ECOLOGY LETTERS

Ecology Letters, (2016) **19**: 191–200 doi: 10.1111/ele.12553

LETTER

Local contagion and regional compression: habitat selection drives spatially explicit, multiscale dynamics of colonisation in experimental metacommunities

William J. Resetarits Jr[1,2]* and Alon Silberbush[2,3]

Abstract

Habitat selection, including oviposition site choice, is an important driver of community assembly in freshwater systems. Factors determining patch quality are assessed by many colonising organisms and affect colonisation rates, spatial distribution and community structure. For many species, the presence/absence of predators is the most important factor affecting female oviposition decisions. However, individual habitat patches exist in complex landscapes linked by processes of dispersal and colonisation, and spatial distribution of factors such as predators has potential effects beyond individual patches. Perceived patch quality and resulting colonisation rates depend both on risk conditions within a given patch and on spatial context. Here we experimentally confirm the role of one context-dependent processes, spatial contagion, functioning at the local scale, and provide the first example of another context-dependent process, habitat compression, functioning at the regional scale. Both processes affect colonisation rates and patterns of spatial distribution in naturally colonised experimental metacommunities.

Keywords

Community assembly, context dependence, *Culex*, habitat selection, metacommunities, metacommunity paradigms, oviposition site choice, patch quality, predation risk, spatially explicit processes.

Ecology Letters (2016) **19**: 191–200

INTRODUCTION

A growing body of evidence identifies habitat selection as an important driver of community assembly in freshwater systems. Factors determining patch quality can be assessed by many colonising organisms and strongly affect colonisation rates of individual patches, the spatial distribution of prey and resulting community structure (Binckley & Resetarits 2005, 2007; Resetarits & Binckley 2009, 2013; Vonesh *et al.* 2009; Kraus & Vonesh 2010). Of particular importance in determining patch quality in aquatic systems is the presence and identity of predators (Wellborn *et al.* 1996; Wilbur 1997). Thus, habitat selection is a non-lethal, direct effect of predators that, unlike induced phenotypes or changes in prey performance, produces differences in local prey distribution and abundance rivalling lethal effects of predation (Binckley & Resetarits 2005; Resetarits & Binckley 2009; Vonesh *et al.* 2009).

Patch quality is simply patch specific fitness (Fretwell & Lucas 1970). Perceived patch quality is a complex function of expected fitness, sensory capabilities and evolved or learned behavioural algorithms. Recent work in the context of predation risk has demonstrated that perceived patch quality and resulting colonisation rates depend not only on risk conditions within a given patch but also on spatial context – nearby patches of high risk may strongly impact the colonisation rate of associated habitat patches (Resetarits 2005; Resetarits & Binckley 2009).

Two context-dependent processes that can affect patch-specific colonisation rates are spatial contagion and habitat compression (see Box 1) (Resetarits *et al.* 2005). In spatial contagion characteristics of nearby patches effect the perceived quality of focal patches, while under compression reduction in patch quality in neighbouring patches increases colonisation rate of remaining high-quality patches (Resetarits *et al.* 2005). Risk contagion can lead to cascading habitat loss, as discrete, high-quality patches associated with high-risk patches are avoided, further reducing available habitat. Compression potentially generates strong density-dependent effects, as more individuals are concentrated into fewer patches. These two processes can interact, with contagion leading to increased compression, and both potentially affect distribution and abundance (Resetarits *et al.* 2005).

Risk contagion affects oviposition site choice by treefrogs (Resetarits 2005) and chironomids (Wesner *et al.* 2012), and colonisation by aquatic beetles (Resetarits & Binckley 2009). Rates of colonisation for predator-associated patches (predator-free patches near predator patches) are far below those of predator-free patches lacking nearby predators. Reward contagion has been demonstrated for frogflies (*Megaselia randi*)

---

[1] *Department of Biology, The University of Mississippi, University, MS 38677-1848, USA*

[2] *Department of Biological Sciences, Texas Tech University, Lubbock, TX 79409, USA*

[3] *Current address: Department of Life Sciences, Center for Biological Control (CBC), Ben-Gurion University of the Negev, P.O. Box 653, Beer-Sheva 8410501, Israel and Department of Life Sciences, Achva Academic College, Achva 7980300, Israel*

**Correspondence: E-mail: wresetar@olemiss.edu*

© 2015 John Wiley & Sons Ltd/CNRS

Box 1 Clarification of spatial terminology and processes (see Fig. 1)

Patch – equivalent to 'patch' or 'habitat' in habitat selection literature (Fretwell & Lucas 1970; Rosenzweig 1981) and 'patch' or 'locality' in metacommunity literature (Wilson 1992; Leibold *et al.* 2004). In the context of our experimental landscape of small ponds, and the natural system on which it is based, a patch consists of a single habitat type and contains a community.

Locality – A geographical area containing multiple patches; a nested subset of all the patches within a larger region (Leibold *et al.* 2004). Nearest neighbour distances are smaller among patches within a locality than among patches at the scale of the region. Local scale decisions are made among patches within localities (Resetarits 2005).

Array – Experimental equivalent of a region in metacommunity parlance (Leibold *et al.* 2004). An array contains multiple localities with greater spatial separation than among individual patches within a locality. Regional scale decisions are made among localities within arrays (Resetarits 2005).

Contagion (Figs 2 and 3) – The effect of characteristics of nearby patches on the perceived quality of a given focal patch – this can be either negative (risk contagion) or positive (reward contagion) (Resetarits *et al.* 2005). This can occur locally, among individual patches within a locality, or regionally, among localities within a larger landscape.

Compression (Figs 2 and 3) – An increase in colonisation rate of suitable patches resulting from a reduction in the local or regional availability of such suitable patches through either changes in actual patch quality or perceived quality (Resetarits *et al.* 2005).

Compromise – When preferred habitats do not exist, or are co-opted by incompatible species, habitat selection forces species either to local extinction or habitat compromise. Species select the best remaining habitat (best of a bad situation), though average fitness may be considerably below that seen in the preferred habitats (*sensu* the Ideal Despotic Distribution (Fretwell & Lucas 1970)) and may even be below replacement rates, resulting in a sink population. This process may also place species into new ecological contexts and into new sets of species interactions (Resetarits *et al.* 2005).

colonising egg clutches of the red-eyed treefrog (*Agalychnis callidryas*); frogflies colonise undamaged clutches adjacent to damaged clutches (preferred oviposition habitat) at a higher rate than those near other undamaged clutches (Hughey *et al.* 2012). To date, no clear examples of habitat compression exist, yet, given a finite number of suitable patches in a landscape and finite dispersal abilities, factors that reduce quality and resulting colonisation of any given patch must redirect colonists to other suitable patches at some spatial scale. The alternative is compromise (see Box 1), where the algorithm for determining patch quality is altered to a 'best of a bad situation' scenario in which individuals simply take the best (or only) available local option, even at the cost of reduced fitness (Resetarits *et al.* 2005).

Oviposition site selection is a form of colonisation particularly important in aquatic systems, as a large proportion of species arrive via seasonal oviposition by species with complex life cycles (insects and amphibians) whose adults are not confined to the aquatic habitat (Merritt & Cummins 1984; Duellman & Trueb 1986; Schneider & Frost 1996; Wellborn *et al.* 1996; Wilbur 1997). Among these, mosquitoes are ubiquitous in many lentic habitats and are an excellent model system for examining questions regarding oviposition site choice in response to variables affecting patch quality. Mosquitoes possess highly sensitive chemosensory apparati, breed across a broad range of patch sizes, and can be quite selective with regard to fine-scale variation in habitat characteristics (Blaustein 1999; Blaustein & Whitman 2009; Juliano 2009; Vonesh & Blaustein 2010). Since adult life expectancy is often measured in days and oviposition opportunities are limited, it is assumed that, for species which oviposit via egg rafts, their entire reproductive output may be limited to a single pool (Clements 1999; Spencer *et al.* 2002). Thus, oviposition decisions are critical to offspring performance and adult fitness.

Females of the mosquito genus *Culex* lay conspicuous egg rafts that allow direct assay of oviposition, which is critical to separate oviposition responses from post-oviposition sorting. Species of *Culex* have been shown to strongly avoid certain fish species, including mosquitofish (*Gambusia*), responding primarily via chemical cues (Van Dam & Walton 2008; Eveland *et al.* 2015, unpublished data). Because of the sensory sensitivity of *Culex* species, compression should be more likely than contagion over relatively small spatial scales. Ovipositing females repelled from a specific predator patch should choose the nearest similar predator-free patch.

We conducted a field experiment using natural populations of two species of *Culex* as a model system to examine spatial context dependence in response to predatory fish. We specifically designed our experiment to examine the potential for both contagion and compression across multiple spatial scales (Fig. 1). Because we are dealing with naturally colonised experimental landscapes over a relatively large spatial scale, it is of necessity an open system. The average size of regions in experimental studies of metacommunities was found to be only 8X larger than the patches of which they were comprised (Logue *et al.* 2011). In contrast, our Localities were > 8X the size of our patches, and regions were $\gg 100$X the size of our patches. The estimated effective sampling area for gravid mosquitoes (Greenberg *et al.* 2012) was $\gg 100\,000$ m^2.

Natural oviposition sites are limited under typical July conditions in Eastern Missouri, but specific drought conditions in July 2013 worked in our favour and guaranteed that most small, natural pools were dry and the nearest competing water bodies to our arrays were a few larger, much older mesocosms (older pools attract far fewer ovipositing *Culex*: pers. obs.) > 100 m away to the NE of the northernmost array. *Culex* are considered relatively weak flyers (Becker *et al.* 2010; Clements 2012), and flight is a significant constraint for female mosquitoes following a blood meal, with females moving on

© 2015 John Wiley & Sons Ltd/CNRS

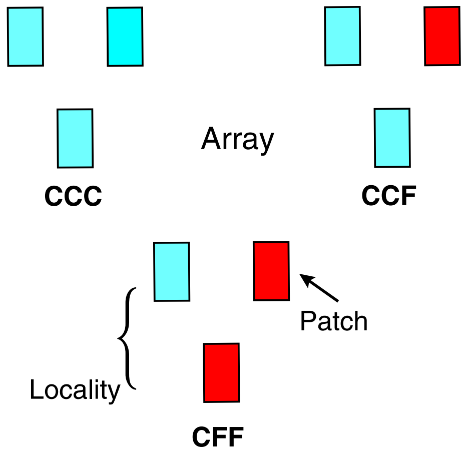


Figure 1 Schematic of 1 of 6 Arrays (blocks) comprising the experimental landscape (not to scale). Area of Patch = .034 m^2, area of Array > 43 m^2. Distance between Patches in a locality = 1.5 m, distance between Localities = 5 m, distance between Arrays > 40 m. Estimated capture area for the experimental landscape based on mean estimated flight distance of gravid females (Greenberg *et al.* 2012) ≈ 100 000 m^2. Locality type (all Control [CCC], 2 Control and 1 Fish patch [CCF] and 1 Control and two Fish patches [CFF]) was randomised among the three positions in each Array. Patch type (Control or Fish) was randomly assigned to positions within each Locality. See Box 1.

average only ~ 100 m (Greenberg *et al.* 2012): this presumably applies to gravid females as well. Thus, given the paucity of alternative oviposition sites, we make the assumption that our landscape has 'captured' the majority of ovipositing females within this ≫ 100 000 m^2 area, and that females which enter the capture space of a given array will choose to oviposit in that array. Should females leave an array and move to the next, they are faced with the same set of choices, thus exchange among them should be symmetrical.

Females approaching individual spatial Arrays within our experimental landscape are faced with a choice among Localities of three associated patches, and among individual Patches within those Localities (Fig. 1, Box 1). Our operating assumptions are that expected value for each Patch is the mean of all patches in that Array, and, in the absence of spatial context dependence, the number of egg rafts in Control (preferred) patches should be equal across Locality types. Four possible scenarios exist at the local scale (among Patches within a Locality): a) Ovipositing mosquitoes are oblivious to the presence of fish (Fig. 2a), b) oviposition is only dependent on Patch characteristics; number of egg rafts in a Patch depends solely on the presence or absence of fish (Fig. 2b), c) decisions occur primarily among Patches within a Locality. Females repelled from Fish patches would select nearby, within-Locality Controls, leading to higher Patch-specific densities (Fig. 2c), d) Fish patches negatively affect perceived quality of associated Control patches, resulting in reduced patch-specific oviposition rates (Fig. 2d). Figure 2e illustrates the expected pattern of oviposition in Control patches with increasing frequency of Fish patches.

If both mosquito species avoid Fish patches, and there is local context dependence, there are six potential scenarios at the larger scale of the individual Array (Fig. 3). Three of these are based on local compression (Figs 2c and 3a,c,e) and three on local contagion (Figs 2d and 3b,d,f); the latter also apply under scenario Fig. 2b – no local context dependence, only with lesser expected magnitude of potential effects at the larger scale. Figure 3 (table) details the expectations under the scenarios illustrated above.

Herein, we demonstrate that the colonisation rate of individual patches in an experimental metacommunity is a complex function of the presence/absence of predators in a given patch, the presence and frequency of nearby predator patches, and the regional distribution of predators among localities. Spatial contagion occurs at the local scale, among individual patches within localities (Fig. 2d), whereas spatial compression is evident at the regional spatial scale, among localities within arrays (Fig. 3f).

MATERIALS AND METHODS

We conducted a mesocosm field experiment in a large, naturally colonised, experimental metacommunity at Tyson Research Center of Washington University, during July 2013. Tyson consists of 795.8 fully fenced, access controlled, hectares along the Meramec River in Saint Louis County, Missouri. Tyson lies in the Ozark Border region and consists largely of oak-hickory secondary forest with sycamore, maple and cottonwood bottomlands. It also has patches of old field and a few permanent and temporary ponds and intermittent streams.

Our experiment was set up using artificial pools in a linear arrangement of 6 arrays (= blocks) of 9 pools each, spaced > 40 m apart (total linear distance > 300 m) along West Valley Rd., which parallels a seasonal stream. Individual arrays occupied forest gaps along the road on the side opposite the stream. Pools were at least 15 m from the stream, which was largely dry during the course of the experiment.

We used rectangular black plastic pools containing approximately 51 L (66 × 51 × 15 cm) as oviposition pools. Pools were filled with treated well-water, and 10 g of rabbit chow (16% protein) were added to each pool to encourage oviposition (Silberbush & Blaustein 2008, 2011). A plastic cylindrical cage (32 cm diameter), with sides removed and covered by insect screen, was glued to the centre of each pool. Pools (Patches) were placed in groups of three (Localities), positioned at the three corners of an equilateral triangle, with 1.5 m between pools (Fig. 1, Box 1). Three Localities were placed 5 m apart in an equilateral triangle ≈ 10 m on a side to form an Array; thus each Array (= block) was comprised of nine Patches. Pools contained either a single *Gambusia affinis* (Baird & Girard) placed inside the cage, or were fishless controls. Number of controls in each Locality ranged from 1 to 3, thus an Array consisted of three Locality types: all Control patches (CCC), two Control and one Fish patch (CCF) or one Control and two Fish patches (CFF). The Locality type within an Array and the Fish patches within each Locality were randomly assigned. Fish were not fed during the field test, and any observed macrofauna (Notonectids, beetles, etc.) were removed immediately (pools were checked daily) – few colonised the pools, likely due to their small size and the distance to other ponds. Pools were emptied and reset after 1 week to further

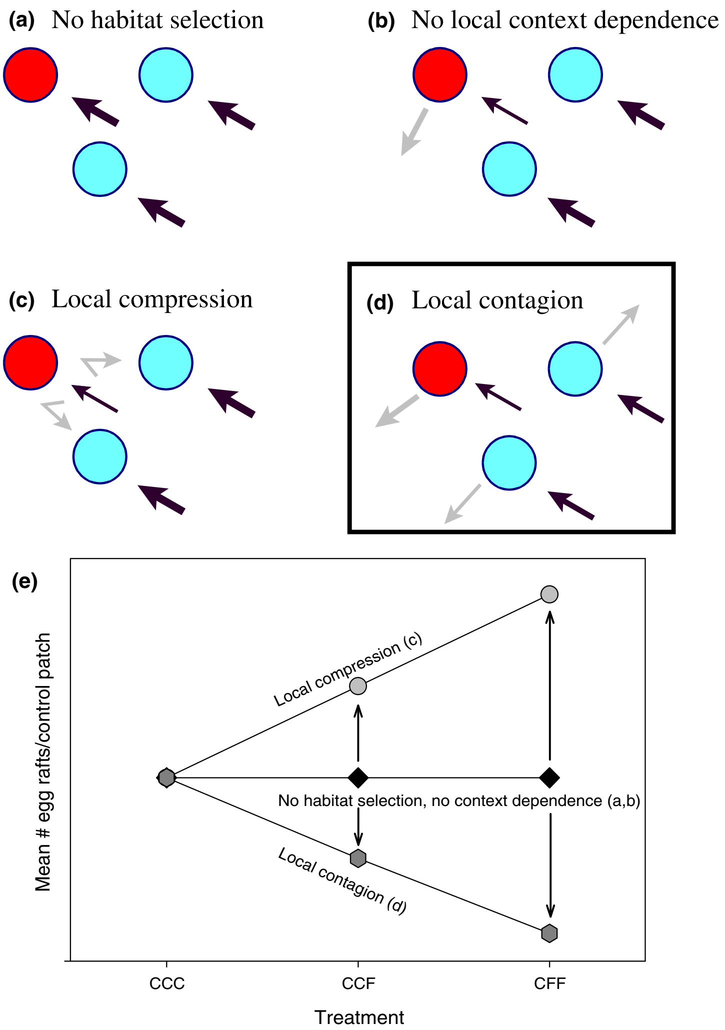


Figure 2 (a–d) Local scenarios (among Patches within a Locality), CCF locality used for the purpose of illustration (see Fig. 1, Box 1). Red = Fish, Blue = Control. Arrows are additive and indicate flow of ovipositing females (and hence egg rafts) through system; thickness of arrows indicates relative magnitude of flows. Black arrows = incoming females, grey arrows = females that leave that Patch or Locality without ovipositing, showing expected destination either within (c) or outside (b,d) the Locality. Square is observed scenario. e) Expected qualitative pattern of egg rafts per control patch with increasing frequency of fish patches.

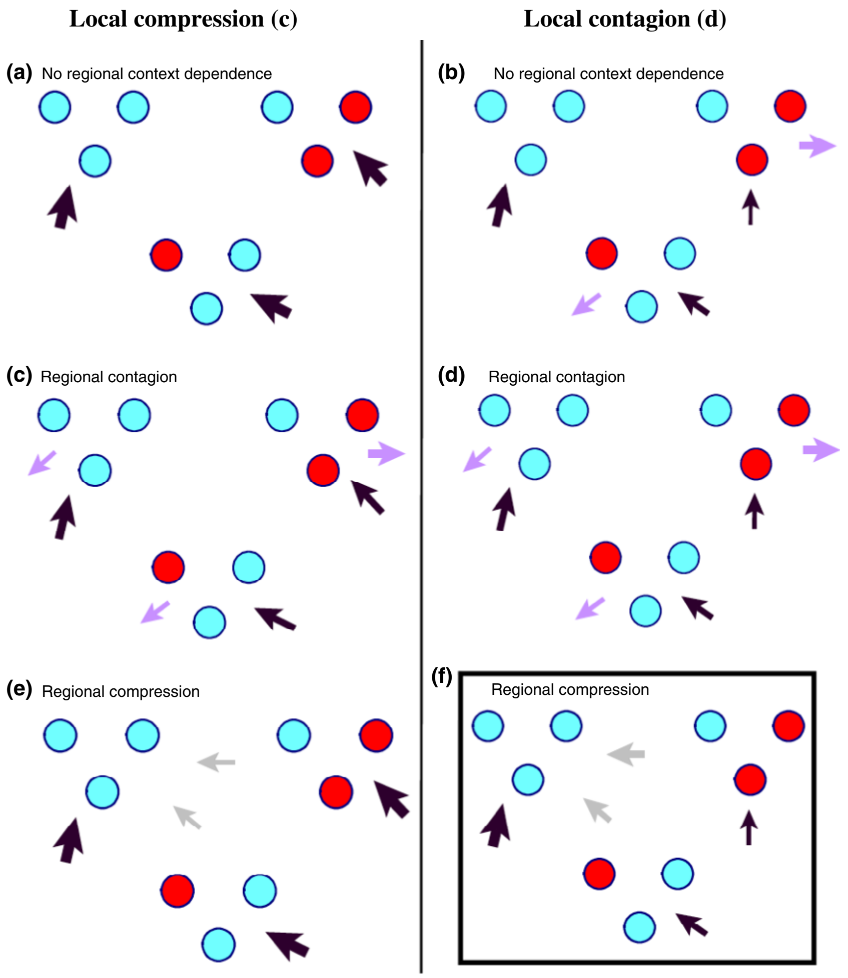
obviate any historical effects of community assembly and the experiment ended after the second week (total duration 16 July – 30 July 2013). We removed and counted *Culex* egg rafts from all pools daily to eliminate density effects. Egg rafts were then hatched, raised to fourth instar and identified to species following Darsie & Ward (2005). With very few exceptions, egg rafts were either *Culex restuans* (Theobald) or from individuals belonging to a widespread, introgressed hybrid population of *Culex pipiens* (Linnaeus) and *C. quinquefasciatus* (Say). We refer to the latter hereafter as *C.* p × q.

Data analysis

We used separate univariate ANOVAS for each mosquito species, since Array (= block) was significant in all analyses for *C. restuans*, but not close to significant (all $F < 1.0$, $P > 0.75$) in any analyses for *C.* p × q. Thus, block was included in the model for *C. restuans*, and rolled into the error term for *C.* p × q. For all analyses we used total number of egg rafts over the duration of the experiment; Patch or Locality were the unit of analysis and determined degrees of freedom. We used a two-stage analysis, first analysing the mean number of egg rafts/Patch for the two Patch types, Fish and Control, using only Localities containing both Patch types (CCF & CFF) to address the basic question of whether the two *Culex* species detect and avoid ovipositing in pools with *Gambusia*. This analysis ignored Locality type, treating the design as a randomised complete block design with equal replication of fish and fishless patches. This simply established fish avoidance to provide the basis for the primary hypothesis tests.

The primary hypothesis tests comprised a randomised complete block design with three treatments (Locality types: CCC, CCF, CFF) each occurring once in each of six spatial blocks (Arrays). We analysed two variables, (1) mean total number of egg rafts/Locality type, testing whether the frequency of

© 2015 John Wiley & Sons Ltd/CNRS



	Local	Regional	Egg rafts in CCF and CFF controls	Egg rafts in CCC controls	Egg rafts in Fish patches	Total egg rafts in localities
a	Compression	No context dependence	Increase	No effect	No effect	No effect
c	Compression	Contagion	Increase	Decrease	Decrease(?)	All decrease
e	Compression	Compression	Increase	Increase	No effect	CCC (and CCF?) increase
b	Contagion	No context dependence	Decrease	No effect	No effect	Reduced in CCF and CFF
d	Contagion	Contagion	Decrease	Decrease	Decrease(?)	All decrease
f	Contagion	Compression	Decrease (no net effect on CCF?)	Increase	No effect	CCC increase (no net effect on CCF?)

Figure 3 Regional scenarios (among Localities within an Array) (see Fig. 1, Box 1) Red = Fish, Blue = Control. Left, (a,c,e) regional outcomes under fish avoidance and compression at the local scale. Right (b,d,f), regional outcomes under fish avoidance and contagion at the local scale. The latter also apply under scenario Fig. 2b – no local context dependence, only with lesser expected magnitude of potential effects at the larger scale. Arrows are additive and indicate flow of ovipositing females (and resulting egg rafts) through system; thickness of arrows indicates relative magnitude of flows. Black arrows = incoming females, grey arrows = females that leave the Locality without ovipositing, showing expected direction, purple arrows = females that leave the Array without ovipositing. Square indicates observed scenario. Table details qualitative expectations under the above scenarios.

Fish vs. Control patches affected total egg rafts per Locality, and (2) mean total number of egg rafts/Control patch/Locality type, examining variation among Locality types in how Control patches were perceived. The latter analysis necessarily had different numbers of Control patches (1–3) contributing to the Control mean for each Treatment. Treatment means ($N = 3$) were compared using Fisher's Protected LSD only when the main effect of Treatment had $P < 0.10$, using $\alpha = 0.05$ for individual LSD comparisons. We also examined the correlation (Pearson's Product Moment) between abundance of *C. restuans* and *C.* p × q in Controls to test for possible interspecific avoidance. All analyses used (SAS Institute Inc., Cary, NC, USA) with Type III sums of squares and $\alpha = 0.05$.

© 2015 John Wiley & Sons Ltd/CNRS

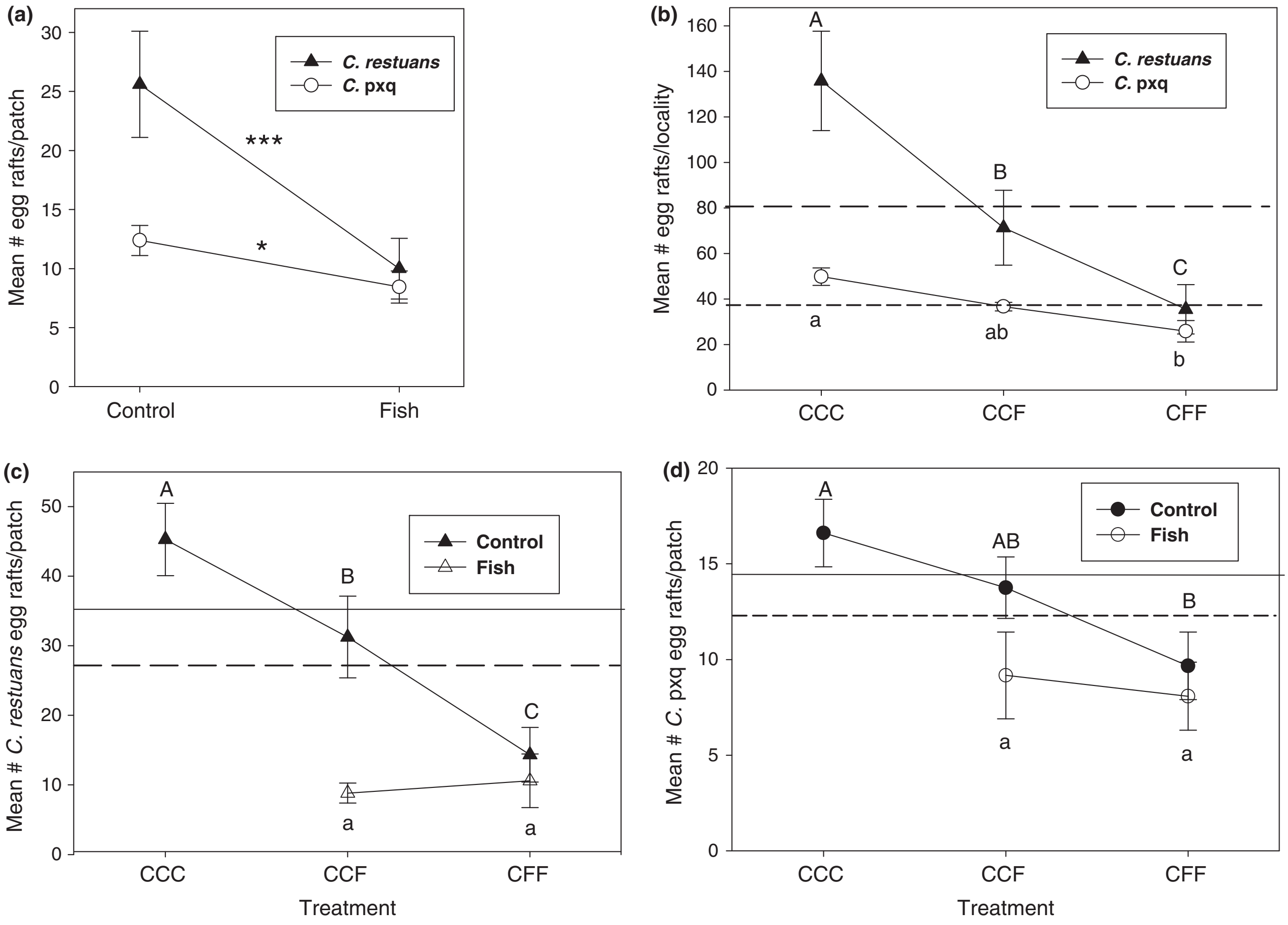


Figure 4 (a) Distribution of egg rafts between the 2 Patch types (Control & Fish) using data from CCF and CFF localities only, showing Patch-level habitat selection in response to Fish (mean ± 1 SE, $***P < 0.001$, $*P < 0.05$.). (b) Mean number (± 1 SE) of egg rafts/Locality showing significant effects of Locality type (CCC, CCF, CFF) for both species. Long-dashed line = overall per patch mean for *C. restuans* and short-dashed line = mean for *C.* p × q. Letters indicate treatments that are significantly different, uppercase for *C. restuans* and lowercase for *C.* p × q. (c & d) Mean (± 1 SE) egg rafts in Control and Fish patches in each Locality type showing the disproportional increase with increasing number of controls for *C. restuans* (c) and *C.* p × q (d). Letters indicate significantly different treatments, uppercase for Controls, lowercase for Fish. Dashed lines = overall patch mean, solid lines = overall Control patch mean. In the absence of context dependence, number of egg rafts in Control patches should be equal across Locality types. Results support local contagion and regional compression (see Figs 2 and 3).

RESULTS

Patch

Our arrays received a total of 1456 egg rafts of *C. restuans* and 674 egg rafts of *C.* p × q. Examining only Localities with both patch types (CCF & CFF), ovipositing mosquitoes of both species avoided individual Fish patches, thus establishing the basis for our examination of spatial context dependence. *Culex restuans* showed strong avoidance, with Controls (25.61 ± 4.49, mean ± 1 SE) receiving 150% more egg rafts than Fish patches (10.0 ± 2.58) ($F_{1,29} = 16.21$, $P = 0.0004$; Fig. 4a). *Culex* p × q showed a relatively weaker, but significant, response to Fish, with Controls (12.39 ± 1.28) receiving 47% more egg rafts than Fish patches (8.44 ± 1.37) ($F_{1,34} = 5.49$, $P = 0.025$; Fig. 4a). Overall there were 106% more egg rafts of the two species in Controls, and there was a significant positive correlation between numbers of egg rafts of the two species in Control patches, suggesting interspecific avoidance is not overriding predator avoidance in determining egg raft distribution ($r = 0.47$, $P = 0.0043$).

Locality

The makeup of a Locality (CCC, CCF, CFF) had a significant effect on the mean total number of egg rafts/Locality for both mosquito species. For *C. restuans* the effect was strong and significant ($F_{2,10} = 16.89$, $p = 0.0006$); increasing number of Controls led to disproportionately more egg rafts/Locality, with all three Locality types significantly different from one another (Fig. 4b). *Culex* p × q again showed a less dramatic, but significant, response ($F_{2,15} = 9.95$, $P = 0.0018$). Increasing number of Controls also led to disproportionately more egg rafts/Locality, with all Locality types significantly different (Fig. 4b).

Increasing number of egg rafts/Locality was not simply a result of more Control patches, but a consequence of more egg rafts per Control in Localities with fewer Fish patches, as

© 2015 John Wiley & Sons Ltd/CNRS

shown in Fig. 4c,d. Mean egg rafts/Control patch increased with decreasing number of Fish patches/Locality for both mosquito species. For *C. restuans* the increase with the number of Control patches was more pronounced and significant ($F_{2,28} = 11.52$, $P = 0.0002$), with all three Locality types significantly different from one another (Fig. 4c). *Culex* p × q had a much weaker response than *C. restuans* that was marginal overall ($F_{2,33} = 2.66$, $P = 0.085$), but paired comparisons showed that CCC and CFF Localities were significantly different (Fig. 4d). For both species Fish patches received the same number of eggs whether in CCF or CFF Localities, and Control and Fish patches received equivalent numbers of egg rafts in CFF Localities (Fig. 4c,d).

DISCUSSION

Theoretical and empirical studies of habitat selection have typically focused on species responses to patch specific characteristics and patch specific fitness (e.g. Fretwell & Lucas 1970; Rosenzweig 1991; Abrams *et al.* 2007). Small freshwater ponds form especially discrete habitat patches, but the communities they contain do not exist in isolation either from the surrounding matrix or from other ponds in the surrounding landscape (Knight *et al.* 2005; Resetarits 2005; Binckley & Resetarits 2007; Resetarits & Binckley 2009; Burkle *et al.* 2012). We know that habitat selection in response to patch quality can drive colonisation rates and determine community structure at multiple spatial scales, but does the effect of spatial context on the perception of patch quality also drive variation in colonisation rate among habitat patches at local and regional scales? The answer is important to assessing the role of habitat selection in the distribution and abundance of species, and in the structure and dynamics of communities and metacommunities (Resetarits & Wilbur 1989; Resetarits *et al.* 2005; Resetarits & Binckley 2009; Vonesh *et al.* 2009; Kraus & Vonesh 2010).

Our results clearly establish that ovipositing mosquitoes avoid patches containing *Gambusia*, and are sensitive to the spatial context of patches. Colonisation of high-quality (Control) patches in the vicinity of high-risk (Fish) patches was reduced, confirming scenario d) (Fig. 2d) at the local scale. Risk contagion has been previously demonstrated for ovipositing treefrogs (Resetarits 2005) and chironomids (Wesner *et al.* 2012), as well as colonising aquatic beetles (Resetarits & Binckley 2009). However, we expected *Culex* species to discriminate on a much finer scale and not be strongly affected by spatial context, resulting in either proportional colonisation of Control patches or local compression; individuals approaching a Locality with fish would avoid the Fish patches and select the nearest available Control. Thus, Controls associated with Fish patches would have a greater number of egg rafts than those only associated with other Controls. Instead, we saw strong contagion (Fig. 4 c,d); Controls associated with Fish patches (CCF & CFF) had lower colonisation than those in CCC Controls. For both species, Fish and Control patches in CFF Localities did not differ – effects of contagion on Controls were as strong as if fish were actually present. And while the number of egg rafts in Fish patches did not differ between CCF and CFF Localities for either species, Controls received significantly more *C. restuans* egg rafts in CCF localities than in their CFF counterparts.

It is clear that the different scenarios in Fig. 2 have differing consequences for larval mosquitoes and the communities they inhabit. Avoidance of high-quality patches associated with high risk patches may constitute an adaptive response if proximity translates into a higher risk of fish invasion. Alternatively, it may be maladaptive, resulting in repulsive sources: high fitness patches avoided because of misperception of quality (Resetarits *et al.* 2005). Offspring of females that avoid predator-associated patches may experience reduced predation risk, but also experience higher intra and interspecific larval densities due to compression. Interestingly, as a result of contagion, larval mosquitoes deposited in Control patches in CCF and especially CFF localities may avoid predation AND experience lower densities than their counterparts in the CCC Control patches. Fitness should be higher in such patches. Thus, a conservative approach of avoiding both fish and fish-associated patches seems a highly invasible evolutionary strategy. However, in natural systems movement of fish between neighbouring pools across metre scale distances with rain events is not uncommon, so there is likely a trade-off between overcompensation for predation risk/reduced growth conditions vs. total reproductive failure if fish do invade subsequent to colonisation (Trexler *et al.* 2001; Pearl *et al.* 2005; Petranka & Holbrook 2006, pers. obs.).

At the regional scale, the greater number of egg rafts per Control in CCC localities appears to be a function of regional compression (Fig. 3e); colonists displaced from Fish patches and fish associated (Control) patches in CCF and especially CFF localities preferentially move to pools of the CCC Localities, greatly increasing average egg raft density/pool. Since contagion effects are clearly related to the relative frequency of Fish patches, the intermediate values for the Controls in CCF localities likely reflect a balance between local contagion, clearly observed in the CFF Localities, and regional compression, as observed in CCC localities. A smaller proportion of arriving females chose CCF Control patches because of contagion, but more females arrive at those CCF localities because of the strong avoidance of all patches in CFF localities.

We should point out that we see no evidence of either reward contagion or of compromise (Resetarits *et al.* 2005; Hughey *et al.* 2012) (Box 1). The presence of more Control (fishless) patches does not positively influence oviposition in nearby Fish patches, as expected with reward contagion, nor are the values for fish patches in CFF, where there are fewer good options, higher than in CCF fish patches, as expected for compromise (Fig. 4c,d).

Contagion may result from a simple misperception of which patches are actually producing fish cues, from a generalised avoidance of areas producing fish cues, or from a behavioural algorithm in which females recognise the difference between closely associated fish and fishless patches but avoid the fishless patches specifically because of that spatial association. Certain mosquitoes, including our two *Culex*, discriminate among patches of different quality, including predator and predator-free patches, as well as among different fish species, at much smaller scales than those represented here (Van Dam & Walton 2008; Silberbush & Blaustein 2011; Eveland *et al.* 2015). They

© 2015 John Wiley & Sons Ltd/CNRS

typically oviposit under relatively still conditions, have very sensitive chemosensory apparati, and are mobile enough to thoroughly sample the chemospace above and surrounding closely associated patches (Silberbush & Blaustein 2008, 2011). These two species of *Culex* utilise a broad range of oviposition sites, albeit at the smaller end of the scale, and given that the frequency of habitat patches declines exponentially with increasing size (Semlitsch & Bodie 1998), the ability to discriminate successfully among small patches at small spatial scales should be paramount. The probability of simple discrimination failure should increase with decreasing spatial separation, and depend on wind direction, velocity, direction of approach, cue intensity, etc. It comes down to whether mosquitoes are being fooled by aspects of spatial context, or utilising that spatial context in making adaptive decisions. We simply do not have the data to determine this, but lean towards the latter.

Habitat selection and metacommunities: a fifth paradigm?

Our experiment demonstrates that spatial contagion of predation risk occurs even in species with highly sensitive sensory systems capable of using small habitat patches for oviposition, and presumably adapted to making critical oviposition choices across small spatial scales. The observed contagion within Localities leads to spatial compression at the larger spatial scale of the Array via a shifting of oviposition activity to localities with fewer or no Fish patches. Thus, presence/absence of fish in any Patch in a Locality not only affects oviposition rate in other Patches in the Locality, but potentially affects every Patch in the Array. The frequency and importance of such phantom interactions–where the presence of a species affects patches, subpopulations, and even species with which it does not co-occur (Resetarits *et al.* 2005; Orrock *et al.* 2010)–, reinforce the idea that metacommunities are sets of communities linked by *processes* of dispersal (processes that affect the distribution of individuals among communities) (Box 2; Resetarits & Binckley 2013) and not simply by *dispersal* per se (exchange of individuals among communities) (Leibold *et al.* 2004; Logue *et al.* 2011). This further emphasises the idea that habitat selection behaviour, in this case specifically oviposition site choice, is a fundamental process driving community assembly in aquatic systems (Resetarits *et al.* 2005; Vonesh *et al.* 2009; Kraus & Vonesh 2010; Resetarits & Binckley 2013), and its inclusion should move us closer to a more general predictive framework for metacommunity ecology.

Box 2 Refining the metacommunity narrative

Metacommunities (re)defined – *A set of local communities that are linked by processes of dispersal of multiple interacting species* (modified from Wilson 1992; Leibold *et al.* 2004). Redefining metacommunities in terms of processes that link communities, rather than exchange of individuals, *per se*, is made necessary by the fact that immigration rates of species are not independent among communities. Especially for species that actively choose habitats, an individual that chooses a given community (patch) is not available to colonise another community. Any process that increases the colonisation rate of a given patch of necessity decreases the colonisation rate in other patches, thus linking those communities. Furthermore, species interactions may cross community boundaries and spatial scales via habitat selection. Species that do not co-occur in individual communities interact at the metacommunity scale via so-called 'phantom interactions' (Resetarits *et al.* 2005), or 'remote effects' (Orrock *et al.* 2010). The original metacommunity definition may not have been intended to be quite so restrictive, but operationally metacommunity studies have taken it quite literally (see Logue *et al.* 2011).

A Fifth Metacommunity Paradigm? – An often overlooked feature of the four original metacommunity paradigms is that spatially explicit processes were expressly excluded (Leibold *et al.* 2004) This was not because of presumed lack of importance, but as a simplifying assumption to jump start thinking from a metacommunities perspective. Even 'spatially explicit' was defined only in terms of arrangement or distance between patches, without mention of patch quality, which itself can be defined in terms of a spatially explicit distribution of fitness across patches.

The four paradigms were presented as 'perspectives' – ways of looking at communities in a new way (Leibold *et al.* 2004). Thus, the paradigms are themselves very general and overlap in their predictions, so testing them *per se* is a very difficult proposition (Leibold *et al.* 2004; Chase *et al.* 2005; Logue *et al.* 2011; Winegardner *et al.* 2012). In any given metacommunity we expect different paradigms to apply to different species, taxonomic subunits, or guilds within the metacommunity (Leibold *et al.* 2004; Logue *et al.* 2011). One paradigm does not fit all, nor or the paradigms set in stone (Holt *et al.* 2005). A complementary approach is to identify and incorporate processes occurring in nature that are not incorporated into the existing paradigms or establish new paradigms (perspectives) based on spatially explicit processes (writ large), which then allows us to craft a more realistic and predictive science of metacommunity ecology. Habitat selection is defined in terms of differential immigration, and immigration (dispersal) is the grist of metacommunity dynamics. Thus, a fifth paradigm (perspective?), based on adaptive and interactive variation in immigration rate as a driver of metacommunity dynamics, might look like this:

Habitat matching perspective – *A perspective which assumes that habitat patches (communities) are heterogeneous, immigration rates are a function of patch characteristics that are variable over space and time, and processes of habitat selection may link communities across space (and time) without the requirement of shared species. Essentially this is species-sorting at the immigration stage and can be expected to interact with post-immigration species-sorting and mass effects.*

It remains difficult, however, to fit habitat selection into the existing metacommunity paradigms, either conceptually

© 2015 John Wiley & Sons Ltd/CNRS

or in terms of the predictions (Resetarits *et al.* 2005; Box 2). Habitat selection depends upon spatial (and/or temporal) heterogeneity among patches, thus it can only fall under the species-sorting or mass effects paradigms. However, neither can accommodate the explicit link between immigration rate (as the consequence of dispersal) and existing patch heterogeneity, nor the rapidly changing nature of habitat heterogeneity as a driver of, and driven by, habitat selection. Thus, perhaps a fifth paradigm is necessary to fuel our thinking in a different, but complementary direction (Box 2). Nature is complex and messy. Pattern challenges us and guides our questions, but we ultimately require knowledge of process to understand community and metacommunity dynamics, and to be able to suggest, plan and implement management strategies. Habitat selection is proving a critical process in the assembly of communities across multiple spatial scales. Metacommunity concepts have played a critical role in fundamentally altering the way we think about communities, but examining the paradigmatic framework and the limitations of its infancy is at least as important as testing the existing paradigms in moving the field forward (Holt *et al.* 2005; Logue *et al.* 2011).

Together with data from a variety of aquatic insects and amphibians (Resetarits 2005; Binckley & Resetarits 2007; Resetarits & Binckley 2009; Hughey *et al.* 2012; Wesner *et al.* 2012), our data specifically reinforce the importance of spatial context dependence in habitat selection. We know that for both aquatic and terrestrial systems, characteristics of the surrounding habitat matrix influence colonisation rates and community structure (Knight *et al.* 2005; Binckley & Resetarits 2007; Burkle *et al.* 2012). We can add to that aspect of spatial context dependence the fact that how any specific habitat patch is perceived by colonising/ovipositing organisms depends not simply on the intrinsic characteristics of that particular patch, but on the characteristics, spatial distribution, proximity and frequency of other patch types in the environment. For many dispersing aquatic species, ponds (writ large) are not islands in the biogeographic sense (MacArthur & Wilson 1967), but patches (Levin & Paine 1974; Whittaker & Levin 1977) with varying levels of resources and risk. These ponds are embedded not only in complex terrestrial matrices, but also in metacommunities comprised of equally complex matrices of aquatic patches that vary in resources, risk, and spatially-explicit, context dependent linkages.

ACKNOWLEDGEMENTS

Washington University's Tyson Research Center, particularly K. Smith and B. Schaal, provided logistical support and a stimulating research environment. M. Pintar, J. Bohenek and L. Eveland helped set up the experiment and collect egg rafts. J. Bohenek and L. Eveland helped raise and identify larval mosquitoes. M. Pintar, J. Bohenek, L. Eveland and R. Bruner commented on earlier versions of the manuscript.

AUTHORSHIP

WJR designed the experiment, analysed the data and wrote the manuscript. AS conducted the experiment and contributed to the writing and analysis.

REFERENCES

Abrams, P.A., Cressman, R. & Krivan, V. (2007). The role of behavioral dynamics in determining the patch distributions of interacting species. *Am. Nat.*, 169, 505–518.

Becker, N., Zarate, B., Petric, D., Zgomba, M., Boase, C., Minoo, M. *et al.* (2010). *Mosquitoes and Their Control*. Springer-Verlag, Berlin.

Binckley, C.A. & Resetarits, W.J. Jr (2005). Habitat selection determines abundance, richness and species composition of beetles in aquatic communities. *Biol. Lett.*, 1, 370–374.

Binckley, C.A. & Resetarits, W.J. Jr (2007). Effects of forest canopy on habitat selection in treefrogs and aquatic insects: implications for communities and metacommunities. *Oecologia*, 153, 951–958.

Blaustein, L. (1999). Oviposition site selection in response to risk of predation: evidence from aquatic habitats and consequences for population dynamics and community structure. In: *Evolutionary Theory and Processes: Modern Perspectives* (ed Wasser, S.). Kluwer, Dordrecht, pp. 441–456.

Blaustein, L. & Whitman, D. (2009). Behavioral plasticity to risk of predation: oviposition site selection by a mosquito in response to its predators. In: *Phenotypic Plasticity of Insects: Mechanisms and Consequences* (eds Whitman, D. & Ananthakrishnana, T.N.). Science Publishers Inc., New Hampshire, pp. 263–280.

Burkle, L.A., Mihaljevic, J.R. & Smith, K.G. (2012). Effects of an invasive plant transcend ecosystem boundaries through a dragonfly-mediated trophic pathway. *Oecologia*, 170, 1045–1052.

Chase, J.M., Amaraskare, P., Cottenie, K., Gonzalez, A., Holt, R.D., Holyoak, M. *et al.* (2005). Competing theories for competitive metacommunities. In: *Metacommunities: Spatial Dynamics and Ecological Communities* (eds Holyoak, M., Leibold, M.A. & Holt, R.D.). University of Chicago Press, Chic.

Clements, A.N. (1999). *The Biology of Mosquitoes, Volume 2. Sensory Reception and Behaviour*. CABI Publishing, Wallingford, UK.

Clements, A.N. (2012). *The Biology of Mosquitoes: Volume 3. Transmission of Viruses and Interactions with Bacteria*. CABI Publishing, Wallingford, UK.

Darsie, R.F. & Ward, R.A. (2005). *Identification and Geographical Distribution of the Mosquitoes of North America, North of Mexico*. University of Florida Press, Gainesville.

Duellman, W.E. & Trueb, L. (1986). *Biology of Amphibians*. McGraw-Hill, New York.

Eveland, L.L., Bohenek, J., Silberbush, A. & Resetarits, W.J, Jr. (2015). Detection of fish and newt kairomones by ovipositing mosquitoes. In: *Chemical Signals in Vertebrates 13* (eds Schulte, B.A. & Goodwin, T.). Springer, Cham, Switzerland, pp. 247–260.

Fretwell, S.D. & Lucas, H.L.J. (1970). On territorial behavior and other factors influencing habitat distribution in birds. I. Theoretical development. *Acta. Biotheor.*, 19, 16–36.

Greenberg, J.A., Dimenna, M.A., Hanelt, B. & Hofkin, B.V. (2012). Analysis of post-blood meal flight distances in mosquitoes utilizing zoo animal blood meals. *J. Vector Ecol.*, 37, 83–89.

Holt, R.D., Holyoak, M. & Leibold, M.A. (2005). Future directions in metacommunity ecology. In: *Metacommunities: Spatial Dynamics and Ecological Communities* (eds Holyoak, M., Leibold, M.A. & Holt, R.D.). University of Chicago Press, Chicago.

Hughey, M.C., McCoy, M.W., Vonesh, J.R. & Warkentin, K.M. (2012). Spatial contagion drives colonization and recruitment of frogflies on clutches of red-eyed treefrogs. *Biol. Lett.*, 8, 887–889.

Juliano, S.A. (2009). Species interactions among larval mosquitoes: context dependence across habitat gradients. *Annu. Rev. Entomol.*, 54, 37–56.

Knight, T.M., McCoy, M.W., Chase, J.M., McCoy, K.A. & Holt, R.D. (2005). Trophic cascades across ecosystems. *Nature*, 437, 880–883.

Kraus, J.M. & Vonesh, J.R. (2010). Feedbacks between community assembly and habitat selection shape variation in local colonization. *J. Anim. Ecol.*, 79, 795–802.

Leibold, M.A., Holyoak, M., Mouquet, N., Amarasekare, P., Chase, J.M., Hoopes, M.F. *et al.* (2004). The metacommunity concept: a framework for multi-scale community ecology. *Ecol. Lett.*, 7, 601–613.

© 2015 John Wiley & Sons Ltd/CNRS

Levin, S.A. & Paine, R.T. (1974). Disturbance, patch formation, and community structure. *Proc. Natl. Acad. Sci. U. S. A.*, 71, 2744–2747.

Logue, J.B., Mouquet, N., Peter, H. & Hillebrand, H. (2011). Empirical approaches to metacommunities: a review and comparison with theory. *Trends Ecol. Evol.*, 26, 482–491.

MacArthur, R.H. & Wilson, E.O. (1967). *The Theory of Island Biogeography*. Princeton University Press, Princeton.

Merritt, R.W. & Cummins, K.W. (1984). *An Introduction to the Aquatic Insects of North America*. Kendall/Hunt, Dubuque.

Orrock, J.L., Dill, L.M., Sih, A., Grabowski, J.H., Peacor, S.D., Peckarsky, B.L. *et al.* (2010). Predator effects in predator-free space: the remote effects of predators on prey. *Open Ecol.*, 3, 22–30.

Pearl, C.A., Adams, M.J., Leuthold, N. & Bury, R.B. (2005). Amphibian occurrence and aquatic invaders in a changing landscape: implications for wetland mitigation in the Willamette Valley, Oregon, USA. *Wetlands*, 25, 76–88.

Petranka, J.W. & Holbrook, C.T. (2006). Wetland restoration for amphibians: should local sites be designed to support metapopulations or patchy populations? *Restor. Ecol.*, 14, 404–411.

Resetarits, W.J. Jr (2005). Habitat selection behaviour links local and regional scales in aquatic systems. *Ecol. Lett.*, 8, 480–486.

Resetarits, W.J. Jr & Binckley, C.A. (2009). Spatial contagion of predation risk affects colonization dynamics in experimental aquatic landscapes. *Ecology*, 90, 869–876.

Resetarits, W.J. Jr & Binckley, C.A. (2013). Patch quality and context, but not patch number, drive multi-scale colonization dynamics in experimental aquatic landscapes. *Oecologia*, 173, 933–946.

Resetarits, W.J. Jr & Wilbur, H.M. (1989). Choice of oviposition site by *Hyla chrysoscelis*: role of predators and competitors. *Ecology*, 70, 220–228.

Resetarits, W.J. Jr, Binckley, C.A. & Chalcraft, D.R. (2005). Habitat selection, species interactions, and processes of community assembly in complex landscapes: a metacommunity perspective. In: *Metacommunities: Spatial Dynamics and Ecological Communities* (eds Holyoak, M., Leibold, M.A. & Holt, R.D.). University of Chicago Press, Chicago, pp. 374–398.

Rosenzweig, M.L. (1981). A theory of habitat selection. *Ecology*, 62, 327.

Rosenzweig, M.L. (1991). Habitat selection and population interactions: the search for mechanism. *Am. Nat.*, 137, S5.

Schneider, D.W. & Frost, T.M. (1996). Habitat duration and community structure in temporary ponds. *J. North Am. Benthol. Soc.*, 15, 64–86.

Semlitsch, R.D. & Bodie, J.R. (1998). Are small, isolated wetlands expendable? *Conserv. Biol.*, 12, 1129–1133.

Silberbush, A. & Blaustein, L. (2008). Oviposition habitat selection by a mosquito in response to a predator: are predator-released kairomones air-borne cues? *J. Vector Ecol.*, 33, 208–211.

Silberbush, A. & Blaustein, L. (2011). Mosquito females quantify risk of predation to their progeny when selecting an oviposition site. *Funct. Ecol.*, 25, 1091–1095.

Spencer, M., Blaustein, L. & Cohen, J.E. (2002). Oviposition habitat selection by mosquitoes (*Culiseta longiareolata*) and consequences for population size. *Ecology*, 83, 669–679.

Trexler, J.C., Loftus, W.F., Jordan, C.F., Chick, J., Kandl, K.L., McElroy, T.C. *et al.* (2001). Ecological scale and its implications for freshwater fishes in the Florida Everglades. In: *The Everglades, Florida Bay, and Coral Reefs of the Florida Keys: An Ecosystem Sourcebook* (eds Porter, J.W. & Porter, K.G.). CRC Press, Boca, Raton, pp. 153–181.

Van Dam, A.R. & Walton, W.E. (2008). The effect of predatory fish exudates on the ovipostional behaviour of three mosquito species: *Culex quinquefasciatus*, *Aedes aegypti* and *Culex tarsalis*. *Med. Vet. Entomol.*, 22, 399–404.

Vonesh, J.R. & Blaustein, L. (2010). Predator-induced shifts in mosquito oviposition site selection: a meta-analysis and implications for vector control. *Isr. J. Ecol. Evol.*, 56, 123–139.

Vonesh, J.R., Kraus, J.M., Rosenberg, J.S. & Chase, J.M. (2009). Predator effects on aquatic community assembly: disentangling the roles of habitat selection and post-colonization processes. *Oikos*, 118, 1219–1229.

Wellborn, G.A., Skelly, D.K. & Werner, E.E. (1996). Mechanisms creating community structure across a freshwater habitat gradient. *Annu. Rev. Ecol. Syst.*, 27, 337–363.

Wesner, J.S., Billman, E.J. & Belk, M.C. (2012). Multiple predators indirectly alter community assembly across ecological boundaries. *Ecology*, 93, 1674–1682.

Whittaker, R.H. & Levin, S.A. (1977). The role of mosaic phenomena in natural communities. *Theor. Popul. Biol.*, 12, 117–139.

Wilbur, H.M. (1997). Experimental ecology of food webs: complex systems in temporary ponds. *Ecology*, 78, 2279–2302.

Wilson, D.S. (1992). Complex interactions in metacommunities, with implications for biodiversity and higher levels of selection. *Ecology*, 73, 1984–2000.

Winegardner, A.K., Jones, B.K., Ng, I.S.Y., Siqueira, T. & Cottenie, K. (2012). The terminology of metacommunity ecology. *Trends Ecol. Evol.*, 27, 253–254.

Editor, Tim Wootton
Manuscript received 1 September 2015
First decision made 9 October 2015
Manuscript accepted 3 November 2015

© 2015 John Wiley & Sons Ltd/CNRS