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The impact of land-use change on larval insect communities: Testing the role of habitat elements in conservation[1]

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Abstract: Conservationists have proposed that maintaining key elements of the original land-cover type in modified landscapes may mitigate the detrimental effects of land-cover change on residual species. We tested this hypothesis for aquatic insect communities in tank-forming bromeliads in forested and non-forested habitats in Costa Rica. Bromeliad tanks hold much of the standing water in this region and therefore provide an important resource for insects with aquatic larval stages. We quantified the relative importance of land-use type and the bromeliad-specific "local" environment on the insect community, and also the effect of land-use type on this local environment. Insect species responded to both land-use type and the local environment, with these variables explaining a total of 36% of species densities. The local environment independently explained 19% of insect densities, while land-use type explained 17%, mainly through its modification of the local environment. Local environmental conditions were strongly correlated to land-use type ($r^2 = 0.64$), with non-forest habitat having a higher average temperature, a greater variation in temperature, and a lower density of bromeliads. Our results indicate that the land-use type in which bromeliads occur influences the relative densities of insects by altering the local environment of bromeliads. Therefore, maintaining bromeliads under land-use conversion will not necessarily maintain the bromeliad insect community of the original forested habitat.

Keywords: countryside biogeography, deforestation, habitat element, phytotelmata, species diversity, tropical forest.

Résumé : Des environnementalistes ont proposé que le maintien, éléments clés de l'habitat original des paysages modifiés puisse atténuer les effets nuisibles de cette modification sur les espèces résiduelles. Nous avons testé cette hypothèse sur des communautés d'insectes aquatiques de réservoirs de broméliades dans des habitats forestiers et non forestiers au Costa Rica. Les réservoirs de broméliades contiennent une grande proportion de l'eau stagnante dans cette région et représentent donc une ressource importante pour les insectes ayant des stades larvaires aquatiques. Nous avons quantifié l'importance relative du type d'utilisation du territoire et de l'environnement « local » spécifique des broméliades sur les communautés d'insectes et aussi l'effet du type d'utilisation du territoire sur cet environnement local. Les espèces d'insectes ont répondu autant au type d'utilisation du territoire qu'à l'environnement local, ces variables expliquant au total 36 % des densités d'espèces. L'environnement local expliquait à lui seul 19 % des densités d'insectes, alors que le type d'utilisation du territoire en expliquait 17 %, principalement par sa modification de l'environnement local. Les conditions environnementales locales étaient fortement corrélées au type d'utilisation du territoire ($r^2 = 0.64$), l'habitat non forestier ayant une température moyenne plus élevée, une plus grande variation de température et une densité moindre de broméliades. Nos résultats indiquent que l'utilisation du territoire au sein duquel on retrouve les broméliades influence les densités relatives d'insectes en modifiant l'environnement local des broméliades. Donc, la conservation des broméliades lors d'une modification d'utilisation du territoire ne maintiendra pas nécessairement les communautés d'insectes associées aux broméliades dans l'habitat forestier original.

Mots-clés : biogéographie du paysage, déforestation, diversité des espèces, éléments de l'habitat, forêt tropicale, phytotelmate.

Nomenclature: Croat, 1978; Rzedowski, 1978.

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Introduction

Conservation of species diversity depends on understanding the causes of species distributions (Noss & Cooperrider, 1994). Land-use change, such as conversion of forest to pasture, may influence species richness and abundances by changing the environmental conditions on which species rely (Laurance & Bierregaard, 1997). With rapid land-use modification occurring in the tropics, a basic understanding of the impacts of this change is necessary to ensuring species' persistence (Laurance, 1991; Gascon *et al*., 1999; Daily, Ehrlich & Sanchez-Azofeifa, 2001).

The clearing and fragmentation of forested land is predicted to become more common globally as demand for agricultural land increases, particularly in tropical countries where much of the world's biodiversity is found (Jackson *et al*., 2005). As such, there is a growing interest in the potential for modified or "countryside" habitats such as cropland, pasture, and managed forests to complement extensive primary habitats in the conservation of native biodiversity (Daily, 2001; Rosenzweig, 2003). Recent research on the factors governing the use of countryside habitats by diverse groups of native forest fauna has thus far yielded few generalities (Ricketts *et al*., 2001; Goehring, Daily & Şekerçioğlu, 2002; Perfecto & Vandermeer, 2002; Steffan-Dewenter, 2002; Horner-Devine *et al*., 2003; Daily *et al*., 2003; Ricketts, 2004; Numa, Verdu & Sanchez-Palomino, 2005). The lack of a general response among taxonomic groups emphasizes the need for studies of additional species, including non-charismatic and little-known species that may nevertheless play important ecological roles (Janzen, 1987; Hughes, Daily & Ehrlich, 2000).

In addition to the effects of land-use type on species, recent research has explored the effects of maintaining habitat elements that native species require for foraging, shelter, or reproduction as one conservation action that could contribute to the persistence of native biota in modified landscapes (Guevara, Purata & Vandermaarel, 1986; Toh, Gillespie & Lamb, 1999; Dean, Milton & Jeltsch, 1999; Davidar, Yoganand & Ganesh, 2001; Tews *et al*., 2004; Solis-Montero, Flores-Palacios & Cruz-Angón, 2005). For example, Luck and Daily (2003) examined foraging by avian frugivores on one species of tree growing in both forest remnants and agricultural habitats in Costa Rica. Despite significant differences in the composition of frugivore assemblages among habitats, they showed that this tree species could be an important resource to native frugivores foraging in agricultural landscapes. Likewise, Ricketts *et al*. (2001) suggested that the similar composition of moth species assemblages in 4 agricultural land-use types in their study area may reflect the similar microhabitats that these land-use types provide the moths, despite apparent differences in the human use of the land-use types.

Shade-grown coffee plantations, with large shading trees serving as the habitat element, are also found to have higher species diversity of many taxa than unshaded plantations (though still less than natural forest: Perfecto *et al.*, 1996; Greenberg, Bichier& Sterling, 1997), and reductions in the amount of shade and shading vegetation are strongly correlated with declines in species diversity (Perfecto *et al*., 1996; Moguel & Toledo, 1999; Perfecto & Armbrecht, 2003; Donald, 2004). Cruz-Angón and Greenberg (2005) have experimentally shown that the presence of epiphytes in coffee plantations increases the abundance of many forest bird species. These positive effects on species diversity by shade-grown coffee are enhanced when the plantations are near to or otherwise strongly connected to intact natural and primary forest (Vandermeer & Carvajal, 2001; Perfecto & Vandermeer, 2002; Steffan-Dewenter, 2002).

Few studies have attempted to quantify the relative importance of land-use *versus* microhabitats in determining species distributions. However, such an understanding may be important to predicting species responses to land-use change and to mitigating the negative effects of this change. The relationship between the two is complicated by the fact that land-use change may eliminate certain habitat elements, or it may change the fundamental nature of these resources.

In this study we aim to disentangle the effects of land-use and smaller-scale environmental factors on the use of tank-forming bromeliads by insect species with aquatic larvae. Bromeliads hold the majority of standing water in this region, particularly during the pronounced dry season that runs from December to May, and therefore represent a resource that many insect species with aquatic larval stages require for reproduction (Benzing, 2000). Because the insect communities in bromeliads have clearly defined boundaries, fine- and coarse-scale environmental variables are easily distinguishable, making bromeliads an ideal model system in which to examine habitat influences on communities at different scales. Moreover, these insect communities are not overwhelmingly diverse and, as such, are an extremely tractable system for studying differences in community composition. We sampled the species assemblages of bromeliad tanks in forested (primary and secondary forest) and non-forested (pasture and road) land-use types in northern Costa Rica. We explore (1) the total effect of land-use type and local environment on species distributions, (2) the independent effects of local environmental conditions and land-use type on species distributions, and (3) the degree to which land-use type drives local environmental conditions.

Methods

NATURAL HISTORY

Bromeliaceae occur as both epiphytes and soil-bound plants; for those that are epiphytic, modified roots serve mainly as holdfasts rather than for nutrient uptake (Benzing, 2000). These arboreal plants obtain their nutrients from atmospheric inputs or by trapping falling plant litter in their tightly interlocking leaves, with the relative importance of these sources varying between genera and with bromeliad size (Reich *et al*., 2003). In addition to leaf litter, these bromeliad wells also collect water and serve as an oviposition site for many insect groups with immature stages that are aquatic. Many of these insects are detritivores, and their feeding, along with their subsequent consumption by predatory insects, enhances the availability of nutrients for the bromeliad (Ngai & Srivastava, 2006).

The growth of bromeliads is limited by both water (Laube & Zotz, 2003) and nutrient availability (Laube &

Zotz, 2003; Ngai & Srivastava, 2006), with the availability of light being important for survival (Winkler, Hülber & Hietz, 2007). For many epiphytic bromeliads, particularly those in the outer canopy, collapse of their tree substrates was found to be the most substantial cause of mortality (Zotz, Laube & Schmidt, 2005; Winkler, Hülber & Hietz, 2007). Because of increasing forest fragmentation and collection of ornamental species, bromeliads are thought to be increasingly threatened in some areas (Siqueira Filho & Tabarelli, 2006).

FIELD SITE

Field work was conducted in the vicinity of the Estación Biológica Pitilla (10º 92' N, 85º 62' W) in the Area de Conservación Guanacaste, in northwestern Costa Rica. While this site is a wet tropical forest, it experiences a distinct dry season from December to May. This mid-elevation site (700 m elevation) is a mixture of primary forest (forest that does not appear to ever have been cleared and which local residents report has not been selectively logged for at least 50 y), secondary forest (16–30 y since clearing), and open pasture. One tertiary road provides vehicle access to the station. The vegetation in the primary forest is dominated by the trees *Calophyllum brasiliense*, *Sloanea faginea*, *Rinorea* sp., and *Pourouma bicolor*, while that of the secondary forest consists largely of *Hedyosmum bonplandianum*, *Clethra mexicana*, *Vernonia triflosculosa*, and *Siparuna andina*. Pastures are sparsely vegetated, with scattered small trees and forested hedgerows. Trees include *Conostegia xalapensis*, *Nectandra hihua*, *Hampea appendiculata*, and *Vochysia ferruginea*. Roadside vegetation is regularly thinned, such that the road is bordered by shrubs and young secondary vegetation, similar to that in the pastures.

SAMPLING PROTOCOLS

In October and November 2004, we sampled tank-forming bromeliads of the genera *Guzmania* and *Vriesea* from primary forest (*n* = 5 plants, a low sample size because of the small number of medium-sized bromeliads that were accessible in the primary forest), secondary forest (23), open pasture (4), and roadside habitats (7), restricting our sampling to water-filled plants. Bromeliads were naturally clustered, and we sampled from multiple clusters within each land-use type to increase the spatial independence of samples. However, because we were interested in sampling bromeliads with a range of well volumes from each land-use type (see below), we also in some cases sampled more than one bromeliad from a single cluster. The average number of bromeliads sampled per cluster was 1.69 (range 1 to 3), with bromeliads within a cluster generally within about 5 m of one another. Our sampling represents a complete census of 39 invertebrate communities that consisted of 9791 larval individuals. Bromeliads were removed from the ground or trees (up to 3 m above the ground) and taken back to the field station in buckets, which collected any spilled tank water. Once at the station, the maximum well volume, which is hereafter referred to as “volume”, was determined for each plant.

The bromeliads were dissected and rinsed out, leaf by leaf, and the collected water was poured through fine soil sieves. The resulting detritus was rinsed onto white trays and searched for insect larvae, which were sorted to family and then to morphospecies. With the exception of dytiscid larvae (Coleoptera: Dytiscidae), aquatic insects only occur in bromeliad wells as larvae and emerge as winged, terrestrial insects.

A number of vegetation and environmental variables were measured at each collection site to characterize bromeliad habitat. Daily maximum and minimum temperatures were recorded at each sample site from November 11 to 24 using max/min thermometers. In addition, canopy cover was scored on a scale of 0 (open) to 5 (closed canopy). For each bromeliad collected, height above ground and the number of other bromeliads on the host tree and within a 3-m radius were recorded. Although we measured microclimate for a comparatively brief period, we are confident that these differences between forested and open sites reflect consistent differences between these habitat types. Species identity and diameter at breast height were recorded for all overstory trees and lianas falling within a 3-m radius around each collection site. This survey was restricted to those plants higher than the location of the sampled bromeliad to provide an indication of possible sources of detrital inputs for the bromeliad.

ANALYSES

Analyses were first performed to investigate the relationship between local environmental conditions at the bromeliad level, the land-use type in which each bromeliad was found, and the insect community within each bromeliad. Land-use types sampled were primary forest, secondary forest, pasture, and roadside; however, due to low replication within primary forest stands and pastures, land-use was subsequently placed into “forest” (primary or secondary forest) or “non-forest” (pasture and roadside) groups for analysis. Local environmental variables included average, minimum, and maximum temperature, bromeliad location (tree or ground), canopy openness, number of bromeliads on same tree, bromeliad density in 3-m radius, bromeliad volume, and 2 axes describing tree species composition (explained below). Variables were log transformed as necessary to ensure normal distributions.

The tree and liana survey contained data for 323 individuals of 108 species. We used non-metric multidimensional scaling (NMDS) to represent the variation in tree and liana species frequencies in fewer dimensions, using PCOrd (McCune & Mefford, 1999). Only species present in at least 3 sites were included in this analysis. We retained the first 2 axes of the NMDS, which explained a total of 58% of tree and liana composition. These 2 axes representing the different tree and liana communities occurring in our sites were included as local environmental variables in the canonical correspondence analyses (CCA) and redundancy analysis (RDA), which are described below.

Canonical correspondence analyses of species abundance (number of individuals per litre) were performed to test (1) the correlation among species and local environmental conditions, (2) correlations among species and land-use, (3) the independent contributions of 1 and 2, and (4) the total variation in species densities explained by both sets of variables. Species density was used to avoid weighting large bromeliads more strongly than small bromeliads, as happens in a CCA when total abundance varies among sample units (Legendre & Legendre, 1998). The land-use and local environmental variables were used as explanatory variables for the appropriate tests, and morphospecies that occurred in at least 10% of samples were used as response variables (22 morphospecies in total; Table I). One oligochaete species (Olig C; Table I) that met the minimum inclusion requirement was subsequently removed from the CCAs because it had a large leverage that greatly inflated the variation explained by a single environmental variable.

For CCAs testing 1 and 2 (above), local environmental conditions and land-use types were used, respectively, as the independent matrix. The independent contribution of each of these (test 3) was determined by first using one explanatory matrix as a covariate and testing the effect of the remaining explanatory matrix on the residuals (Legendre & Legendre, 1998). A fourth test was performed by including the significant variables from both explanatory matrices into a single matrix and thus determining the variation explained by both sets of variables; this final test (test 4) provides an indication of the fit of the complete model (*i.e.*, the variation in community density described by all explanatory variables considered).

Independent variables for all CCAs were added to the model through a forward selection ($\alpha = 0.05$) with a sequential Bonferroni correction, such that the first variable entered if the P value was less than 0.05, the second if the P value was less than 0.05/2, and so on. This correction was applied to limit the effect of having more explanatory variables in the "local environment" matrix. The roles of independent variables and specific ordination axes on individual species were determined with the CANOCO output by calculating variable correlations with each axis and the percent variation within each species explained by a given axis (ter Braak & Smilauer, 1998).

Following a significant result from the CCA, we did tests on individual species to check for significant differences in abundance between land-use types and with bromeliad volume. These univariate tests were run using mixed models,

Table I. Mean densities (number of individuals per litre) and standard deviations (SD) of morphospecies and overall species richness and abundance in each of the 4 land-use types. Morphospecies abbreviation, taxonomic description, and functional group are also listed (functional groups adapted from Merritt & Cummins, 1996; Thompson & Townsend, 2003). Results from univariate analyses testing for differences between species abundance in forested and non-forested habitats and for the effect of bromeliad volume on insect abundance are also provided.

Abbreviation	Morphospecies name (taxonomic description)	Pasture		Road		Secondary forest		Primary forest		Forest *vs* non-forest difference†	Effect of bromeliad volume‡
		mean	SD	mean	SD	mean	SD	mean	SD		
PREDATORS											
Tany	Tanypodinae (Chironomidae, Diptera)	1.1	2.3	0.7	1.2	6.6	20.2	2.8	6.2		
Taba	Tabanidae (Diptera)	1.2	2.4	0.9	1.3	2.2	2.5	1.0	1.4		*
Cera	Ceratopogonidae (Diptera)	0	-	0.4	0.8	12.3	21.0	14.6	17.3	**	
Meci	*Mecistogaster* sp. (Pseudostigmatidae, Odonata)	0.8	1.5	9.1	10.4	4.8	7.0	0.7	1.0		***
COLLECTOR-GATHERERS											
Chir A	Chionomidae A (Diptera)	5.1	6.8	7.8	12.2	192.4	327.9	208.1	90.8	***	*
Chir B	Chironomidae B (Diptera)	12.3	16.5	82.8	49.9	8.3	25.9	0	-		***
Chir C	Chironomidae C (Diptera)	98.3	66.2	45.0	70.9	51.5	62.8	83.1	65.6		**
Chir D	Chironomidae D (Diptera)	17.5	35.1	3.1	5.7	0.1	0.2	0	-		***
Olig A	Oligochaeta A	0	-	0.1	0.4	2.1	4.5	0	-		
Olig B	Oligochaeta B	3.8	2.6	0.1	0.3	0	-	0	-	**	*
Olig C	Oligochaeta C	2.8	4.6	1.9	3.9	35.1	157.5	0	-		
Olig D	Oligochaeta D	4.8	9.6	12.6	31.4	1.5	2.9	0.9	2.0		
Dipt A	Diptera A	4.7	5.4	25.6	42.3	2.2	4.7	0.8	1.8	**	**
Dipt B	Diptera B	3.0	6.1	10.2	8.6	0.9	3.0	0	-	***	**
Syrp	Syrphidae (Diptera)	0.4	0.8	1.8	4.1	2.6	4.8	0.3	0.7		*
Peri	*Pericoma* sp. (Psychodidae, Diptera)	0	-	2.3	4.1	1.3	2.8	0	-		
FILTER FEEDERS											
Anop	*Anopheles* sp. (Culicidae, Diptera)	25.5	17.9	16.6	17.8	15.7	29.2	9.6	13.1	*	
Cule	*Culex* sp. (Culicidae, Diptera)	53.9	61.0	10.5	6.3	20.9	36.0	5.2	8.8		
Wyeo	*Wyeomia* sp. (Culicidae, Diptera)	94.6	140.9	16.7	26.6	16.9	25.7	17.5	26.2	**	
SCRAPERS											
Scir	Scirtidae (Coleoptera)	95.0	92.7	163.4	74.1	175.4	117.1	173.2	93.1		***
Dyti	Dytiscidae (Coleoptera)	0	-	0	-	0.9	2.5	0	-		
SHREDDERS											
Tipu	Tipulidae (Diptera)	76.4	66.7	55.1	73.0	55.7	35.6	40.6	30.7		***
SUMMARY BY LAND-USE TYPE											
Average richness (morphospecies per bromeliad)		9.3	5.9	14.0	2.2	11.0	3.3	7.6	1.7		
Average abundance (individuals per bromeliad)		147.2	142.8	415.4	158.4	229.5	158.4	192.2	144.2		

† *** $P < 0.01$, ** $P < 0.05$, * $P < 0.1$, blank - non-significant effect.

‡ In all cases where there was a significant relationship, morphospecies density increased with increasing volume.

with the bromeliad cluster considered a random factor and land-use type or bromeliad volume considered a fixed factor. Species abundances and bromeliad volumes were log transformed for these analyses.

An RDA was used to examine the correlation between land-use type and the local environmental variables that were significant in the CCA (Legendre & Legendre, 1998). Local environmental variables were entered into the RDA as dependent variables, and land-use type (forested or non-forested) was entered as a binary explanatory variable. All CCAs and the RDA were tested using permutations (ter Braak & Smilauer, 1998). Regressions of species richness and abundance on log-transformed bromeliad volume were performed with $\alpha = 0.05$.

Results

The 9791 larval individuals that we collected were identified into 43 morphospecies (hereafter referred to as species), of which 22 were common enough to include in further analyses (Table I). On average, bromeliads contained 246.7 individuals (range 8–698) and had a species richness of 12.1 (range 2–20). Both species richness and abundance were significantly related to bromeliad volume (species richness *versus* volume: $r^2 = 0.30$; $P < 0.001$; $n = 39$; total abundance *versus* volume: $r^2 = 0.39$; $P < 0.001$; $n = 39$), with the sampled bromeliad volumes ranging from about 50 to 3000 mL.

Overall, land-use type and local environmental conditions explained 36% of insect species distributions ($P = 0.001$; Figure 1). The significant local environmental conditions (Table II) explained 19% of species distributions independent of land-use type ($P = 0.001$). Land-use type explained 17% of insect distributions ($P = 0.001$), indicating that the insect community as a whole changes from one land-use type to another. The effect of land-use was mainly through the modification of local environmental conditions; once the effect of local environmental conditions was statistically controlled, land-use type did not explain species distributions ($r^2 = 0.03$, $P = 0.09$). Overall, the first axis of the CCA was most strongly related to 3 environmental conditions: number of bromeliads in the surrounding area, bromeliad volume, and maximum temperature. The first of these was greatest in forested areas, while the latter 2 were greater in cleared areas (Figure 2, Table II). The second axis of the CCA mainly reflects the effects of temperature and volume. Species showed diverse responses to the environmental conditions, with some being most abundant in cooler, smaller bromeliads (*e.g.*, Chironomidae A and Oligochaeta A) that tend to occur in the forest, while others occur predominantly in hot, open areas (*e.g.*, Oligochaeta B and Diptera B).

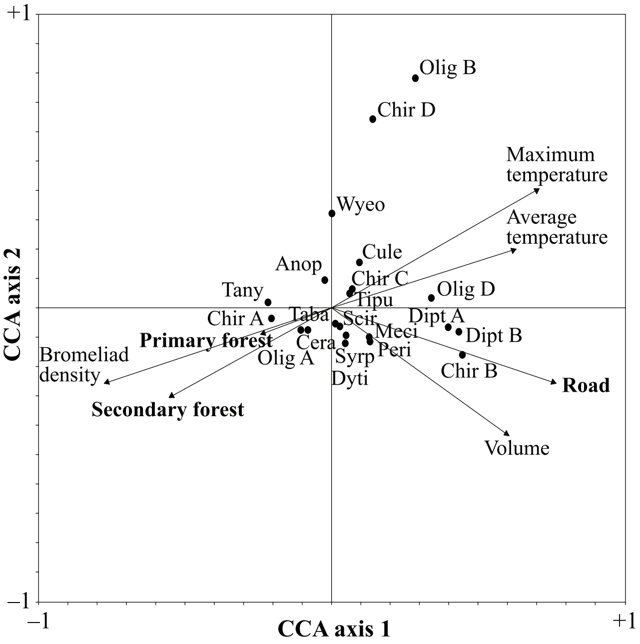

FIGURE 1. Biplot of CCA output showing species (points) and environmental gradients (vectors: land use and fine-scale environmental variables). Here, we show each land-use type separately although they were grouped into forested and non-forested land-use types for analyses. Environment and land use combined explained 36% of species distributions. The "Pasture" land-use type is not visible in the biplot because it is included in the intercept. See Table I for abbreviations.

Although the 2 axes representing variation in overstory tree and liana species explained significant amounts of variation in insect species abundances and land-use types when tested alone, they were non-significant ($P > 0.05$) when included in the larger matrix of local environmental variables. This indicates that the variation in the species composition of surrounding trees was only weakly correlated to insect species densities relative to other local environmental factors. It should be noted that unique tree species (occurring only once in the survey) were removed from the analysis; these individuals may be important for specific insect species, but our data do not allow us to test this possibility.

Land-use type was strongly related to the local environmental variables that were significant in the CCA ($r^2 = 0.64$, $P = 0.001$; Figure 2). Forested sites had higher densities of bromeliads ($r = 0.78$) and lower average and maximum temperatures ($r = –0.85$ and $r = –0.84$; Table II). Bromeliad volume was not strongly correlated to land-use type ($r = –0.20$). The first axis of the RDA shows a strong correlation between non-forested land-use types and temperature, both of which are negatively correlated to forested land-use types and bromeliad density. In contrast, the weak correlation between volume and land-use indicates that the effects of bromeliad volume should be apparent in both forested and open areas.

TABLE II. Statistically significant environmental variables in the CCA with mean (SD) values in forested and non-forested sites. Correlations indicate the degree to which species distributions correspond to changes in each variable.

Local environmental conditions	Correlation[†] to species densities (r)	Non-forest	Forest
Number of bromeliads in 3-m radius[††]	0.38	1.00 (1.00)	24.5 (23.7)
Maximum temperature (ºC)	0.37	29.7 (1.64)	25.0 (1.30)
Average temperature (ºC)	0.34	23.3 (0.75)	21.1 (0.59)
Volume[††] (mL)	0.33	990 (1041)	433 (216)

[†] Does not account for the effects of other variables. See ter Braak and Smilauer (1998) for details on generating the multivariate correlation coefficient.

[††] Mean and SD values are for raw data. Log-transformed data were used in the CCA and to generate the correlation.

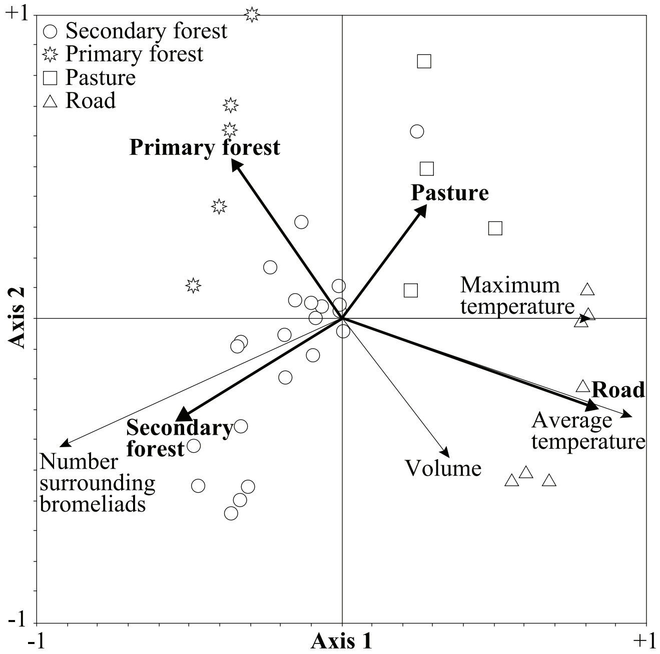

FIGURE 2. Triplot of RDA output showing linear correlations between land use (thick vectors) and environmental variables (thin vectors).

Specific species groups illustrate the range of species' responses to land-use type and local environmental variables. For example, among the detritivore chironomids of the collector–gatherer feeding guild, Chironomids A and B are segregated along the first CCA axis, with Chironomid A more abundant in forest bromeliads with lower average temperatures and Chironomid B more abundant in larger, warmer bromeliads (Figure 1; Table I). Chironomid D is segregated from Chironomids A and B along the second CCA axis, showing preference for small volume bromeliads with high maximum and average temperatures (Figure 1). Similarly, the predators showed varying abundances among habitats. For example, the tanypodine chironomids, the smallest of the predators, were most common in smaller bromeliads in forest habitats. The largest predator, the damselfly larvae *Mecistogaster modesta*, was found more frequently in larger bromeliads in warm, roadside areas.

Discussion

Maintaining crucial resources in otherwise-modified landscapes is one approach that may help to maintain native biodiversity in altered landscapes (Luck & Daily, 2003; Davidar, Yoganand & Ganesh, 2001; Tews *et al*., 2004). However, before such an approach can be adopted as a conservation tool, we need to understand the factors that control the distributions of target species in these areas. In tropical regions where there are few ponds or other sources of standing water and an array of insect species that obligately oviposit in standing water, bromeliad tanks represent such a habitat element (Benzing, 2000). Here we show that the local environment of a given habitat element is responsible for most of the explained variation in insect community composition. Land-use type makes no significant independent contribution to insect distributions but is important in determining the local environment. This suggests that the use of habitat elements may help to conserve the forest community of aquatic insects but only if local environmental conditions can be maintained under changing land use.

In the landscape we studied, we found substantial differences in environmental conditions around bromeliads in forested *versus* non-forested habitats, indicating that managing the local environment would likely need to be an explicit focus of conservation efforts that aim to maintain forest insect species in cleared areas. In particular, temperature was strongly correlated to land-use type and was also a strong predictor of insect community composition in bromeliads (Figure 1). Temperature may determine species' competitive hierarchies, as has been documented in fresh water habitats (Tilman, 1982), or may act as an abiotic filter for specific species (*sensu* Weiher & Keddy, 1995) by changing available oxygen levels. In either case, the correlation between temperature and species' relative abundances noted here has been found in other studies, most notably with chironomids (Lotter *et al*., 1999). Temperature of bromeliads in non-forested land-use types could potentially be managed by creating larger patches of trees within the open landscape, thus minimizing the environmental extremes that often occur at the edges of forest remnants (Laurance *et al*., 1998). Similarly, increasing the use of live fences, which are already common in the area, could increase the availability of shaded habitats for bromeliads and the insect populations that they host (Harvey *et al*., 2005). One caveat is that there are other environmental variables that we have not measured, such as food for adult insects or refuges from predators, that are important to insect fitness and that are affected by changes in land use. Some additional variation in the insect community is likely explained by these unmeasured variables.

In addition to changing insect species composition, land-use type has a marked effect on bromeliad population dynamics. Previous studies have documented differences in the number of bromeliad species in disturbed *versus* mature habitats, although the overall effect of habitat type remains uncertain. For instance, while Barthlott *et al*. (2001) found higher bromeliad diversity in disturbed habitats, Cascante-Marin *et al*. (2006) and Martin *et al*. (2004) both found the opposite. Heitz (2005) found similar numbers of epiphyte species in natural forest and coffee plantations in Veracruz, Mexico, although plantations had a more homogenous epiphyte community and those that had smaller shade-tree species had lower numbers of epiphytes as well. Clearly, species composition does change with land use. Both increased abundance and size of bromeliads have also been observed in secondary *versus* primary forest (Srivastava, Melnychuk & Ngai, 2005). Moreover, Merwin, Rentmeester, and Nadkarni (2003) have found that the abundance and distribution of bromeliads change with the composition of host trees, a habitat characteristic that will shift with land use.

Given that bromeliad volume strongly impacts insect community composition (Figure 1, Table I, and Armbruster, Hutchinson & Cotgreave, 2002), and that different bromeliad species have different average sizes, any shifts in the species composition of tank-forming bromeliads that result in changes in the size of bromeliads present in different land-use types would likely affect the insect community as well. In the vicinity of our study area, for example, larger species of bromeliads (*e.g.*, *Vriesea sanguinolenta*) are generally found in the open habitats and early successional forests. In our study we were careful to select a range of sizes of bromeliads from each land-use type; however, it will be important to determine how the characteristics and total number of bromeliads in different land-use types may be compounding the shifts in insect populations that we have documented in this study.

An issue related to land-use change and insect distributions is how the spatial configuration of habitat elements and land-use types may affect their use by insects. Several studies of forest species in countryside habitats have documented a shift in species composition with distance from forest sites, indicating that forest species are less present at sites further from the forest (Ricketts *et al*., 2001; Horner-Devine *et al*., 2003; Luck & Daily, 2003; Ricketts, 2004). A similar pattern is observed amongst well-studied pollinators in tropical agro-ecosystems. Proximity to rainforest enhances pollination and ecosystem services, as the agricultural lands themselves do not necessarily provide habitat to species present before agricultural intensification (Aizen & Feinsinger, 1994; Steffan-Dewenter & Tscharntke, 1999; Cunningham, 2000; Kleijn *et al*., 2001; Klein, Steffan-Dewenter & Tscharntke, 2003; Aguilar *et al*., 2006; Blanche, Ludwig & Cunningham, 2006; Chacoff & Aizen, 2006; Klein, Steffan-Dewenter & Tscharntke, 2006; Priess *et al*., 2007). At the same time, the scale of forest proximity can depend on the species studied (Becker, Moure & Peralta, 1991; Aizen & Feinsinger, 1994; Steffan-Dewenter *et al*., 2002; Tonhasca, Blackmer & Albuquerque, 2002), making any general pattern difficult to discern. Although our study provides strong evidence for the importance of local environmental factors in determining the composition of insect communities in bromeliads, we suspect that dispersal-related factors would explain some of the currently "unexplained" variation in insect community composition and should be a focus of further research.

Overall, our study indicates that for bromeliads in open habitats to conserve forest-associated species, care must be taken to ensure that the local environmental conditions required by these species are maintained. However, in cases where conservation of forest species is not a concern, our results indicate that bromeliads in open habitats increase the beta diversity of aquatic insects in the landscape by hosting a community with low relative abundances of forest insects (*e.g*., Cera, Chir A; Table I). A fundamental question that remains in the event of large-scale deforestation is whether the lower densities of forest species currently observed in open land-use types (pastures and roadsides) are sufficient to maintain viable populations. If not, the open land-use types could act as a "sink" for forest species (Pulliam, 1988). Studies of species' population growth rates would be needed to definitively answer whether bromeliads in open areas are acting as sources or sinks for forest species. Research that manipulates the locations of bromeliads and that monitors community dynamics could be used to explore the mechanisms underlying the patterns that we observed in this study.

Our study can be combined with the findings of other work in the field of countryside biogeography to begin to develop a general framework for the management of residual species in so-called "countryside" habitats. Our study emphasizes that such a framework must, at the very least, consider the quality of habitat elements within the agricultural matrix. In the case of species with distinct life stages, such as the insects that we studied, consideration should be given to the habitat and resource requirements of each life stage. Finally, a large body of work emphasizes the importance of considering the spatial configuration of modified habitats relative to patches of the original land-cover type. Not only is this configuration likely to affect the dispersal of residual species into modified habitats, but the survival of residual species in modified habitats may in some cases depend on their utilization of patches of the original land-cover type at some stage in their life cycle.

In conclusion, the significant role the local environment plays in explaining species distributions indicates that community composition can be maintained under changing land use, as long as the local environment stays the same. However, our results show that land use has a large effect on fine-scale environmental variables, such that the environment surrounding habitat elements is likely to be altered with changes in land use. Indeed, our results indicate that bromeliads found in different land-use types tend to host different insect communities. Therefore, if habitat elements are to be used successfully in conservation strategies, considerable attention will need to be paid not only to the availability and distribution of the elements, but also to the environmental conditions that species will encounter when using them.

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