Variation in the distribution and abundance of species across gradients of canopy cover suggests that canopy may prove to be a dominant behavioural filter inducing community structure by influencing dispersal and colonisation at multiple spatial scales.

We experimentally examined the colonisation dynamics of a diverse assemblage of aquatic insects (primarily beetles) and oviposition site selection in a natural population of an aquatic beetle (*Tropisternus lateralis*), to assess the importance of habitat selection as a mechanism underlying changes in species distribution and abundance with changes in canopy cover. We specifically addressed whether open and closed canopy sites represent distinctly different habitat types in terms of colonisation/oviposition, and how such dynamics might change seasonally in response to leaf phenology.

Methods

Study organisms

At our study site, aquatic beetles are abundant in ponds from early spring to late fall (Binckley & Resetarits, 2005). They feed and reproduce in the water, and adults of most species immigrate and emigrate to and from ponds if local conditions change (pond drying) or aestivate in the dry pond basin. Many species of aquatic insects, including coleopterans, show increased abundance and richness correlated with the amount of open canopy at ponds (Matta, 1979; Nilsson & Svensson, 1995; Batzer *et al.*, 2000, 2004; Palik *et al.*, 2001; Fairchild *et al.*, 2003; Tuno *et al.*, 2005). 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. For example, *T. lateralis* is a hydrophilid beetle with obligate aquatic adults, larvae, and egg cases (Zalom *et al.*, 1979; Resetarits, 2001). After a semi-terrestrial pupal stage along the periphery of ponds, adults disperse aerially amongst ponds for feeding and reproduction (Zalom *et al.*, 1979). Females lay conspicuous silken egg cases (3–4 mm) containing 12–24 eggs that hatch into predacious larvae (Zalom *et al.*, 1979; Resetarits, 2001). Egg deposition occurs at our study site from early April to October. It is unknown if adults modify their habitat use prior to oviposition or simply deposit egg cases where they forage (see Mayhew, 1998).

Experimental design

We utilised experimental mesocosms (cattle watering tanks approximately 1.65 m in diameter, 0.61 m in depth, and 1000 litre

total volume) to control for local (quantity, quality, and age of both water and substrate, competitors and predators) and regional factors (the number and spatial arrangement of patches of each potential habitat type) that often co-vary with canopy coverage and complicate the identification of mechanisms generating patterns along this gradient.

We established 24 experimental ponds organised into six rectangular spatial blocks of four ponds each at the Naval Security Group Activity Northwest (NSGANW) base in Chesapeake, Virginia. Experimental ponds mimic natural ponds to the extent that natural populations of numerous aquatic insects and amphibians readily colonise them for feeding and reproduction. Each block was established at a field/forest boundary with two ponds located 5 m into the woods (closed canopy) and two located 5 m into the clearing (open canopy). Ponds in the same block and in the same canopy category were approximately 1.5 m from each other, and blocks were located approximately 30 m apart. Forest was ≈25 years post-agricultural abandonment and dominated by red maple (*Acer rubrum*), sweetgum (*Liquidambar styraciflua*), and loblolly *pine (Pinus taeda);* the field was regularly mowed. Our manipulations represent the endpoints of a gradient in canopy cover, from fully open in the clearing, to essentially fully closed in the forest. All possible positions between these are possible at natural ponds.

We covered all ponds with fibreglass mesh screen lids (2 mm × 2 mm) to prevent premature colonisation by aquatic insects before filling them with tap water on 16/17 March 2002. Three days later, 1.0 kg of dried leaf litter and 1.0- litre aliquots of pond water collected from six temporary ponds were randomly added to each tank. The addition of pond water inoculates the experimental units with bacteria, algae, and zooplankton. However, these trophic levels were not quantified by taxa. On 29 March 2002, we pushed the mesh screen lids down into the water to allow for aquatic insect colonisation and oviposition. We collected insects from above the screens once a week for 6 weeks, and preserved insects and egg cases in glass vials containing 95% ethanol. The experiment ended on 15 May 2002. Insects were identified to species when possible at the Division of Entomology, U.S. National Museum of Natural History, using voucher specimens collected from Chesapeake, VA (Matta, 1979).

This experiment employed a randomised complete block design for multivariate analysis of variance with two treatments, closed and open canopy. We examined the effect of block and treatment on two response variables, the mean beetle abundance and species richness. We did not analyse the number of *Tropisternus lateralis* egg cases, as all were oviposited in open canopy ponds. A single MANOVA was performed using SAS for Windows version 8.0 with type III sums of squares and α = 0.05, followed by separate univariate ANOVAS for each response variable.

Leaf emergence was initiating when the experiment began, and as time progressed, closed canopy ponds received less direct solar radiation and experienced deeply shaded conditions. We performed a repeated measures MANOVA (RMANOVA) for the two response variables, followed by profile analysis for each separate variable to test if these changes affected the data structure. The RMANOVA tests whether time affected the response variables and interacted with canopy coverage. Profile analysis tests

three hypotheses sequentially, and if any hypothesis is rejected the analysis stops (Khattree & Naik, 1999). Specifically, this analysis tests (1) whether means for the treatments are parallel through time, and if so (2) are they coincidental, and (3) whether they are horizontal. In this experiment, for example, profile analysis first tested if the plots of weekly mean beetle abundance, and species richness for open and closed canopy were parallel. This hypothesis was rejected for both response variables.

Results

During the 6 weeks of the experiment, a total of 3791 insects comprised of 39 species were collected, along with 360 *T. lateralis* egg cases (Figs 1 and 2). All but one species, *Gerris marginatus*, were aquatic beetles. The three most abundant species, *Copelatus glyphicus*, *Laccophilus fasciatus rufus*, and *Enochrus ochraceus*, comprised 61.6% of the total sample, with the 10 most abundant species comprising 90.2% of the total (Fig. 2).

When the data were analysed without respect to time, significantly more individuals and species were collected from the open canopy ponds (Table 1, Figs 1 and 2). Open canopy sites contained 2667 individuals of 37 species, comprising 70.4% of the total sample. In contrast, 1124 individuals of 21 species, of which 66.7% were *C. glyphicus*, were collected in closed canopy sites. Canopy also affected species composition; 18 species were found only in open canopy ponds, whereas only two were unique to closed canopy sites. Furthermore, only 10 species had higher total abundance under a closed canopy (Fig. 2), and no *T. lateralis* egg cases were collected from closed canopy ponds (Fig. 1).

Canopy, time, and the time × canopy interaction were significant in the RMANOVA model, as profile plots for both response variables were not parallel (Table 2). Significantly more beetles were captured in open canopy ponds only after week 3 (Fig. 1, $P < 0.05$ weeks 4–6), whereas significantly more species were collected in open canopy ponds after week 1 (Fig. 1, $P < 0.05$ weeks 2–6). The most abundant species, *C. glyphicus*, had similar abundance in open and closed ponds during the first 3 weeks of the experiment, but then its abundance declined markedly, and other abundant species began colonising primarily open canopy sites (e.g., *L. rufus*, Fig. 3). Open canopy ponds continually added species through time, whereas species richness in closed canopy sites remained essentially constant (Fig. 1). *Tropisternus* oviposition did not occur until week 3 and all egg cases were deposited in open canopy ponds (Fig. 1).

Discussion

Canopy coverage has been increasingly implicated in the performance, abundance, distribution, and diversity of a variety of aquatic species (Nilsson & Svensson, 1995; Skelly *et al.*, 1999; Grether *et al.*, 2001; Hill *et al.*, 2001; Halverson *et al.*, 2003; Batzer *et al.*, 2004; McCauley, 2005; Schiesari, 2006; Werner *et al.*, 2007; Williams *et al.*, 2007). Changes in forest cover associated with changing forestry and agricultural practices, habitat
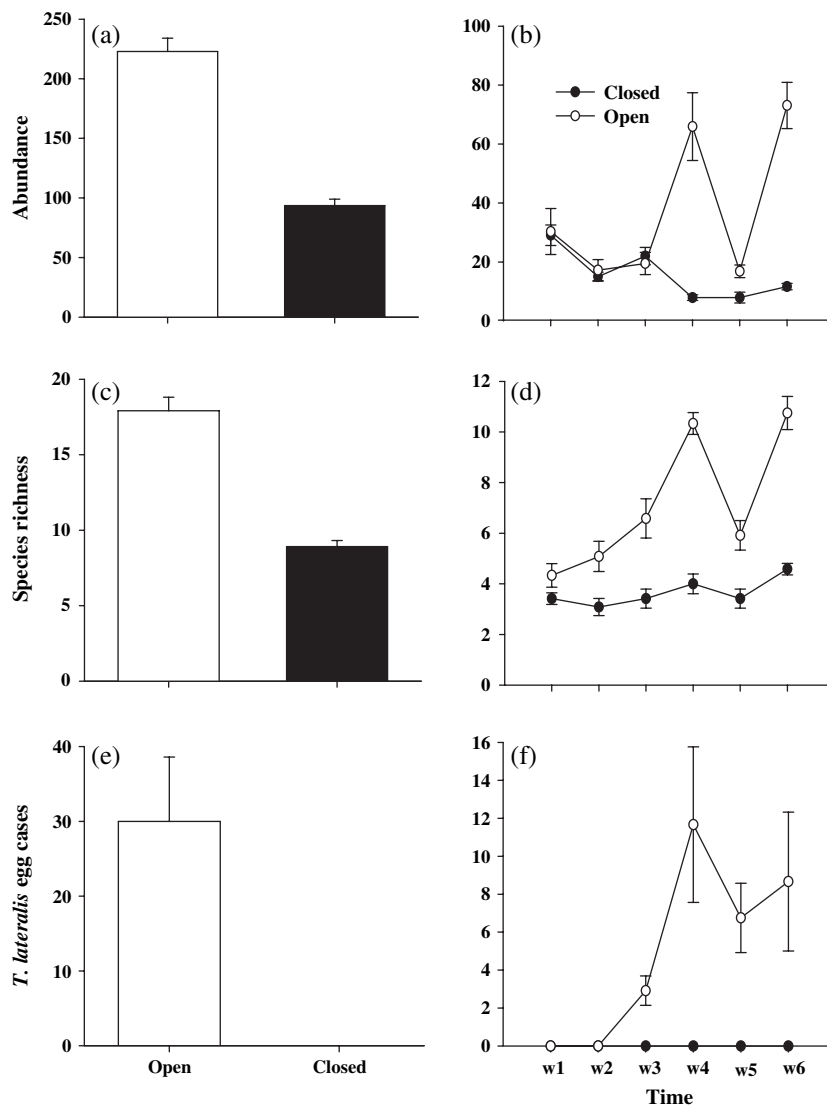
Fig. 1. Mean (±SE) abundance (a, b) and species richness (c, d) of aquatic beetles, and number of *Tropisternus lateralis* egg cases (e, f) in experimental ponds established under either open (white bars and circles) or closed (black bars and circles) forest canopy. Panels a, c, and e show overall means, while b, d, and f show means for each week of the experiment. Open canopy ponds contained significantly more individuals, species, and *T. lateralis* egg cases.

restoration efforts, and alterations of natural disturbance regimes (Frost, 1995; Tilman *et al.*, 2000; Caspersen *et al.*, 2000; Schurbon & Fauth, 2003; Chen *et al.*, 2006) may have unforeseen consequences for associated aquatic systems. Thus, understanding the responses of multiple species to gradients of canopy cover is critical to understanding variation in community structure, and both large and small scale changes in forest cover have important implications for distribution and diversity of aquatic organisms (England & Rosemond, 2004; Binckley & Resetarits, 2007).

Habitat selection is clearly a potential mechanism underlying observed patterns of distribution and abundance across aquatic sites differing in canopy coverage, at least at the endpoints of the gradient (open vs closed). Our observed differences in aquatic beetle abundance, richness, reproduction, and composition between open and closed canopy ponds were generated behaviourally by selective colonisation/oviposition (Figs 1–3). Such behaviour appears widespread both geographically and taxonomically in species representing a variety of trophic levels

(Figs 1–3, see Binckley & Resetarits, 2007; Hocking & Semlitsch, 2007). This ability to track changes in habitat quality and follow the spatial *movement* of high-quality habitats, could offset the fitness reductions observed when species are experimentally placed in closed canopy habitats. If species behaviourally avoid low-quality habitats, expected changes in population or metapopulation size can be mediated, assuming a sufficient high-quality habitat remains accessible. Documented local extinction events in closed canopy ponds (Skelly *et al.*, 1999; Werner *et al.*, 2007) could be behavioural phenomena, depending on the strength of the avoidance or attraction. Although more work is necessary in quantifying colonisation at intermediate canopy levels, we have demonstrated that the extremes of this gradient produce strong spatial variation in colonisation dynamics, as opposed to simply generating local variation in performance and mortality.

Preference for open canopy ponds dominated our results and match published field accounts of species associations with
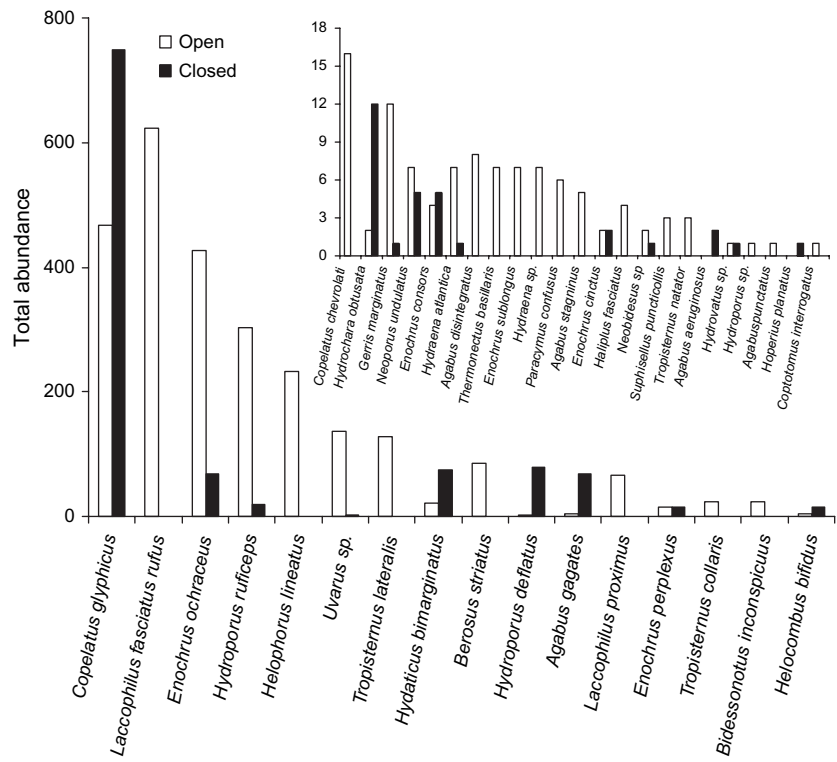
Fig. 2. Total abundance of each species colonising experimental ponds established under open (white bars) or closed (black bars) forest canopy. Most species preferred open canopy ponds, whereas a subset chose closed canopy sites. The most abundant species, *Copelatus glyphicus*, had significantly higher abundance in closed canopy ponds, but was well represented in open canopy sites. Note difference in scale of y axis for insert graph.

canopy coverage (see Matta, 1979; Larson *et al.*, 2000). The regional species pool at our study site appears dominated by species preferring open canopy ponds, with the capacity to detect and differentially colonise this habitat type. However, there was a strong temporal component to colonisation dynamics as canopy treatments progressively diverged with time (Figs 1 and 3). The most numerous species, *C. glyphicus*, heavily colonised both open and closed canopy ponds early in the experiment, effectively offsetting differences in abundance between treatments until week 4, when most other species arrived and primarily colonised open canopy ponds (Figs 1 and 3). The significantly higher abundance of *C. glyphicus* in closed canopy

ponds (almost 70% of the total) resulted from a short, early pulse of intense colonisation, after which it decreased in abundance (Fig. 3). There was a pronounced reduction in the colonisation of open canopy sites during week 5 (Fig. 1), perhaps as a result of heavy precipitation that generated numerous other ponds suitable for colonisation (C. Binckley, pers. obs.). However, the general temporal pattern was that open canopy ponds continually added species through time, whereas closed canopy sites had consistently lower richness, represented primarily by a different composition of species associated with woodland pools (see Matta, 1979; Larson *et al.*, 2000) with lower abundance (Figs 1 and 2).

Table 1. MANOVA using Wilks' Lambda and univariate ANOVAs for the effect of block and canopy on the mean abundance and richness of beetles colonising experimental ponds. Open canopy ponds received significantly more beetles and species than closed canopy sites. Data square root transformed.

Factor	Value	*F* Value	Num DF	Den DF	Pr > *F*
Block	0.5120	1.27	10	32	0.2867
Canopy	0.0698	106.49	2	16	<0.0001
Abundance					
Source	d.f.	ss	ms	*F*	*P*
Block	5	10.6	2.1	1.89	0.1493
Canopy	1	164.9	164.9	145.84	<0.0001
Error	17	19.2	1.1		
Total	23	194.8			
Species richness					
Block	5	0.43	0.08	0.94	0.4816
Canopy	1	8.87	8.87	94.83	<0.0001
Error	17	1.59	0.09		
Total	23	10.9			

Table 2. Multivariate repeated measures ANOVA for the effect of the dependent variables (beetle abundance and richness), canopy, time, and the canopy × time interaction. The significant canopy × time interaction suggests that the significant canopy effect on the two response variables changed during the experiment. Data square root transformed.

Effect	Num DF	Den DF	*F* Value	Pr > *F*
Response variable	1	275	100.62	<0.0001
Canopy	1	275	167.64	<0.0001
Time	5	275	23.51	<0.0001
Canopy × Time	5	275	12.02	<0.0001

This experiment was conducted in early spring, at the onset of leaf emergence, when canopy affects on aquatic systems should be at their weakest (Hill *et al.*, 2001). The seasonal development of canopy coverage, from sparse in winter to full in summer, should enhance differences between open and closed canopy ponds as they increasingly diverge in productivity. The specific cue(s) used to assess differences in canopy are unknown. However, reflectance (Bernath *et al.*, 2002) and visual cues associated with canopy itself (e.g. branches leaves see Binckley & Resetarits, 2007) are two hypothesised cues that would reduce searching costs if species avoid or target woods when colonising ponds, and the reliability of these cues would strengthen seasonally as well. Taken together, closed canopy ponds might become harder to locate, and less valuable, as the season progresses. For example, leaf emergence began during week 3 and this greatly reduced light reaching the forested experimental ponds (personal observation). Further work is needed to identify and better quantify specific cues potentially influencing selective colonisation/oviposition in response to forest canopy. However, preference for open canopy sites by multiple species is strong early in the season and appears to strengthen as time progresses (Figs 1 and 3).

Globally, aquatic systems are experiencing multiple changes to their surrounding terrestrial landscapes, whether through widespread deforestation, or via increases in per cent forest cover through suppression of natural disturbance regimes, such as fire, and conversion of abandoned agricultural land to forest (Frost, 1995; Tilman *et al.*, 2000; Chen *et al.*, 2006). This has generated a growing concern over how modification of terrestrial vegetation (see Caspersen *et al.*, 2000; Chen *et al.*, 2006) affects aquatic systems (Skelly *et al.*, 1999; Rubbo & Kiesecker, 2004; Binckley & Resetarits, 2007). Spatial and temporal variation in canopy cover can be generated rapidly by natural or anthropogenic disturbances, gradually by the process of succession, and seasonally via leaf phenology (Hill *et al.*, 2001; Binckley & Resetarits, 2007). We demonstrate that succession in forests only ≈25 years post-agricultural abandonment, results in habitat degradation for many species as canopies close (Figs. 1, 2). Future experimentation is needed to determine how finer gradients of canopy coverage in forests of varying ages, post disturbance, are assessed by colonising aquatic taxa. The behavioural partitioning of aquatic landscapes and how these metacommunities are structured, will depend upon whether canopy cover is perceived and responded to as a continuous variable, or if there are discrete, threshold responses (Rieger *et al.*, 2004).

The behavioural response to canopy coverage by colonising/ovipositing aquatic taxa equals, if not exceeds, that induced by predators such as fish (Blaustein, 1999; Binckley & Resetarits, 2003, 2008). When combined, these two colonisation filters generate four habitat types (open/closed canopy crossed with the presence/absence of predatory fish), which are predicted to have habitat specific colonisation rates. The degree to which spatially discrete communities are connected by processes of dispersal will depend on how spatial factors (area, isolation) modify colonisation rates within these different habitat types. If connectivity is habitat specific, in that ponds of the same habitat type are more strongly linked by dispersal, spatial sub-structure within metacommunities is behaviourally generated and each habitat type occurs in a unique spatial configuration (Fig. 4). Testing these hypotheses requires categorising ponds into different habitat types and examining habitat-specific slopes and intercepts along pond area and isolation gradients (Fig. 4, see Ryberg & Chase, 2007; Werner *et al.*, 2007). The existence of such behavioural landscapes
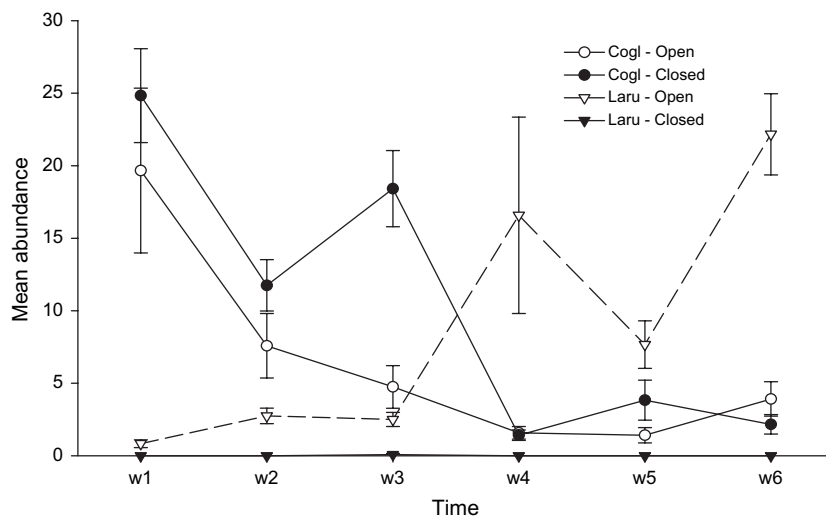

Fig. 3. Mean (±SE) abundance of the two most numerous species, *Copelatus glyphicus* (circles) and *Laccophilus rufus* (triangles), for each week of the experiment for open (white) and closed (black) canopy ponds.
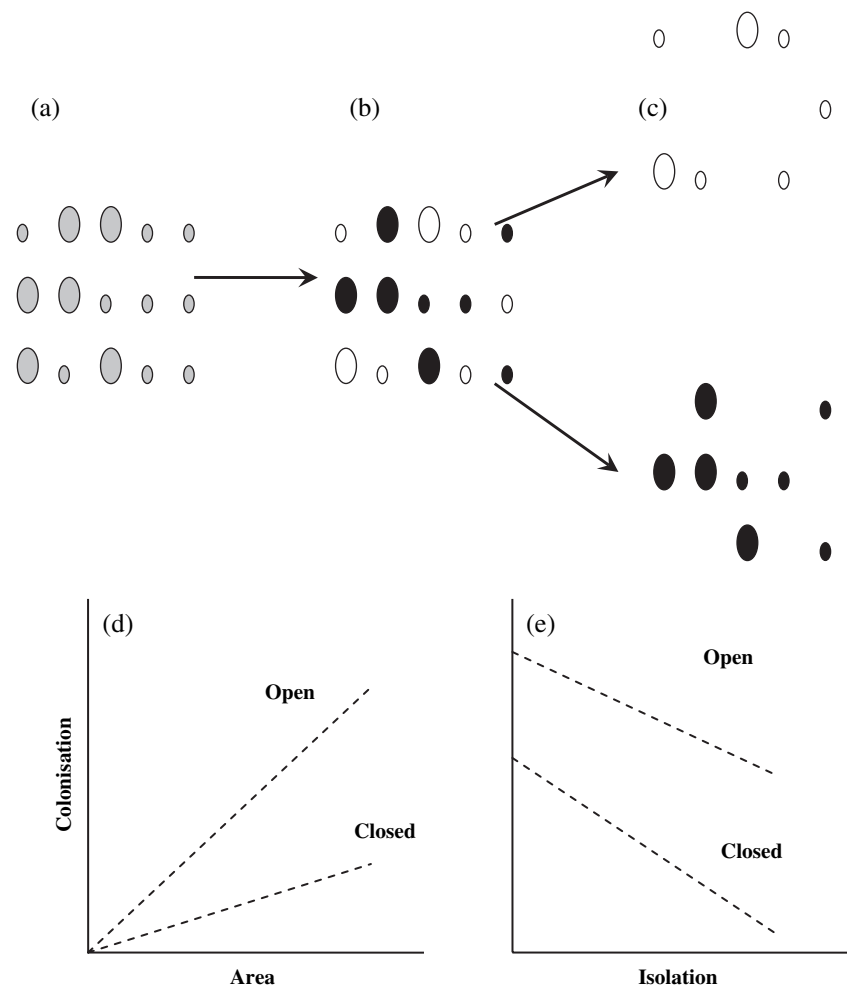
Fig. 4. A landscape of 15 ponds (a) broken up into two habitat types (b) of open (white) and closed (black) canopy. For species selectively colonising/ovipositing in response to canopy, each habitat type occurs in a unique spatial configuration (c). This spatial substructure is hypothesised to generate habitat specific colonisation curves along gradients of (d) area and (e) isolation. Panels d and e represent colonisation of a population, or assemblage of species, preferring open canopy ponds.

(Lima & Zollner, 1996) has clear implications for predicting the response of aquatic taxa to modifications of the terrestrial matrix.

Canopy closure has been increasingly identified as a critical predictor of the performance and diversity of aquatic species (Schiesari, 2006; Werner *et al.*, 2007). Responses to canopy gradients by aquatic taxa have received increased attention given local and regional scale changes to canopy composition and cover (Rubbo & Kiesecker, 2004; Williams *et al.*, 2007). In a growing number of aquatic taxa, responses to forest canopy closure appears to be a behavioural phenomenon, as our data in combination with other recent work demonstrates that species representing a variety of taxonomic and trophic positions selectively colonise open canopy sites for feeding and reproduction (McCauley, 2005; Binckley & Resetarits, 2007; Hocking & Semlitsch, 2007). For most active habitat selectors examined to date, canopy closure at a pond represents a cryptic form of habitat loss, as these ponds remain physically present, but are functionally non-existent. The reverse would be true for species preferring closed canopy sites. However, given the importance of open canopy sites in maintaining diversity in a variety of

aquatic taxa, it is becoming increasingly apparent that specific management strategies that include maintaining open canopy ponds in forested landscapes are needed. Habitat selectors should rapidly respond to restoration efforts that reduce canopy at aquatic sites, as opposed to species that are non-selective or philopatric. Strategically reducing canopy in ponds in close proximity to other open canopy sites, would further facilitate a rapid behavioural increase in aquatic diversity. A basic understanding of how different colonisation strategies are distributed among sets of species, provides both a predictive framework and creative opportunities for restoration efforts aimed at maintaining aquatic habitat quantity and quality.

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