



Niche partitioning at multiple scales facilitates coexistence among mosquito larvae

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A theoretical dichotomy in community ecology distinguishes between mechanisms that stabilize species coexistence and those that cause neutral drift. Stable coexistence is predicted to occur in communities where competing species have niche-partitioning mechanisms that reduce interspecific competition. Neutral communities are predicted to be structured by stochastic processes that are not influenced by species identity, but that may be influenced by priority effects and dispersal limitation. Recent developments have suggested that neutral interactions may be more common at local scales, while niche structuring may be more common at larger scales. We tested for mechanisms that could promote either stable coexistence or neutral drift in a bromeliad-dwelling mosquito community by evaluating A) if a hypothesized within-bromeliad niche partitioning mechanism occurs in the community, B) if this mechanism correlates with local species co-occurrence patterns, and C) if patterns of coexistence at the larger (metacommunity) scale were consistent with those at the local scale. We found that mosquitoes in this community do partition space within containers, and that species with the strongest potential for competition co-occurred least. Species with overlapping spatial niches minimized co-occurrence by specialising in bromeliads of differing sizes, effectively changing the scale at which they coexist. In contrast, we found no evidence to support neutral dynamics in mosquito communities at either scale. In this community, a niche-based mechanism that is predicted to stabilize species coexistence explains co-occurrence patterns within and among bromeliads.

Determining the mechanisms that allow species to coexist is important for understanding community ecology and conserving biodiversity (Chave et al. 2002, Amarasekare et al. 2004). Ecological theory distinguishes between mechanisms that stabilize coexistence among species (sensu Chesson 2000), and those that lead to unstable coexistence and species 'drift' by solely equalizing species' competitive abilities (Chesson 2000, Hubbell 2001). Understanding how each mechanism contributes to coexistence in a community allows for predictions on both the long-term persistence of community members and the processes that will lead to the extirpation of a given species (Chesson 2000). For these reasons, tests of the importance of stabilizing mechanisms and neutral drift have recently gained focus in research on diverse organisms, including forest plants (Gilbert and Lechowicz 2004), intertidal animals (Wootton 2005), and stream insects (Thompson and Townsend 2006).

The scale at which stabilizing mechanisms and neutral drift are expected to function is particularly important to species coexistence (Holyoak and Loreau 2006). Neutral drift may be apparent in local interactions among species in a metacommunity, and when these interactions are considered at the spatial scale of the metacommunity they lead

to spatial clustering so long as individuals have limited dispersal (Chave and Leigh 2002, Gilbert and Lechowicz 2004, Holyoak and Loreau 2006). Stabilizing mechanisms may also lead to scale-dependent coexistence, whereby species that cannot coexist locally due to asymmetric competitive ability or predator avoidance can co-exist at larger temporal or spatial scales that are environmentally heterogeneous (Chesson 2000, Davies et al. 2005). In both scenarios, local coexistence mechanisms may be nested within larger, landscape-level processes that are dominated by environmental heterogeneity (Chave 2004). Tests of coexistence mechanisms should therefore include members of a single metacommunity and test across spatial scales that capture the environmental heterogeneity experienced by those species (Amarasekare 2003).

Here we focus on larvae of bromeliad-dwelling mosquito species in the Guanacaste region of northern Costa Rica. Previous research on mosquito larvae has provided contrasting evidence for coexistence mechanisms. Although several studies of container-dwelling mosquitoes have identified potential stabilizing mechanisms (Livdahl and Willey 1991, Sunahara and Mogi 2002b, Costanzo et al. 2005), others have been either unable to find a stabilizing mechanism of coexistence (Bradshaw and Holzapfel 1983,

Schneider et al. 2000), or have cited priority effects as drivers of species distributions whereby larger or early-arriving individuals are able to outcompete late-arriving individuals for a particular niche space (Livdahl 1982, Sunahara and Mogi 2002a, Lounibos et al. 2003). When priority effects occur without other life history tradeoffs, they are consistent with species drift (Hubbell 2001, Amarasekare et al. 2004).

Such contrasting results from previous studies may have resulted from the scales at which the mosquito community was considered. The most common case for which a stabilizing mechanism was identified involves two species that have different environmental niches, as occurs when species perform best in different habitat types, such as tree holes and tires (Lounibos 1981, Livdahl and Willey 1991). Likewise, temporal fluctuations in environmental conditions, such as drought and rainy periods, have been shown to favour different species at different times (Juliano et al. 2002, Costanzo et al. 2005). However, these mechanisms of habitat specialisation generally lead to species coexisting at large spatial and/or temporal scales (i.e. regional coexistence), by favouring a single species within a single habitat (Costanzo et al. 2005, but see Yee et al. 2007). This pattern is consistent with Leibold and McPeck's (2006) hypothesis that stable coexistence is likely to occur at larger spatial and temporal scales, as observed in mosquito communities, and that neutral dynamics are more likely to occur within single habitats.

The mechanisms promoting the coexistence of mosquito larvae within a single habitat are particularly interesting because all filter feeding species consume the same resources (small particles of detritus and microscopic organisms), with little evidence for differences in feeding preferences or behaviour among species (Yee et al. 2004, 2007, Kesavaraju et al. 2007). Recently, Yee et al. (2004) proposed that mosquito species create 'spatial niches' by specialising in specific vertical strata within a given container habitat. This mechanism could potentially promote within-habitat coexistence by restricting interactions among species, such as resource competition or interference competition (Lounibos et al. 2003). To our knowledge, the spatial niche mechanism for coexistence has not been tested in natural mosquito communities.

In this study we use sampling data to test the degree to which the bromeliad mosquito community shows evidence of niche segregation or neutral dynamics. If partitioning of spatial niches is important in this community, species with similar spatial niches should co-occur less in natural bromeliads, as these species will have the strongest potential for competition (Fig. 1A). In contrast, if neutral processes are dominant and species do not differ in their competitive abilities, we expect species distributions to be random with respect to spatial niches. Neutral dynamics may produce different patterns of co-occurrence, depending on whether dispersal limitation and priority effects are important. In the case of dispersal limitation, species tend to be spatially clustered, and the similarity between any two bromeliads decreases linearly with logarithm of distance (Fig. 1B; Chave and Leigh 2002). Priority effects in mosquito communities are expected to cause high mortality in young cohorts (late-arriving mosquitoes), which would decrease the co-occurrence of different cohorts (Fig. 1C).

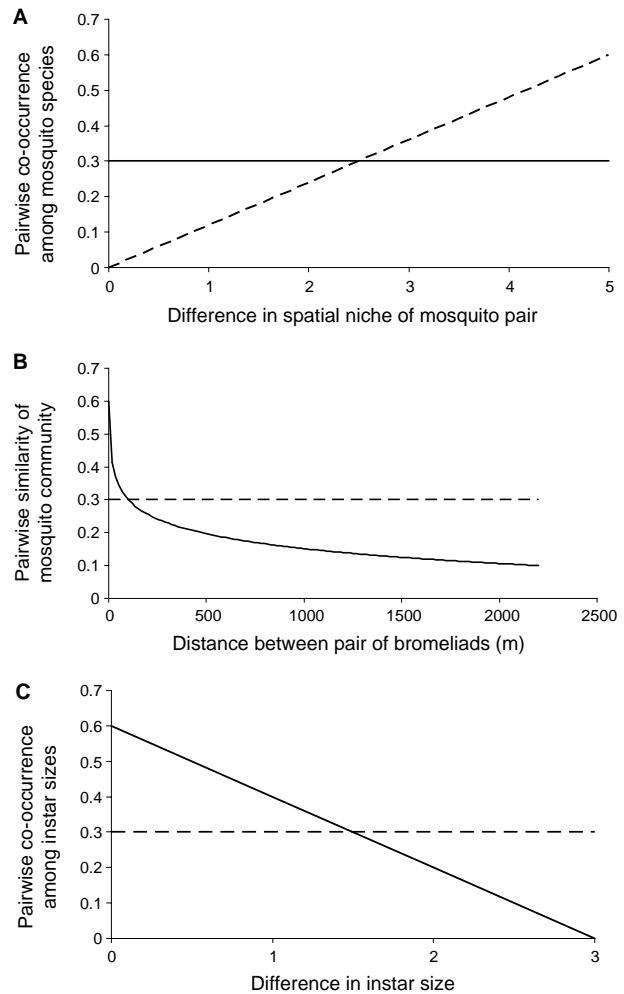


Fig. 1. Hypothetical trends in mosquito community depending on whether neutral dynamics (solid lines) or niche partitioning (dashed lines) determine co-occurrence patterns. (A) neutral prediction: there is no relationship between the areas of the water column that species tend to occupy and their co-occurrence; niche prediction: species that occupy different areas of the water column co-occur, while those with similar spatial niches do not; (B) neutral prediction: the mosquito community changes in species composition as the distance between bromeliads increases due to universal dispersal limitation; niche prediction: species composition is determined by environmental heterogeneity such that geographic distance is not important once environmental heterogeneity is accounted for; (C). neutral prediction: individuals of a given instar do not co-occur with individuals of different instars because of priority effects; niche prediction: inter-specific co-occurrence is not solely related to instar size

Depending on the processes that are most important at local scales, we expect differences in the relationship between species' distributions and the environmental characteristics of bromeliads. If niche processes are important, species' distributions should correspond to environmental differences among bromeliads, allowing specific species to be optimal competitors at distinct points along an environmental gradient. In contrast, if neutral processes determine local coexistence, there will either be no correspondence between species and environment, or environmentally distinct bromeliads will house neutral species groups (Chave 2004).

Here we test 1) if there is evidence for species partitioning of spatial niches within containers, 2) if sampled mosquito communities yield species co-occurrence patterns that are consistent with predictions based on species' spatial niche overlap, priority effects (size differences), or dispersal limitation (spatial clustering), and 3) if among-bromeliad habitat partitioning is consistent with local co-occurrence patterns.

Methods

Two studies were conducted from 6 October to 28 November 2004, in the area immediately surrounding Pitilla biological station (10°59'N, 85°26'W) in the Área de Conservación Guanacaste (<<http://www.acguanacaste.ac.cr/>>). The station is at an altitude of 700 m in the premontane tropical wet forest life zone (Holdridge 1967) and approximately 4000 mm of rain falls between May and February. The landscape surrounding the station is made up of primary forest, regenerating (1–80 year old) forest and pasture. All experiments and sampling were performed in primary or secondary forest. Further details on the area are given in Srivastava et al. (2005).

Study 1. Observation of species' spatial niches within containers

An observational study was designed to detect differences in the spatial positions of the four common mosquito species in the area: *Anopheles neivai*, *Wyeomyia melanopus*, *Culex rejelector* and *Wyeomyia circumcincta*. Two 3rd instar individuals of a species were put into a transparent 50 ml centrifuge tube to which 0.4 g (dry weight) of fine detritus (1 mm < diameter < 5 mm) from the wells of bromeliads in nearby forest and 35 ml of water had previously been added. The top of each tube was covered with mesh. The depth in the water column of each individual larva was recorded after allowing sufficient time for the mosquitoes to acclimatize to the presence of the researcher. This observational study was designed to replicate that of Yee et al. (2004), but using an observer instead of a camera. In total, the experiment consisted of six replicates (tubes) of *A. neivai* and three of each other species, each of which was monitored twice a day over four days. Each monitoring period was considered a single observation, with observations nested within experimental units (Statistical methods). Because of the consistent and clear spatial positioning of the species, we deemed it unnecessary to monitor the larvae beyond this time.

Study 2. Sampling species distributions

A total of 71 bromeliads were sampled to determine species patterns of co-occurrence, and whether these patterns correlated with environmental conditions within or around the bromeliad. Individuals from two genera of bromeliad, *Vriesia* and *Guzmania*, were sampled at ≤ 2.5 m from the forest floor. Sampling was done with a turkey baster and all water from each leaf well in each bromeliad was removed.

More water was added twice to completely flush each leaf well.

Measures of leaf well pH, water holding capacity, and actual water level at time of sampling were taken when possible. Bromeliads were measured for characteristics that predict their water holding capacity (i.e. their maximum volume) based on relationships generated from previous sampling of the two genera encountered in our survey ($r^2 = 0.95$, $DF = 22$ and $r^2 = 0.88$, $DF = 14$, both $p < 0.001$; Srivastava unpubl.). These characteristics included the bromeliad genus, number of leaves, and the maximum width and length of leaves. In addition, bromeliad species, date sampled, geographic location, forest age, forest canopy openness (on a 5 point scale), elevation, and local bromeliad density on the tree sampled and within a 3 m radius (to 10 m height) were quantified. All aspects of leaf wells (species and environmental variables) were grouped within each bromeliad prior to analysis, as leaf wells often share water and therefore are not independent.

All water collected while sampling was scanned using a dissecting scope (10 \times magnification) to ensure that small mosquitoes were not missed. Mosquito larvae were identified at Pitilla with a dissecting scope, with some 1st instar individuals raised in rearing cups to 2nd or 3rd instar for positive identification. Larval traits for identification did not change after the 2nd instar for any of the species. Larvae were identified using a key for Costa Rican mosquitoes generated by G. Chaverri at the Inst. National de Biodiversidad (INBio), and voucher specimens were collected and stored in the INBio Culicidae Collection. Mosquito sizes were measured as the length of the body from the tip of the head to the base of the siphon. Sizes were measured for all common species at each instar except *C. rejelector*, which had its first instar length estimated from the lengths of larger instars (exponential equation, $r^2 = 0.97$, $p < 0.0001$, $DF = 10$) because we were unable to distinguish between *C. rejelector* and *C. jenningsi* in the first instar.

Analysis

The observational study of the spatial niches of mosquito larva was analysed using a general linear model (GLM) with a multinomial distribution and a cumulative logit link. The multinomial distribution was used because the spatial distribution of individuals was not normal, with larvae occurring either at the water surface, at the bottom of the water column (on the detritus) or in a small band in the centre of the water column. Observations were aggregated within experimental units and the dispersion parameter was set as the Pearson's χ^2 statistic divided by the degrees of freedom for computing standard errors and likelihood ratio statistics. Aggregating within experimental units corrects for multiple observations from a single unit by treating them as a single observation when calculating standard errors and likelihood ratios.

Sampling data was used to evaluate two niche-based (spatial partitioning of the water column and habitat partitioning among bromeliads) and two neutral (priority effects and dispersal limitation) mechanisms. The two neutral mechanisms could not be tested simultaneously

because of different predictor variables in each relationship; however, because of the different predictor variables, these effects should both be detectable if they occur. In each of these tests, co-occurrence patterns or community similarity were calculated using the Steinhaus coefficient (Legendre and Legendre 1998); this similarity coefficient is the complement of the Bray–Curtis distance, and measures the relative co-occurrence of two species based on their individual abundances across all bromeliads and their joint abundances in bromeliads in which they co-occur. It can also be used to measure community similarity by comparing species relative abundances on a per bromeliad basis. The Steinhaus coefficient ranges from 0 (no co-occurrence or no similarity) to 1 (two species have identical abundances in all bromeliads, or two bromeliads have identical abundances of all species). Uncommon species are not appropriate for these analyses, thus species that occurred in less than five bromeliads were removed from the analysis. These species were *Wyeomyia abebela*, *W. pseudopecten*, *Culex jenningsi*, and an unidentified species of *Wyeomyia*.

The role of priority effects in determining coexistence patterns were evaluated by correlating size differences between any two instars with the co-occurrence of these two instars. If priority effects alone determine competitive outcomes, then we would expect that early instar individuals (1st and 2nd instar) would occur less with later instar individuals (4th instar) than with each other (Sunahara and Mogi 2002a; Fig. 1C). When priority effects are considered a neutral mechanism, species identity should not matter. Therefore we ignored species identity in this analysis, with one exception: we did not include comparisons among instars within a species, as different growth rates among individuals from the same oviposition event could cause spurious differences. Instar co-occurrences were compared with two metrics: differences among instars based on mosquito size measurements from samples, and differences among instars treating a given instar of all species as equivalent (i.e. all 1st instar individuals had a size of 1, 2nd instars were 2, etc.). To test this relationship, a randomization was performed by generating correlation coefficients for the pairwise relationship between instar size differences and a randomized instar co-occurrence matrix. To minimize the risk of type 1 error, randomizations were constrained by keeping the total abundances of all instars of each species constant (Gotelli 2000). This and all other randomization tests were run 9999 times. This analysis was subsequently repeated with 1st instar individuals removed, and then with 1st and 2nd instar individuals removed, to insure that the lack of effect shown was not due to a time lag in mortality. These subsequent analyses did not differ qualitatively (all had $p > 0.05$), and we therefore only present results from the first analysis.

We evaluated the role of dispersal limitation by testing for spatial clustering of species with a Mantel test (Legendre and Legendre 1998). The neutral hypothesis was that species similarity between bromeliads decreases with geographic distance (Chave and Leigh 2002; Fig. 1b). Both linear distances and logarithmically transformed distances were used for this test.

We then evaluated whether species co-occurrences increase with differences in spatial niches, (Fig. 1A) to test for a niche-based explanation of species co-occurrence.

Differences in spatial niches were measured as the absolute difference in depth between each species pair from the observational study, and species co-occurrences were calculated from the sampling data. As with the test for priority effects, a randomization test was used to evaluate the pairwise correlation between species co-occurrence patterns and species spatial niche differences.

Following the analysis of similarities, we tested whether species partition niches at larger scales (i.e. between bromeliads) by examining species' distributions among bromeliads. In particular, we tested for correlates of species densities using a canonical correspondence analysis (CCA), which is able to model linear or unimodal species distributions along environmental gradients (Legendre and Legendre 1998). Densities were used to prevent large bromeliads with more individuals from dominating the ordination, with density calculated as $\text{density} = (\text{no. individuals}) / (\text{bromeliad water holding capacity})$. The densities of species that occurred in five or more bromeliads were used as the dependent matrix, and the explanatory matrix consisted of the following environmental variables: water pH, Julian date, water holding capacity of bromeliad, forest canopy openness, forest canopy height, forest age, local bromeliad density and bromeliad species. Explanatory variables were included through a forward selection process with an $\alpha = 0.05$ cut-off. Because total species density showed a slight decrease with bromeliad size ($r^2 = 0.08$, $p < 0.04$), sampling analyses were rerun with this trend removed statistically to test their sensitivities to this effect; the results did not change, so the initial test is reported.

Analyses were conducted using SAS for GLMs, CANOCO for the CCA (ter Braak and Smilauer 1998), and PC-ORD (McCune and Mefford 1999) and our own code in visual basic for Mantel tests, randomization tests and distance matrices.

Results

Species showed significant differences in their vertical distributions in the water column (multinomial GLM, $F_{3,25} = 18.74$, $p < 0.0001$), with *A. neivai* occurring mainly at the water surface, *W. circumcincta* occurring in or on the detritus at the base of the container, and the other species occurring in the middle of the water column (Fig. 2). All species appeared to feed by both filtering the water column and browsing the detritus or the sides of the container.

Species' pairwise co-occurrence patterns were strongly correlated with differences in their spatial niches ($r = 0.95$, $p = 0.0005$; Fig. 3A). The correlation is consistent with predictions of local niche segregation, with those species most likely to interact within a water column (*C. rejector* and *W. melanopus*) least likely to co-occur, and species least likely to interact (*W. circumcincta* and *A. neivai*) co-occurring most frequently. By contrast, there was no evidence of consistent priority effects. Individuals from small instars were as likely to co-occur with individuals from larger instars as with other individuals of small instars, and this result was consistent whether actual sizes were used or all individuals of a given instar were included in a single rank ($r = 0.06$ and 0.03 , both $p > 0.05$; Fig. 3C). Likewise, there was no evidence of dispersal-limitation at the distances

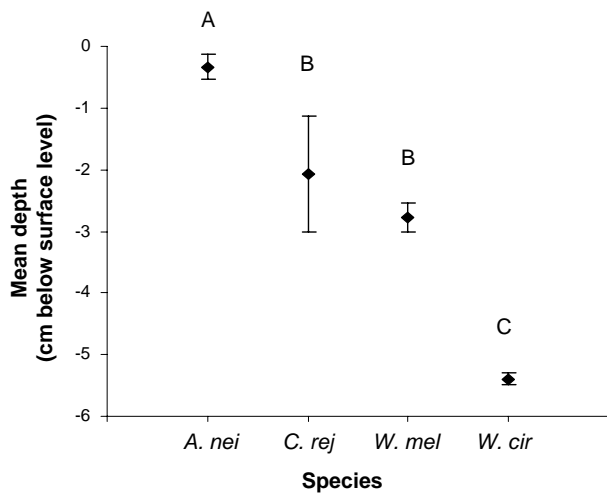


Fig. 2. Mean depth (\pm SE) of individuals below water surface for *Anopheles neivai* (*A. nei*), *Culex rejector* (*C. rej*), *Wyeomyia melanopus* (*W. mel*) and *W. circumcincta* (*W. cir*). Different letters represent statistically significant differences (Bonferroni corrected $\alpha = 0.05$) in vertical habitat use based on frequency of occurrence at the water surface, middle, or bottom of the container.

measured (distances ranged from 0.015 m to 2128 m); spatial clustering in community composition was not significant using linear or log-transformed distances ($r = 0.01$ and 0.04 , both $p > 0.05$; Fig. 3B).

The CCA indicated that bromeliad water holding capacity was the only significant correlate of species-distributions amongst bromeliads, and it explained 36% of the total variation in common species' densities ($p < 0.0001$, Fig. 4). Overall, species that had high overlap in vertical niches (e.g. *C. rejector* and *W. melanopus*, Fig. 2) showed segregation in the size of bromeliad in which they were each most common (*C. rejector* occurred primarily in bromeliads > 60 ml, *W. melanopus* primarily < 60 ml; Fig. 4).

Discussion

The mosquito species studied here are restricted to bromeliads for the larval stage of their life cycles (Dyar 1928), and their coexistence is therefore mediated by their interactions within this habitat. For these species to coexist stably over the long term, species pairs with strong overlap in one niche axis must compensate by segregating along a second niche axis (reviewed by Chesson 2000). The community studied here followed this principle; species had well-defined spatial niches, and species pairs with the most overlap in their spatial niches co-occurred least (Fig. 3). In contrast, a neutral community would show random patterns of species co-occurrence with respect to spatial niches, and species co-occurrence patterns would instead reflect priority effects and dispersal limitation. Our results reject a purely neutral model of coexistence both locally and in the larger metacommunity.

Interference competition has been documented as an important regulator of mosquito density (Broadie and Bradshaw 1991), and may be especially relevant within the limited volume of bromeliad tanks (Lounibos et al.

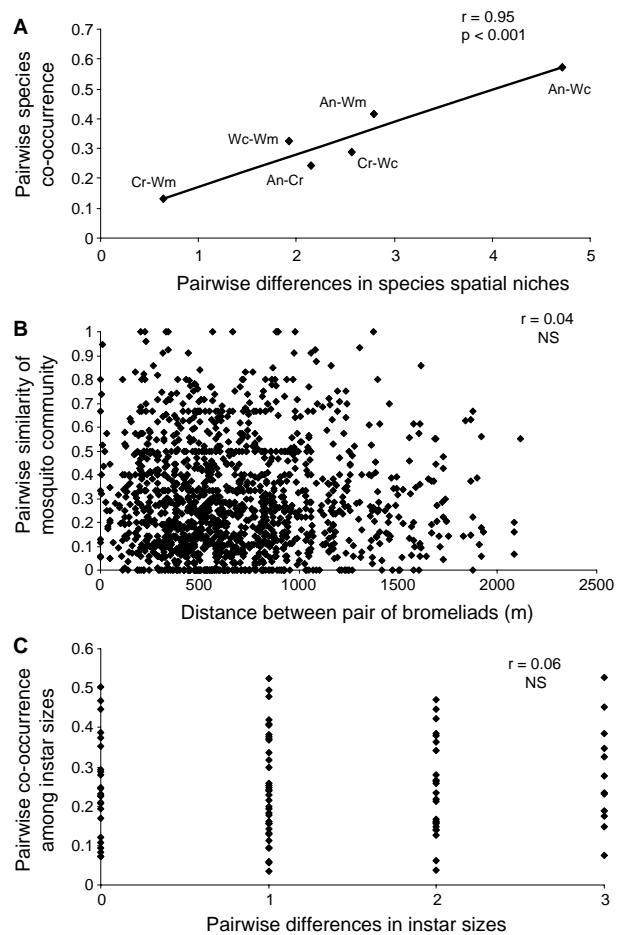


Fig. 3. Tests of the spatial niche hypothesis (A) and two neutral hypotheses (B) and (C). (A) the relationship was significant between species' pairwise difference in spatial niches (vertical distributions) and their pairwise co-occurrence. Species with different niches score high on the x-axis, and frequently co-occurring species score high on the y-axis. Abbreviations for both species in a species pair are labelled with the genus (first letter) and species (second letter). (B) and (C) both tests of neutral hypotheses were not significant (NS, $p > 0.05$).

2003). Spatial partitioning among species has been proposed as a mechanism that limits interference and potentially resource competition and thus facilitates species coexistence (Yee et al. 2004). The strong correlation between species co-occurrence patterns and overlap in spatial niches supports this hypothesis, and suggests not only that the abundance of each species is affected by the abundance of other species in a bromeliad, but that the strengths of interspecific interactions are determined by species' spatial niches. It has been hypothesized that coexistence among species in many communities is determined by one or two important niche axes (Chase and Leibold 2003). The wide applicability of spatial niche partitioning, not only for mosquitoes but across taxa (MacArthur 1958), suggests that this mechanism may be an important and common stabilizing mechanism for species coexistence (Chesson 2000).

If within-bromeliad co-occurrence relies on differences in species' spatial niches, what causes these different niches?

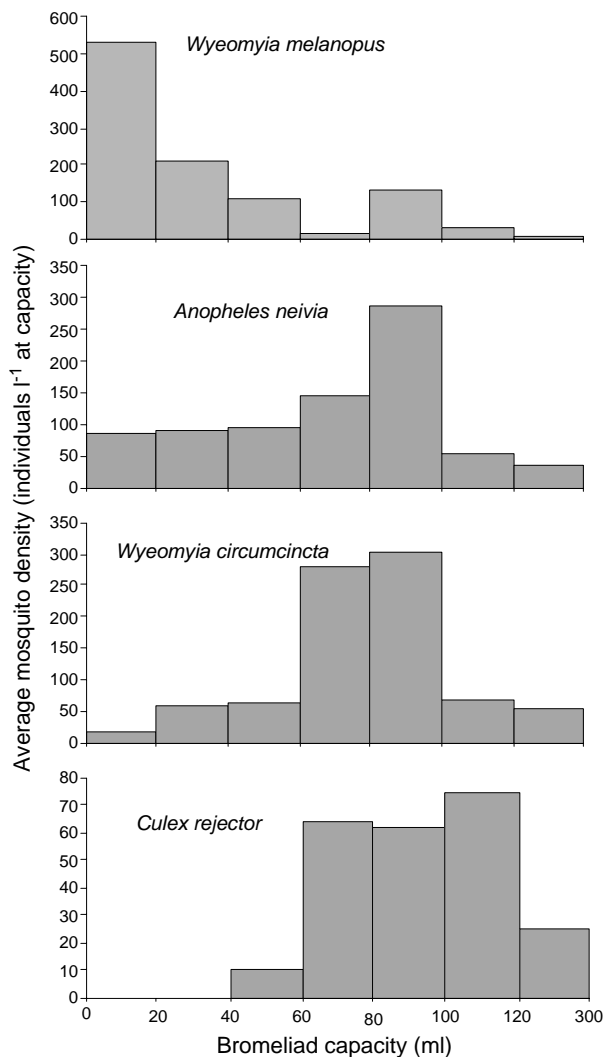


Fig. 4. Histograms of average species densities (individuals per litre of water holding capacity) along a gradient of bromeliad water holding capacities. Bromeliad water holding capacity explained approximately 36% of species densities ($p < 0.001$). Note that the last size category ranges from 120 to 300 ml, and the range of densities (y axis) differs among species.

In some cases the answer to this question is clear: species from the genus *Anopheles* lack respiratory siphons, and thus would be expected to occur more at the surface of the bromeliad. However, for the other species present there is no such limitation and yet even the two *Wyeomyia* species have different spatial niches. These different niches may have evolved from negative interspecific interactions or may instead be related to some other aspect of the biology of the individual species, as appears to be the case with *A. neivai*. However, the cause of these differences may be unimportant to the outcome of ecological interactions: if a difference in life-history traits decreases negative interactions among species, it increases the probability that those species will coexist stably (Chesson 2000). The strong relationship between spatial niche differences and co-occurrence (Fig. 3) suggest that this is indeed the case.

Species with overlapping spatial niches within bromeliads occur in bromeliads of different sizes, effectively

changing the scale at which niche partitioning occurs. For example, species with large microhabitat overlap (*W. melanopus* and *C. rejector*) occur in bromeliads at opposite ends of a size spectrum, while species with little microhabitat overlap (*W. circumcincta* and *A. neivai*) occupy similarly sized bromeliads (Fig. 4) and co-occur frequently (Fig. 3). These differences in occurrence can result from one of two mechanisms: differential survival rates or oviposition differences. Although much of the literature on niche partitioning tests differential survival among species (Costanzo et al. 2005), oviposition preferences can also determine mosquito distributions (Edgerly et al. 1998). For example, the larger scale of spatial partitioning (Fig. 4) is consistent with other species that cue oviposition choices to bromeliads of a certain size (Srivastava et al. 2005), and may be enhanced by females detecting competing species at the time of oviposition (Edgerly et al. 1998). Although our data could not test between these possibilities, patterns of species segregation were fairly consistent across instars, suggesting that much of the observed partitioning among differently sized bromeliads was in fact due to oviposition choice.

Selecting different bromeliad sizes likely represents a tradeoff for some of the species considered, with *C. rejector* (large bromeliads) and *W. melanopus* (small bromeliads) occurring in sub-optimal habitats. Small bromeliads are more likely to dry out (Srivastava unpubl.), which reduces mosquito survival (Juliano et al. 2002). On the other extreme, bromeliads with a water-holding capacity greater than 100 ml usually host the top odonate predator *Mecistogaster modesta* (Srivastava et al. 2005), which consumes mosquitoes (D. Srivastava and J. Ware, fecal dissections) and is likely to have a strong negative impact on mosquito densities (Fincke et al. 1997, Chase and Knight 2003). Neutral theory assumes that other trophic levels do not impact species distribution patterns, and further study would need to be undertaken to test this assumption directly. Nonetheless, from the data presented here we speculate that the effects of predators (*C. rejector*) and drought (*W. melanopus*) could impact competitive outcomes at different bromeliad sizes (Chase and Knight 2003, Costanzo et al. 2005), and may represent tradeoffs between resistance to stress-induced mortality (predation or drought) and competitive ability (Chase and Leibold 2003).

As with many studies that correlate pattern with process (Karst et al. 2005, Thompson and Townsend 2006), we did not experimentally test the effects of competition among species across the range of bromeliad sizes to ensure that the observed patterns match the predicted mechanism. Although such a test is beyond the scope of this study, we suggest that future research focus on the strength of interspecific competition amongst species with different spatial niches and how their competitive asymmetries change with bromeliad volume.

In summary, the bromeliad mosquito community studied shows local co-occurrence patterns that are consistent with spatial niche partitioning, and these patterns scale up to environmental segregation among species. Although partitioning at the local and among-bromeliad scale is related to species richness and species turnover respectively, competitive interactions among species are consistent with the partitioning at both scales. Further

studies should test the underlying mechanism of spatial niche partitioning and its generality in other mosquito communities.

Acknowledgements – Thanks to Jackie Ngai, Jonathan Shurin, Brian Starzomski, Kurtis Trzcinski and Katsky Venter for suggestions on earlier drafts, and to Ross Conner and Aimée Pelletier for field help and discussions. Personnel of the Area de Conservación Guanacaste provided logistical support, particular thanks to Róger Blanco, María Marta Chavarria, Calixto Moraga and Petrona Rios. L.G. Chaverri and INBio provided invaluable assistance with larval identification and sampling advice. NSERC provided personal funding (B. Gilbert) and research funding (D. Srivastava). All experiments and sampling for this research comply with the laws of Costa Rica.

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