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Prey colonization in freshwater landscapes can be stimulated or inhibited by the proximity of remote predators

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Abstract

1. Recent findings suggest that the colonization of habitat patches may be affected by the quality of surrounding patches. For instance, patches that lack predators may be avoided when located near others with predators, a pattern known as risk contagion. Alternatively, predator avoidance might also redirect dispersal towards nearby predator-free patches resulting in so-called habitat compression. However, it is largely unknown how predators continue to influence these habitat selection behaviours at increasing distances from outside of their own habitat patch. In addition, current information is derived from artificial mesocosm experiments, while support from natural ecosystems is lacking.
2. This study used bromeliad landscapes as a natural model system to study how oviposition habitat selection of Diptera responds to the cues of a distant predator, the carnivorous elephant mosquito larva.
3. We established landscapes containing predator-free bromeliad habitat patches placed at increasing distances from a predator-containing patch, along with replicate control landscapes. These patches were then left to be colonized by ovipositing bromeliad insects.
4. We found that distance to predators modulates habitat selection decisions. Moreover, different dipteran families had different responses suggesting different habitat selection strategies. In some families, predator-free patches at certain distances from the predator patch were avoided, confirming risk contagion. In other families, these patches received higher numbers of colonists providing evidence of predator-induced habitat compression.
5. We confirm that effects of predators in a natural ecosystem can extend beyond the patch in which the predator is present and that the presence or absence of remote predator effects on habitat selection depends on the distance to predators. The notion that perceived habitat quality can depend on conditions in neighbouring patches forces habitat selection studies to adopt a landscape perspective and account for the effects of both present and remote predators when explaining community assembly in metacommunities.

KEYWORDS

bromeliads, context dependence, habitat compression, habitat selection, oviposition site selection, predation risk, risk contagion

1 | INTRODUCTION

Habitat selection is a well-documented phenomenon in actively dispersing organisms whereby environments deemed to maximize their fitness are preferentially colonized (Fretwell & Lucas, 1970; Morris, 2003). Until recently, habitat selection studies considered that selection decisions were based on properties of the target habitat patch alone. However, new studies suggest that the landscape context including conditions in neighbouring patches can also be important. Context dependency may arise when perception of target patch quality varies depending on the quality of nearby patches, a process known as spatial contagion, or from habitat compression, when patch colonization rates are elevated due to avoidance of nearby habitat patches (Resetarits, Binckley, & Chalcraft, 2005). For example, predation risk is probably the most important factor influencing colonization decisions of prey (Blaustein, 1999). Earlier studies have shown that prey species avoid patches with predator cues (i.e. local habitat selection; e.g. Binckley & Resetarits, 2005; Blaustein, Kiflawi, Eitam, Mangel, & Cohen, 2004; Vonesh & Blaustein, 2010). However, new studies show that patches in close proximity to patches with predators can also be perceived negatively and consequently receive fewer colonists (Resetarits, 2005; Resetarits & Binckley, 2009; Resetarits & Silberbush, 2016; Wesner, Billman, & Belk, 2012). This negative effect of context on colonization is referred to as risk contagion (Resetarits et al., 2005). Risk contagion may arise from an inability to discriminate between neighbouring habitats, to identify which one the predator cues are coming from (Resetarits & Silberbush, 2016; Wesner et al., 2012). On the other hand, prey may simply avoid general areas in which predators are detected without attempting to discriminate between nearby habitats (Resetarits & Binckley, 2009; Wesner, Meyers, Billman, & Belk, 2015). The presence of risk contagion is then likely to decay with increasing distance from a predator-containing habitat (Resetarits, 2018). Meanwhile, habitat compression in response to predators would be expected to occur at further distances as individuals avoiding the predator habitat and/or those habitats closer to the predator redirect and concentrate in more distant patches. As such, although at one particular distance from a predator it is expected that prey behave either by contagion or compression, both types of context-dependent habitat selection may be observed across a landscape. Previous studies of these remote predator effects on habitat selection have placed patches at a single distance from one another. However, given that the presence as well as the specific type of context-dependent habitat selection (e.g. contagion or compression) likely changes with increasing distances between patches (Resetarits, 2018), it remains largely unknown how predators continue to influence habitat selection behaviour outside their own habitat patch.

In addition, context-dependent habitat selection has only been tested under simplified artificial conditions in mesocosms with a limited set of colonizing species and often focusing on single taxa (Trekels & Vanschoenwinkel, 2018). It is unknown to what extent different taxonomic groups of organisms employ different habitat selection strategies in response to the same predator. Different taxa may differ in their vulnerability to predation. This could drive differences in a predator avoidance response, affecting their ability to detect but also differentiate predation risk between habitats. Additionally, depending on how susceptible they are to predation or on their capacity to reach distant patches, colonists may divert to neighbouring patches (habitat compression) or patches beyond the experimental landscapes.

In this context, simple natural model systems that combine realism with experimental control can play an important role in confirming that a process is also relevant in real ecosystems (Srivastava et al., 2004). Water bodies in bromeliad plants (Bromeliaceae) are an example of a simple aquatic model ecosystem used in many ecological studies (Kitching, 2000). These water bodies, known as phytotelmata, support discrete aquatic ecosystems (Armbruster, Hutchinson, & Cotgreave, 2002; Kitching, 2000). Most bromeliad inhabitants (i.e. the infauna) are aquatic insects with flying adults that complete their larval life stages in the tank. As a result, oviposition habitat selection is an important process that determines establishment and maintenance of bromeliad infaunal communities (LeCraw, Srivastava, & Romero, 2014). The combination of their small size, the discrete nature of the habitat and the relatively complex aquatic communities inside including many different families of insects, makes bromeliads suitable model systems to study habitat selection under natural and manipulated conditions.

This study investigated oviposition habitat selection of aquatic insects in bromeliad microcosms in the presence of an aquatic predator to test for context-dependent habitat selection in a natural model system. For this, we set up replicated landscapes of bromeliad habitat patches with patches placed at increasing distances from a central patch. Landscapes differed in the presence or absence of predator cues released from a caged predator in the central patch. We hypothesized that (H1) habitat patches with predator cues would be avoided by colonists confirming local habitat selection. Second, (H2) we expected that colonization of predator-free patches in landscapes that contain a central patch with a predator would be different than in patches in landscapes where all patches were predator-free. This would confirm context-dependent habitat selection due to the effect of a remote predator. If colonization in a patch located in the vicinity of a predator patch would be higher than in patches in entirely predator-free landscapes, this is evidence for habitat compression.

If colonization would be lower, it reflects risk contagion. Third, (H3) we anticipated that the presence or absence of a remote predator effect as well as the specific type (risk contagion or habitat compression), would be scale-dependent. For example, we would expect contagion to occur in patches closer to the predator and compression to occur farther away. It is assumed, however, that the responses are mutually exclusive at each distance. As such, if a remote predator effect is detected, at each specific distance the response would be either contagion or compression for a given taxonomic group. Finally, (H4) we expected that different taxa might show different oviposition patterns in response to remote predator cues.

2 | MATERIALS AND METHODS

2.1 | Model system

Field work was conducted in July 2016 in Nicaragua in the vicinity of the Waslala municipality, located in the North Caribbean Coast Autonomous Region. The experiment was performed in a cacao plantation (13°17′15″N, 85°23′35″W; 440 m a.s.l.). The regular distribution of cacao trees provided relatively uniform understory conditions. Although common in the study region, there were no naturally occurring bromeliads in the plantation that could have otherwise interfered with the experimental set-up.

Extensive sampling of bromeliads in the study region found high prevalence of a common predator of bromeliad insects, aquatic larvae of the elephant mosquito *Toxorhynchites* spp. (Diptera, Culicidae). It was selected as the model predator for this experiment due to their observed behaviour as voracious generalist predators (Campos & Lounibos, 2000). Furthermore, prey behavioural responses to chemical cues produced by *Toxorhynchites* have been documented (Andrade, Albeny-Simões, Breaux, Juliano, & Lima, 2017; Kesavaraju, Damal, & Juliano, 2007; Zuharah, Fadzly, Yusof, Dieng, & Ni, 2015), indicating the existence of molecular mechanisms needed for its detection and subsequent avoidance.

The experiment consisted of eight landscapes, each containing four bromeliad habitat patches: one central bromeliad and three outer bromeliads arranged around it at 120° angles from one another (Figure S1). These outer bromeliads were positioned at three distances from the central plant: one with its base 5 cm from the base of the central plant, but with overlapping leaves (hereafter the 0 cm position), the second with its leaf tips 5 cm from the leaf tips of the central plant (5 cm position) and the third with 100 cm between leaf tips (100 cm position). In five landscapes, the central bromeliad contained a caged predator and the outer bromeliads had no predator. These landscapes are referred to as predator-associated landscapes. The remaining three landscapes were predator-free controls. Landscapes were positioned at ground level on the edge of a 15 m radius circular plot with a distance of 11.5 m between central plants of each landscape. The circular arrangement controlled for the effect that wind direction may have on the distribution of predator cues. Given the dimensions of the field site, it also allowed to maximize the distance between each landscape to ensure they were independent of one another.

Experimental bromeliads were collected from the study region. Experimental plants were washed thoroughly and then hung inverted to dry for 7 days to eliminate all invertebrates and predator cues. Bromeliads were then positioned in experimental landscapes and filled with mineral water. Care was taken to make sure that bromeliads within the same landscape were similar in volume (maximum holding capacity, ml). Hence landscapes contained either consistently small, medium, or large bromeliads. Volume is known to be an important factor influencing bromeliad insect communities (e.g. Armbruster et al., 2002; Petermann et al., 2015) and thus might also affect oviposition decisions. Therefore, grouping by volume minimized ‘within-landscape’ variation in colonization. Leaf litter collected below cacao trees (200 mg dry weight per 100 ml volume), cleaned with 70% ethanol and left to dry for several hours prior to use, were added to each bromeliad to act as a food source.

Third and fourth instar *Toxorhynchites* larvae were collected from bromeliads within the Waslala area. In central plants receiving a predator treatment, one larva was added to a 50 ml transparent centrifuge tube, acting as a cage to prevent consumptive effects, based on a procedure from Hammill, Atwood, and Srivastava (2015). Four 1-cm diameter circular holes near the base of each tube covered with 80 μm mesh, facilitated predator cue diffusion into the water. The tops of the tubes were covered with mesh to prevent colonization into the tubes themselves and to facilitate atmospheric gas exchange. The tubes were placed in the central tank of the bromeliads such that cues could filter down throughout all lower leaf axils. One caged larva was added to each bromeliad to be consistent with densities of *Toxorhynchites* in bromeliads in the study area (personal observation). Identical empty tubes were added to central plants of the control landscapes.

The experiment was set up on July 11, 2016. Throughout the experiment, predators were fed one culicid mosquito larva every 24–36 hr. On day 5 and 6, two *Toxorhynchites* larvae pupated and were replaced. Bromeliads were left for 9 days to obtain sufficient abundances for analysis yet to restrict nonconsumptive predatory effects to oviposition differences only. In addition, it was not possible to prevent new *Toxorhynchites* from independently colonizing the bromeliads. By restricting the duration of the experiment, it ensured that any *Toxorhynchites* eggs that were oviposited would only be newly hatched and would not be able to affect colonization decisions. Subsequently, tubes attached to 50 ml syringes were used to collect the water from each plant. Plants were then placed in separate plastic bags and transported to a working station where they were washed thoroughly with a pressure hose. Wash water was collected and poured over a 40-μm mesh filter together with the water previously collected with syringes. The residue was preserved on 70% ethanol.

In the laboratory, samples were searched completely for all invertebrates using a stereoscope after adding Rose Bengal (Sigma-Aldrich: Aldrich-330000) to stain animal tissue. All immature Diptera were identified to the lowest taxonomic level possible (family, subfamily, genus) following Merritt, Cummins, and Berg (2008) and Brown et al. (2009). Amongst those groups that actively colonize bromeliads, they were by far the most abundant group; others were found rarely, in abundances too low to analyse.

2.2 | Data analysis

All statistical analyses were performed in R (Version 3.1.3). For all tests, the number of oviposited individuals in a bromeliad habitat patch (hereafter referred to as colonists) was the response unit used. To test our hypotheses, we constructed a generalized linear model (glm function, STATS package) to compare the number of colonists in patches in landscapes with a predator in the central patch to control patches in entirely predator-free landscapes. Bromeliads from the same landscape were not independent from one another and needed to be corrected for by introducing a blocking factor into the models. Given the fact that we made sure bromeliads in the same landscape had similar volume, we used bromeliad volume as the blocking factor to absorb differences among landscapes (i.e. blocks) in the analysis. As such the blocking factor in our model was not a random but a fixed factor and was treated as a continuous rather than a discrete variable. We used a Poisson error distribution and specified a log link function. Tests for overdispersion indicated that colonization responses were best captured by specifying a Poisson distribution. We used the summary function in R to get a model output that shows the coefficients—and associated *t* test statistic and *p* value—of each term in our model (R code provided in Supporting Information). We included a predator term in the model to determine the difference in colonization between central patches with caged predators and control patches in predator-free landscapes. If this term was significant this confirmed our hypothesis of local habitat selection (H1). We also included three distance terms (categorical; either 0, 5 or 100 cm) to determine whether predator-free patches at each discrete increasing distance from the central caged-predator patch had more or less colonization than similar patches in control landscapes (H2). The regression coefficient and associated *p* value for each distance term in the models determined if there was significantly more or less colonization compared to controls. This allowed us to test for risk contagion (i.e. less colonists due to a remote predator) or habitat compression (i.e. more colonists due to a remote predator) at increasing spatial distance (H3). The exponential of the regression coefficients of each distance term was used as a measure of effect size because it directly reflects by how much colonization has increased or decreased compared to the controls. Predicted colonization rates in control patches and in patches at each distance in predator-associated landscapes were also determined from the models.

For each model, pseudo r^2 values were calculated (PseudoR2 function, DESCTOOLS package) based on the traditional Mc Fadden and the Veall–Zimmermann approximations. It has been shown that the former underestimates r^2 and therefore the latter is likely more reliable (Veall & Zimmermann, 1994).

To test for differential colonization responses between taxonomic groups (H4), separate models were constructed for the four most commonly encountered dipteran families (Culicidae, Chironomidae, Psychodidae and Cecidomyiidae). Other dipteran families colonized in abundances that were too low to analyse as separate responses. Differences in the significance of model terms suggested response variation between families. Differences between families were also assessed visually by plotting the regression coefficients (± confidence interval) for each family at each distance class. If the coefficients and their confidence intervals for the different families did not overlap, this is evident that the insect families differed in their habitat selection behaviour.

3 | RESULTS

Colonization through oviposition occurred in all experimental bromeliads, with a total of 2,193 dipteran larvae belonging to 43 taxa (Table S1). Central bromeliad habitat patches with a caged predator were found to have significantly less culicid colonists than habitat patches in predator-free control landscapes, confirming our first hypothesis of local habitat selection for this family (Table 1; H1). A nonsignificant trend was also detected in Cecidomyiidae. No effect was found in Chironomidae or Psychodidae. Besides local habitat selection, a caged predator in the central bromeliad had significant effects on colonization in more distant predator-free bromeliads in the same landscape (Table 1), confirming our second hypothesis of context-dependent habitat selection (H2). Consistent with our third and fourth hypotheses, colonization response varied depending on the distance to the central patch with the caged predator and on the considered taxonomic group (Table 1; H2 and H3 respectively). These differences in observed colonization patterns are illustrated in Figure 1 and Figure S2.

To show the specific remote effect of a caged predator on more distant predator-free patches in a bromeliad landscape we compared patches at each distance in these predator-associated landscapes with patches in control landscapes without a central caged predator (Table 1). Predicted colonization rates for patches at each distance (centre, 0, 5 and 100 cm) and in control patches from control landscapes are shown in Figure 1e. Using this procedure, we could demonstrate that Culicidae showed reduced colonization at all distances from the predator compared to patches in control landscapes, indicative of risk contagion. Similarly, Psychodidae had lower colonization in patches closest to the predator patch (0 cm), and a marginally nonsignificant decrease in colonizers at 5 cm, also suggesting risk contagion. However, increased colonization compared to controls, which is indicative of habitat compression, was not detected in either family at any distance. On the other hand, Cecidomyiidae showed no evidence of risk contagion but did have elevated colonization at 5 cm, indicating compression. Chironomidae were found to have increased colonization at 0 and 5 cm, and a marginally nonsignificant increase at 100 cm. The resultant habitat selection patterns for each taxonomic group are shown in Figure 2.

TABLE 1 Results of generalized linear models (Poisson residuals, log link) showing the effect of a caged predator in a central bromeliad habitat patch on colonization of patches at increasing distances from these predator cues. Effects are shown for different families of Diptera (a. Cecidomyiidae; b. Chironomidae; c. Culicidae; d. Psychodidae). The coefficient estimate of each model term reflects the differences in colonization of patches in these predator-containing bromeliad landscapes compared to patches from control landscapes that lack a central patch with a predator. The predator term shows the effects of the caged predator on colonization in its own central patch. Each distance term (0, 5 and 100 cm) reflects effects of predator cues on colonization in patches at each respective distance from the remote predator. Finally, bromeliad volume (maximum holding capacity, ml) was included as a fixed blocking term to correct for the main differences between landscapes. It is not a random factor and hence this is not a mixed model.
Bold values indicate a significant treatment effect at $\alpha = 0.05$. Pseudo r^2 values are provided based on the Mc Fadden (MF) and Veall Zimmermann (VZ) approximations

Term	Coefficient est.	z	p
(a) Cecidomyiidae			
Int.	1.36 ± 0.14	9.44	<0.001
Predator	−0.56 ± 0.32	−1.72	0.080
0 cm	−0.16 ± 0.28	−0.56	0.570
5 cm	0.72 ± 0.21	3.42	**<0.001**
100 cm	0.31 ± 0.23	1.30	0.190
Volume	0.003 ± 0.001	4.21	**<0.001**
MF pseudo r^2	0.17		
MZ pseudo r^2	0.64		
(b) Chironomidae			
Int.	2.98 ± 0.06	45.90	<0.001
Predator	0.02 ± 0.12	0.14	0.880
0 cm	0.53 ± 0.10	5.29	**<0.001**
5 cm	0.87 ± 0.09	9.48	**<0.001**
100 cm	0.21 ± 0.11	1.85	0.060
Volume	0.0010 ± 0.0003	3.71	**<0.001**
MF pseudo r^2	0.15		
MZ pseudo r^2	0.82		
(c) Culicidae			
Int.	3.36 ± 0.05	62.90	<0.001
Predator	−0.31 ± 0.10	−2.84	**0.005**
0 cm	−0.78 ± 0.13	−5.85	**<0.001**
5 cm	−0.27 ± 0.11	−2.47	**0.010**
100 cm	−0.29 ± 0.11	−2.68	**0.007**
Volume	0.0020 ± 0.0004	5.90	**<0.001**
MF pseudo r^2	0.14		
MZ pseudo r^2	0.75		
(d) Psychodidae			
Int.	1.29 ± 0.15	8.90	<0.001
Predator	0.34 ± 0.23	1.49	0.140
0 cm	−2.34 ± 0.72	−3.25	**0.001**
5 cm	−0.54 ± 0.30	−1.78	0.070
100 cm	0.36 ± 0.22	1.63	0.100
Volume	0.006 ± 0.001	6.99	**<0.001**
MF pseudo r^2	0.31		
MZ pseudo r^2	0.83		

4 | DISCUSSION

In this study, we used bromeliads as a natural model ecosystem to investigate effects of predator cues on oviposition habitat selection of potential prey species. We studied bromeliad habitat patches containing a caged predator, but also neighbouring predator-free patches at increasing distances from this source of the predator cues. We found that bromeliads with a caged predator had lower abundances of some dipteran larval families compared to control predator-free bromeliads. This confirmed our first hypothesis of local habitat selection. In turn, predator cues did not just change colonization rates in these patches but also in the surrounding bromeliads located at increasing distances from predator patches, confirming our second hypothesis of context-dependent habitat selection. The presence or absence of this effect varied with distance from the predator patch, confirming the third hypothesis that effects of remote predators are scale dependent. In line with our fourth hypothesis, habitat selection responses varied depending on the taxa that were considered. While in some families, colonizers compressed into predator-free patches surrounding the predator patch, other families continued to avoid these patches as well (Figure 2).

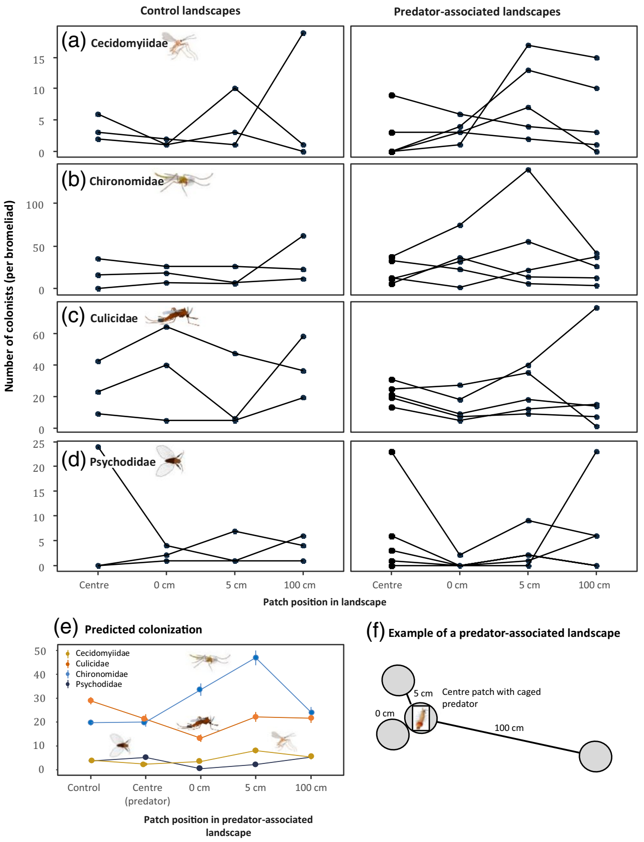

FIGURE 1 Effect of a caged predatory *Toxorhynchites* larva on habitat selection of ovipositing Diptera in replicated landscapes of bromeliad habitat patches. An example of these predator-associated landscapes is shown in panel (f). Control landscapes (not shown) were identical except that they did not have a caged-predator in the central patch. Graphs on the left in panels (a–d) depict colonization in control landscapes ($n = 3$) and on the right, predator-associated landscapes ($n = 5$). Each path connects patches found in the same experimental landscape at increasing distances (0, 5 and 100 cm) from the central patch. Each row shows responses for the dipteran families (a) Cecidomyiidae, (b) Chironomidae, (c) Culicidae and (d) Psychodidae. Variation between replicates at each distance is in part due to variation in bromeliad volume which is also a determinant of colonization decisions. Resultant predicted colonization ($M \pm SE$) for patches at each distance in predator-associated landscapes (centre, 0, 5 and 100 cm) and in control patches from control landscapes are shown in (e), as determined from generalized linear models used to compare colonization between patches in predator-associated versus control landscapes. Differences in predicted colonization between controls and patches at each distance in predator-associated landscapes suggest predator effects on local habitat selection in their own habitat patch (centre) and remote predator effects through context-dependent habitat selection in surrounding predator-associated patches (0, 5 and 100 cm)

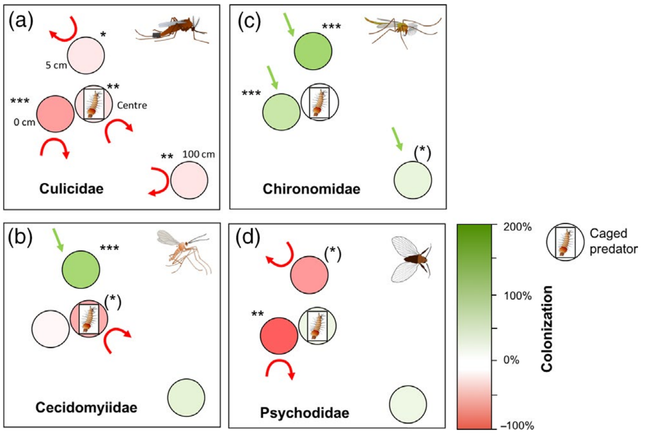

FIGURE 2 Colonization behaviour of ovipositing dipteran insects in landscapes of bromeliads containing a caged predatory *Toxorhynchites* larva in the central bromeliad, including local habitat selection in the predator-containing bromeliad and context-dependent habitat selection in surrounding predator-free bromeliads (positions 0, 5 and 100 cm). Types of context-dependent habitat selection include avoidance of predator-free habitats due to proximity to a predator-containing habitat (risk contagion) and increased colonization of predator-free habitats due to redirection from avoided habitats (habitat compression). Observed behaviour is displayed for the most commonly encountered dipteran families. Each circle represents an individual bromeliad. Red circles indicate colonization which was lower than in controls, green indicates colonization that was higher. The colour gradient represents the effect size of this response, given as a percent difference compared to controls. Therefore, red arrows extending away from a bromeliad represent habitat avoidance and green arrows indicate that colonization was redirected towards that targeted bromeliad. *, **, *** indicate where this behavioural response was found to be significant from generalized linear models at $p < 0.05$, $p < 0.01$ and $p < 0.001$ respectively. (*) indicates a marginally nonsignificant trend ($p < 0.09$). Based on these colonization responses, these panels illustrate the following for (a) Culicidae: local habitat selection avoiding predator bromeliads and risk contagion at 0, 5 and 100 cm (b) Cecidomyiidae: local habitat selection avoiding predator bromeliads and habitat compression at the 5 cm position; (c) Chironomidae: higher oviposition in the 0, 5 and 100 cm positions; (d) Pyschodidae: risk contagion at the 0 and 5 cm position

We found evidence for risk contagion (i.e. habitat avoidance due to spatial association to a poor-quality habitat) in Psychodidae and Culicidae. In addition to previously documented contagion effects in plastic tanks (Resetarits, 2005; Resetarits & Binckley, 2009; Resetarits & Silberbush, 2016; Wesner et al., 2012), our findings show that such effects can also occur under more natural conditions. In Culicidae, this effect was observed at all distances from the predator. This suggests that for this group, contagion may result from general avoidance of areas where a predator is detected, without attempting to discriminate individual habitats (Resetarits & Binckley, 2009; Wesner et al., 2015). In Psychodidae on the other hand, contagion was only detected in the bromeliad closest to the predator, along with a marginally nonsignificant reduction in colonization in the bromeliad slightly farther away, but was absent in the farthest bromeliad. Contagion in this group therefore may reflect an inability to discriminate the origin of predator cues at such small spatial scales (Resetarits & Silberbush, 2016; Wesner et al., 2015). These cues are likely to be volatile chemicals, as has been confirmed for predator cues released by the hemipteran predator *Notonecta* (Silberbush et al., 2010), as we are confident there was no physical exchange of water with predator cues between bromeliads in our experiment.

Besides risk contagion, our results provide evidence of habitat compression (i.e. increased colonization due to redirection from avoided poor quality patches) resulting from predator avoidance within a set of habitat patches. This was observed in Cecidomyiidae. This group did not demonstrate contagion but rather responded to predators locally by redirecting colonization towards other patches within a bromeliad landscape. This effect was observed not in the predator-free bromeliad closest to the predator but in one located slightly farther away at a distance of 5 cm.

We expected a pattern of risk contagion at distances closest to the predator followed by compression farther away. Contrary to this, however, Cecidomyiidae only demonstrated compression. Likewise, in Culicidae and Psychodidae, predator-avoiding individuals did not compress at farther distances from the predator. These diverging and family-specific responses may have different explanations. Culicidae and Psychodidae may be more preferred types of prey. Therefore in turn, they may have a stronger avoidance response (Kraus & Vonesh, 2010; Vonesh & Blaustein, 2010) than Cecidomyiidae and redirected individuals may choose to colonize and compress in habitat patches beyond the experimental landscapes. Additionally, the pronounced response of culicids avoiding all bromeliads in predator landscapes may be due to the fact that predators were fed with culicid larvae. Previous research has shown that cues of consumed conspecifics, rather than heterospecifics, can increase the prey avoidance behaviour compared to predator cues alone (Gall & Brodie Jr., 2009; Schoeppner & Relyea, 2005, 2009; but see Marino, Srivastava, & Farjalla, 2016). Finally, the pattern can also be due to taxon-specific dispersal ranges. After detecting predator cues, better flyers could cover larger distances before colonizing safer patches.

Unlike other taxonomic groups, Chironomidae behaviour diverged from our expectations. We found no indications that they avoided central patches when a caged predator was present and instead oviposited more in bromeliads near a central predator patch. Such behaviour suggests indifference to predator cues and possibly even some attraction to landscapes with predators. This is consistent with Kraus and Vonesh (2010) who reported chironomid attraction to the fish predator *Enneacanthus gloriosus* while other studies have also found no response at all (Blaustein et al., 2004 for the hemipteran predator, *Notonecta maculata*; Wesner et al., 2012 for dragonfly *Ophiogomphus severus* and fish *Salmo trutta* predators). It has been suggested that more benthic chironomids that burry in the sediment and often form protective cases, are less sensitive to pelagic predators and therefore their oviposition behaviour may not strongly respond to predator cues (Wesner et al., 2012). Hence, potentially some chironomids may benefit from lower competition in patches with predator cues that are avoided by more predation-sensitive dipterans.

The presence of risk contagion in culicids and psychodids could suggest a maladaptive response to predators whereby suitable habitats are unnecessarily avoided (Resetarits et al., 2005). On the other hand, it may be an adaptive behaviour if for example, predator presence in one bromeliad increases the likelihood that a neighbouring bromeliad will be colonized by another predator. Future studies on colonization patterns of *Toxorhynchites* and other bromeliad-dwelling predators would be useful to test these two possibilities. If the latter is the case, the benefits from a decreased likelihood that a predator will colonize may outweigh the costs of increased competition from compression in the more distant safe habitats (Trekels & Vanschoenwinkel, 2018).

Overall, it appears that the presence of a single predator in a landscape of bromeliad habitat patches leads to changes in colonization behaviour in surrounding predator-free patches. This is the first study to evaluate such context-dependent habitat selection behaviour across multiple different taxonomic groups. From our results it is clear that the specific response to the predator and the spatial scale at which it occurs varies between dipteran families. How these different families differ in their ability to detect aquatic habitats and predators is unknown and despite the fact that we found consistent differences between families, intra-family differences in colonization behaviour are also likely. For instance, for Culicidae in our system, 90% of individuals belonged to the genus *Wyeomyia*. It is clear that the detected responses for this family were mainly driven by this genus.

Despite the important role dispersal plays in maintaining animal populations that live in the dynamic environment of bromeliad phytotelmata (LeCraw et al., 2014; Srivastava, Trzcinski, Richardson, & Gilbert, 2008), this is one of the first studies to show the importance of habitat selection during this process (see also Breviglieri, Oliveira, & Romero, 2017). The focus on predators is particularly relevant as they are emerging as one of the most important structuring determinants of these communities (Breviglieri et al., 2017; Dézerald et al., 2014; Hammill, Atwood, Corvalan, & Srivastava, 2015). Hammill, Atwood, and Srivastava (2015) have demonstrated that nonconsumptive effects are an important component of the total impact of damselfly predators on bromeliad aquatic communities. This present study suggests that the same is true for the elephant mosquito *Toxorhynchites* and that oviposition avoidance in response to this predator can explain species distribution patterns. In addition, our results show that the influence of predators is not restricted to bromeliads in which they are found but extends to surrounding communities. Such remote effects (Orrock et al., 2008) or 'phantom interactions' (Resetarits et al., 2005) of predators may be particularly relevant for bromeliad infaunal communities as they are often found aggregated in landscapes rather than in isolation (Cascante-Marín et al., 2006). Therefore, to explain community composition in small aquatic habitats such as bromeliads, it would be necessary to include information about predator presence in surrounding patches located at different distances.

The effect of habitat context on perceived habitat quality during habitat selection complicates current attempts in the field of metacommunity ecology to explain and predict spatiotemporal variation in the composition of ecological communities (Leibold & Chase, 2017). The present results strongly support the notion that new frameworks are needed to assess effects of habitat selection on species distribution patterns in nature (Resetarits & Silberbush, 2016). While including habitat quality and spatial location in species distribution models is challenging enough, the fact that spatial context determines how local patch quality is perceived, represents a level of complexity that is yet to be included in predictive models. We conclude that landscape context including the distance to predators can alter colonization rates in landscapes with discrete habitat patches. While we only observed one type of context-dependent habitat selection within the scale of this study for each Dipteran family, a general trend of local predator avoidance with or without risk contagion followed by habitat compression at increasing distances is likely as shown for the mosquito *Culex pipiens* in response to fish predation (Trekels & Vanschoenwinkel, 2018). However in the field, the situation is more complex. Not all taxa responded to habitat context in the same way, complicating generalization. Additionally, in real landscapes, habitat quality is not a unidimensional property and different cues, both positive and negative, are presented simultaneously and together affect the habitat selection behaviour of dispersing animals. Understanding exactly which cues are more important than others and how this information is integrated during the decision-making process remains an open question.

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AUTHORS' CONTRIBUTIONS

All authors conceived the experiment ideas and designed the methodology; B.T. and M.V. collected the data; B.T. and B.V. analysed the data; B.T. and B.V. lead the writing of the manuscript with substantial input from H.T. All authors contributed critically to the drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

Raw data are accessible from the Dryad Digital Repository https://doi.org/10.5061/dryad.zw3r2285k (Turner, Trekels, Vandromme, & Vanschoenwinkel, 2020).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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