



Lizard habitat partitioning on islands: the interaction of local and landscape scales

Lauren B. Buckley* and Joan Roughgarden

Department of Biological Sciences, Stanford University, Stanford, CA, USA

ABSTRACT

Aim This study addresses how species resolve environmental differences into biological habitats at multiple, interacting spatial scales. How do patterns of local habitat use change along an elevation gradient? How do patterns of local habitat partitioning interact with partitioning at a landscape scale?

Location Northern and southern Lesser Antilles islands, West Indies.

Methods We document how *Anolis* Daudin, 1802 lizards partition habitat locally at sites along a landscape-scale elevation gradient. We examine habitat partitioning both with and without interspecific interactions in the predominately flat northern Lesser Antilles islands and in the more mountainous southern islands.

Results Anoles partition local habitat along perch-height and microclimate axes. Northern-group sympatric anoles partition local habitat by perch height and have overlapping distributions at the landscape scale. Southern-group sympatric anoles partition local habitat by microclimate and specialize in particular habitats at the landscape scale. In both the northern and southern groups, species use different perch heights and microclimates only in areas of species overlap along the elevation gradient.

Main conclusions We demonstrate the interaction between local- and landscape-scale habitat partitioning. In the case of microclimate partitioning, the interaction results from the use of thermal physiology to partition habitat at multiple scales. This interaction prompts the question of whether habitat partitioning developed 'local-out' or 'landscape-in'. We pose this dichotomy and present a framework for its resolution.

Keywords

Altitudinal gradient, *Anolis*, environmental gradient, habitat partitioning, Lesser Antilles, landscape scale, lizard, local scale, microclimate, thermal physiology.

*Correspondence: Lauren B. Buckley, Department of Biological Sciences, Stanford University, 371 Serra Mall, Stanford, CA 94305, USA.
E-mail: lbuckley@stanford.edu

INTRODUCTION

Species resolve environmental differences into biological habitats at multiple, interacting spatial scales (Case *et al.*, 2005; Holt *et al.*, 2005; Parmesan *et al.*, 2005; Rahbek, 2005). The influences of climate, habitat complexity, topography, and resources on habitat partitioning vary spatially (Gaston, 2003), and species distribution patterns change with spatial resolution in response to these variables (Kotliar & Wiens, 1990). Mechanisms of local habitat partitioning along niche axes are well documented (Gurevitch *et al.*, 1992); however, few studies have examined local habitat partitioning from a landscape-scale perspective. We evaluate how patterns of

local habitat partitioning shift along an elevation gradient. We then introduce a framework for considering the interaction between habitat partitioning at local and landscape scales.

We consider three spatial scales: 'local', the scale of within-habitat partitioning; 'landscape', the scale of partitioning along a habitat gradient; and 'regional', the scale at which extinction and speciation rates and geographic dispersal determine regional species pools (Ricklefs & Schluter, 1993; Willis & Whittaker, 2002). Scales of local and landscape habitat partitioning vary by species (Kotliar & Wiens, 1990). We define the local scale to encompass adult home ranges. The landscape scale encompasses inter-generational movement,

such as juvenile dispersal along the elevation gradient. Regional processes may predispose species to partition along particular resource axes, and result in differences in local and landscape habitat partitioning between islands (Ricklefs & Schluter, 1993).

In order for an environmental variable to influence habitat partitioning at multiple spatial scales, the variable must vary sufficiently (often in patches) within a local site, while also varying in a systematic manner along a spatial gradient. Environmental variables that vary in this manner and influence both local and landscape habitat partitioning include temperature, precipitation, habitat complexity, exposure to disturbance, and nutrients. For example, the warmest microclimates within a site may be warmer than the coolest microclimates in sites at a substantially lower elevation, leading to overlapping ranges of thermal microhabitats between elevations. Complex interactions between microclimate partitioning at local and landscape scales may result.

To examine the interaction of local- and landscape-scale habitat partitioning among communities of *Anolis* Daudin, 1802 on the Lesser Antilles islands, we compare habitat use by solitary anole species to habitat use on two-species islands. On the two-species islands, size-dimorphic species pairs compete for resources as the result of overlapping insectivorous diets (Schoener, 1970; Rummel & Roughgarden, 1985). Solitary anoles are of intermediate size (Schoener, 1970). While the northern Lesser Antilles islands are predominately low elevation with steep mountains in the centre of the island, the southern islands tend to be more uniformly mountainous (Roughgarden, 1995). This enables us to address how abundance patterns are influenced by how evenly area is distributed into elevation classes. Hence, we are able to isolate the influence of species interactions and topography on habitat partitioning. Observations of habitat partitioning are facilitated by high anole abundance and territorial sit-and-wait insect predation (Roughgarden, 1995).

At the landscape scale, a greater degree of broad-scale habitat partitioning occurs in the southern islands (Roughgarden *et al.*, 1983a). On the northern sympatric study island, both species are present in approximately equal abundance at low elevation. However, on the southern sympatric study island, species are spatially patchily distributed at low elevation (Buckley & Roughgarden, 2005). Adaptation of the smaller southern species to warmer conditions enables specialization to low-elevation habitat (Buckley & Roughgarden, 2005) as well as to warmer microsites (Schoener & Gorman, 1968).

Lesser Antillean anoles partition local habitat along two recognized axes: microclimate (one species perching in a warmer microclimate than the other); and perch height (one species perching above the other in the vegetation; Schoener & Gorman, 1968). Perch-height separation acts primarily to divide territories rather than to partition prey (Roughgarden, 1995). These axes are independent. For example, higher perches tend to be both sunnier and more windy, eliminating

covariance between perch height and temperature (Roughgarden *et al.*, 1981). Southern-group anoles partition local habitat along a microclimate axis (Schoener & Gorman, 1968). Northern-group anoles do so along a perch-height axis (Roughgarden *et al.*, 1981, 1983a).

Previous studies have documented local-scale habitat partitioning at several randomly located sites (Schoener & Gorman, 1968; Roughgarden *et al.*, 1981). The question of whether patterns of local habitat partitioning change along the elevation gradient with shifts in landscape-scale factors has not been addressed. We systematically document local habitat partitioning by perch height and microclimate in sites along the elevation gradient, spanning the range from low-elevation coastal scrub to montane rain forest.

Optimal perch height may shift with elevation. For example, more complex forests at higher elevation may afford higher perch heights than low-elevation scrub. However, little morphological adaptation to the use of different perch heights has occurred in the Lesser Antilles (Knox *et al.*, 2001; Glor *et al.*, 2003). Mid-range perch heights tend to be energetically optimal as they afford both access to and a view of prey. Shifts in optimal microclimate are less likely, owing to constant thermal physiology (VanBerkum, 1986; Sultan & Spencer, 2002). We can detect shifts in optimal perch height and microclimate by documenting habitat use by solitary anole species along the elevation gradient. The paired one- and two-species islands chosen for observation in both the northern and southern islands are inhabited by anoles that are phylogenetically closely related (Poe, 2004).

How do patterns of local habitat partitioning vary along an elevation gradient? We hypothesize that interspecific differences in local habitat preferences will only occur when either (1) species overlap exists or (2) differential morphology or physiology leads to differential habitat preferences. In the case of perch-height partitioning on the northern sympatric island, morphological adaptation to the use of different perches is limited (Knox *et al.*, 2001; Glor *et al.*, 2003). Hence, we hypothesize that the smaller species will shift to an energetically optimal mid-range perch height, because this species becomes solitary with increasing elevation. In the case of microclimate partitioning on the southern sympatric island, we expect differential microclimate use in areas of species overlap. Whether the smaller, warm-adapted species continues to use warmer microclimates when alone in a site depends on whether doing so is energetically optimal. The smaller species may use warmer microclimates to partition habitat and enable coexistence in areas of species overlap, but may use cooler or a wider breadth of microclimates when solitarily occupying a site. Where the two species are patchily distributed at low elevation on the southern sympatric island (Buckley & Roughgarden, 2005), we can evaluate whether they use different microclimates when solitarily occupying a site. This enables us to ascertain whether the microclimate differences primarily act to enable species coexistence at a local or landscape scale.

METHODS

Site selection

Phylogenetic relatedness (Poe, 2004) and similar habitat use (Williams, 1972) enable a comparison of habitat use on the paired one- and two-species islands. The northern-group one- and two-species study islands are Montserrat and St Kitts, respectively. The southern-group one- and two-species study islands are St Lucia and Grenada, respectively. All study islands have comparable topographic reliefs (but different topographies), vegetation types, and areas (with the two-species islands being somewhat larger than their one-species counterparts). The relatively small difference in areas between the one- and two-species islands is not anticipated to influence the interaction between local and landscape habitat partitioning, because the topographic shapes of the islands remain constant. On St Kitts, the larger and smaller species are *A. bimaculatus* Sparrman, 1784 and *A. schwartzi* Lazell, 1972, respectively. The northern solitary species is *A. lividus* Garman, 1887 on Montserrat. On Grenada, the larger and smaller species are *A. richardi* Dumeril & Bibron, 1837 and *A. aeneus* Gray, 1840, respectively. The southern solitary species is *A. luciae* Garman, 1887 on St. Lucia.

Both windward and leeward elevation gradients were surveyed on each island. Sites were distributed along the gradients and chosen to contain representative habitat types, a low abundance of cultivated crop species, relatively undisturbed habitat with a minimum of edge effects, and canopies less than approximately 10 m high in order to facilitate anole observation. The influence of restricting canopy height to 10 m on perch-height partitioning should be negligible because all of the Lesser-Antilles anoles are considered trunk-ground ecomorphs and few are observed high on the trunks (Williams, 1972). Site elevations were measured by GPS and confirmed with topographic maps. Microclimate and perch-height measurements were taken for each individual observed while pacing an approximately 100-m transect during a 2-h period (Diaz, 1997). All anoles within 2 m of each side of the transect were recorded. If 100 m was travelled in less than 2 h, an additional transect was surveyed parallel to and approximately 5 m from the original transect. Observations were conducted from June to August in 2002 and 2003, which is within the wet season. We surveyed between the hours of 10:00 and 16:00 to maintain temperature and light-intensity distributions that are reasonably constant and adequate for microclimate partitioning. Day and time of observation were randomized with respect to site elevation. All surveys were conducted by the first author, while the distribution of available microclimate was simultaneously measured.

Perch-height and microclimate measurements

Perch heights of observed lizards were visually classified into one of the following categories: 0–1.5 ft; 1.5–3 ft; 3–6 ft; 6–12 ft; >12 ft. (Perch-height categories were chosen and are

reported in feet to correspond with previous studies.) The following microclimate measurements were taken as close to the perch location as feasible: air temperature (Extech type K thermal couple, 0.1 °C resolution, ± 0.3 °C $\pm 0.05\%$ of reading accuracy), humidity (Extech 3-in-1 meter, 0.1 RH resolution, $\pm 4\%$ RH accuracy), wind speed (Extech 3-in-1 meter, 0.1 m s⁻¹ resolution, ± 0.1 m s⁻¹ $\pm 3\%$ of reading accuracy), and light intensity (Omega HHLM-1 light meter, 0.01-lux resolution, $\pm 3\%$ accuracy). Measurements for the high perches were taken at the highest similar perch location that it was feasible to climb to. Microclimate measurements and species mass (assuming an intermediate mass of 10 g; Schoener, 1970) were used to calculate the grey-body temperature index (*GBTI*), the equilibrium body temperature of a lizard at a perch location (method detailed by Roughgarden *et al.*, 1981). We independently measured grey-body temperature (*GBT*) by allowing a solid metal object of approximately the same size and shape as a lizard to come to equilibrium at the perch location. We only report results for *GBTI*, as the *GBT* results correspond well with those derived using *GBTI*.

We assessed the distribution of available site microclimates by locating a 12 × 12 m grid in a random direction from the transect starting point at each site. Microclimate measurements were recorded at 4-m intervals at a height of 3 m. The scale of the grid was chosen because microclimate variation tends to occur at a scale of less than a metre to several metres and is associated with variation in canopy cover. The spatial pattern of variation in the grid confirmed the occurrence of small-scale microclimate variation. *GBT* was measured at heights of 1 ft, 3 ft, and 6 ft at each grid point. We examine microclimate partitioning by plotting histograms of the delta grey-body temperature index, $\Delta GBTI$. Each observation in the $\Delta GBTI$ plot is the difference between the *GBTI* of an observed anole and the mean available *GBTI* of the site.

Statistical analysis

Microclimate observations were designated 'low-elevation' (<300 m) and 'high-elevation' (≥ 300 m). Microclimate differences were tested using two-tailed *t*-tests to compare means and one-tailed *t*-tests to test for microclimate selection. Welch's approximate *t*-tests were used to accommodate unequal variances. *F*-tests were used to compare variances in $\Delta GBTI$.

Perch-height trends were analysed by partitioning observations into elevation classes: 0–30 m, 30–150 m, 150–300 m, 300–450 m, and 450–750 m. These classes roughly correspond to empirically observed habitat types. A two-tailed *t*-test was performed to test differences in the mean perch height for each elevation class. *P*-values were adjusted to account for multiple comparisons using the Hochberg (1988) and Hommel (1988) methods. Analyses of variance were used to evaluate the influence of species and elevation class on perch height. We report ANOVA results derived by dividing the perch-height observations into discrete elevation classes. Considering elevation as a continuous variable yielded the same results. This

enabled greater statistical power given the small sample sizes in the higher-elevation classes. Effect sizes are indicated for significant effects by η^2 , the ratio of effect sum of squares to total sum of squares. All analyses were performed using R (R Foundation for Statistical Computing).

RESULTS

Microclimate partitioning

A comparison of the ranges of available and utilized microclimates as a function of elevation reveals microclimate selection (Fig. 1). The ranges indicate that microclimate choices at local and landscape scales interact, because the warmest microclimates within a site may be warmer than the coolest microclimates in sites at a substantially lower elevation. We examine microclimate partitioning by plotting histograms of $\Delta GBTI$, the difference between the GBTI of an observed anole and the mean available GBTI of a site (Fig. 2). Non-random habitat selection with respect to temperature was observed for all species on all islands. Lizards chose significantly warmer than average microsites. $\Delta GBTI$ is significantly greater than zero at $P < 0.05$ for both high and low elevations on all islands (adjusted t -test).

In the northern island of St Kitts, the mean microclimates utilized by *A. schwartzi* and *A. bimaculatus* are statistically

indistinguishable in the low-elevation (<300 m) sites (mean $\Delta GBTI = 0.69$ and 0.82 , respectively; $t_{0.05[83]} = -0.7$; $P = 0.48$; Fig. 2a). The difference between perch microclimate and the mean available microclimate is greater for *A. schwartzi* at high elevations (≥ 300 m), where it is solitary, than it is at low elevations (<300 m) ($t_{0.05[214]} = -10.7$; $P < 0.001$). Three *A. bimaculatus* individuals observed in sites above 300 m were not included in the analysis because of the low sample size.

In the southern island of Grenada, the mean microclimates utilized by *A. aeneus* and *A. richardi* are statistically indistinguishable in the low-elevation (<300 m) sites (mean $\Delta GBTI = 1.1$ and 0.89 , respectively; $t_{0.05[34]} = 0.91$; $P = 0.37$; Fig. 2b). However, in the high-elevation (>300 m) sites, *A. aeneus* perches in significantly warmer microclimates than does *A. richardi* (mean $\Delta GBTI = 0.97$ and 0.37 , respectively; $t_{0.05[29]} = -10.7$; $P < 0.006$). The smaller southern species, *A. aeneus*, maintains a constant difference between perch microclimate and mean available microclimate across the elevation gradient. This difference for *A. aeneus* is statistically indistinguishable between the higher- and lower-elevation classes ($t_{0.05[39]} = 0.51$; $P = 0.61$). In contrast, the larger species, *A. richardi*, perches in relatively cooler microsites at higher elevation. Individuals of *A. richardi* at high elevations (<300 m) perch in microclimates closer to the mean environmental temperature than individuals at low elevations (≥ 300 m) ($t_{0.05[91]} = 3.61$; $P < 0.001$).

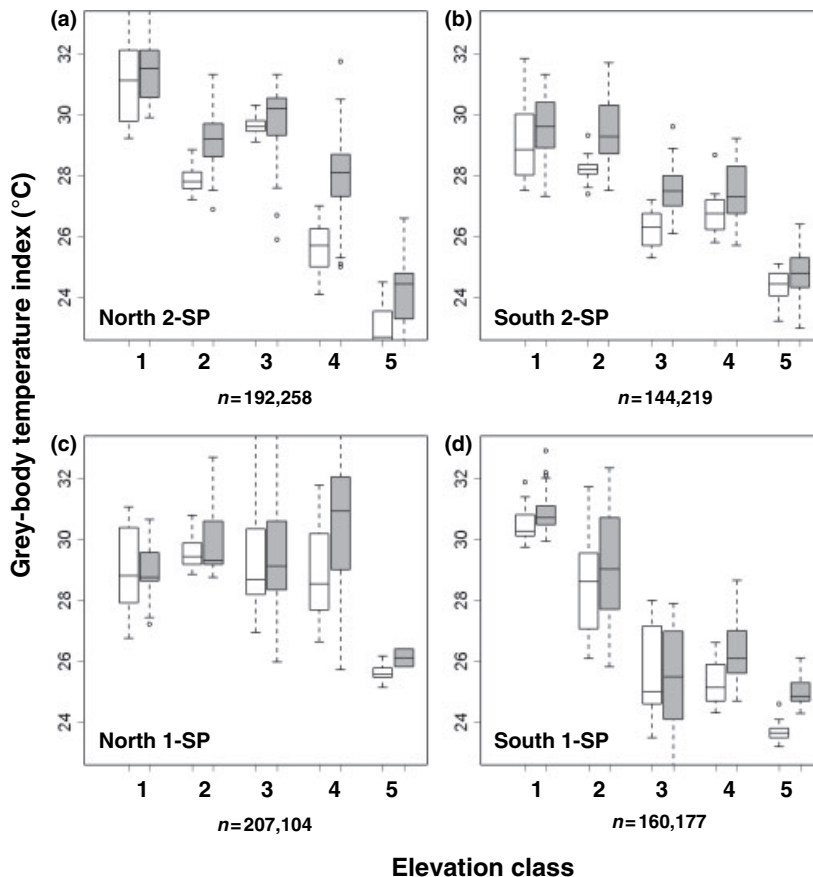
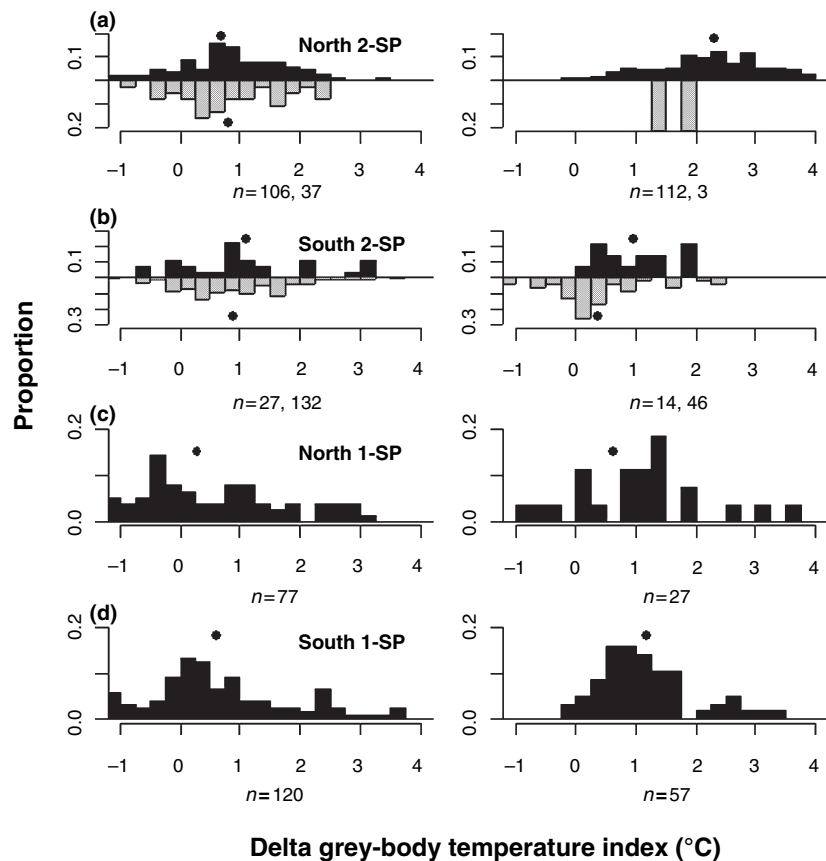


Figure 1 Box plots of the grey-body temperature index (*GBTI*, °C) of random grid points (null microclimate, white bars) and lizard perch locations (grey bars) as a function of elevation class (1–5: 0–30 m, 30–150 m, 150–300 m, 300–450 m, 450–750 m). Temperature trends are depicted for (a) St Kitts (north two-species), (b) Grenada (south two-species), (c) Montserrat (north one-species), and (d) St Lucia (south one-species). The n indicates the number of null microclimate measurements and lizard microclimate measurements, respectively. Lizards perch in warmer-than-average microhabitats, and the available microclimates overlap along the elevation gradient.

Figure 2 Density histograms of the delta grey-body temperature index (Δ_{GBTI} , °C), the difference between the microclimate temperature of each anole and the null microclimate temperature. The left and right columns present data from low-elevation (<300 m) and high-elevation (≥ 300 m) sites, respectively. The Δ_{GBTI} is depicted for (a) St Kitts (north two-species), (b) Grenada (south two-species), (c) Montserrat (north one-species), and (d) St Lucia (south one-species). Bars for the smaller species extend upwards, while those for the larger species extend downwards. The n indicates the number of microclimate measurements for the smaller and larger species, respectively. The asterisks indicate the mean Δ_{GBTI} . Microclimate partitioning is restricted to higher-elevation areas of species overlap in Grenada. Microclimate use is more variable on the one-species islands.



Both northern and southern solitary species perch in variable microclimates (Fig. 2c,d). Variance in the Δ_{GBTI} of northern solitary anoles is significantly greater than the variances of both the smaller and larger northern sympatric species at both low- and high-elevation sites ($P < 0.05$, F -test). Δ_{GBTI} variance for the southern solitary anoles is only significantly greater than that for *A. richardi* at low elevation ($P < 0.01$, F -test).

Perch-height partitioning

In the northern island of St Kitts, species perch at different heights in areas of species overlap (Fig. 3a). *Anolis bimaculatus* perches at intermediate heights throughout its elevation range. The abundance of *A. bimaculatus* steadily declines with increasing elevation (Buckley & Roughgarden, 2005). As the abundance of *A. bimaculatus* declines, the height at which *A. schwartzi* perches increases to an intermediate height. An ANCOVA explaining perch height as linear functions of elevation class, species, and their interaction is highly significant ($F_{[8,705]} = 12.66$; $P < 0.001$). Both elevation class ($F_{[4,705]} = 4.64$; $P < 0.001$) and species identity ($F_{[1,705]} = 80.95$; $P < 0.001$) significantly influence perch height, but the interaction of the two factors is not significant ($F_{[3,705]} = 0.6$; $P = 0.62$). Both elevation class ($\eta^2 = 0.02$) and species ($\eta^2 = 0.10$) have a relatively small effect on perch height. When examining the elevation trend for *A. schwartzi* alone, perch height significantly increases with

increasing elevation ($F_{[1,596]} = 51.19$; $P < 0.001$). The mean perch height of *A. schwartzi* is significantly lower than the mean perch height of *A. bimaculatus* for every elevation class in which the latter species is present ($t_{0.05[165]} = -7.53$, $P < 0.001$; $t_{0.05[36]} = -3.90$, $P < 0.001$; $t_{0.05[6.7]} = -2.84$, $P < 0.03$; $t_{0.05[2.15]} = -5.30$, $P < 0.03$, for elevation classes 1–4, respectively; adjusted t -tests).

In the southern island of Grenada, species perch at a similar height throughout the elevation classes (Fig. 3b). In the lowest-elevation class (<30 m), where scrubby vegetation may provide few high perches, both species perch close to the ground. Both species perch at intermediate heights at higher elevations. An ANCOVA explaining perch height as linear functions of elevation class, species, and their interaction is highly significant ($F_{[9,529]} = 10.87$; $P < 0.001$). While elevation class is a significant determinant of perch height ($F_{[4,529]} = 23.76$; $P < 0.001$), neither species identity ($F_{[1,529]} = 1.06$; $P = 0.30$) nor the species \times elevation interaction ($F_{[4,529]} = 0.44$; $P = 0.78$) has a significant influence. Elevation class ($\eta^2 = 0.15$) has a relatively small effect on perch height. The mean perch heights in each elevation class are statistically indistinguishable between the sympatric anoles (adjusted t -test).

We next look for elevation trends in the perch heights of solitary anoles, which would indicate shifts in optimal perch height. Anoles on the northern one-species island, Montserrat, do not perch in significantly higher perches with increasing

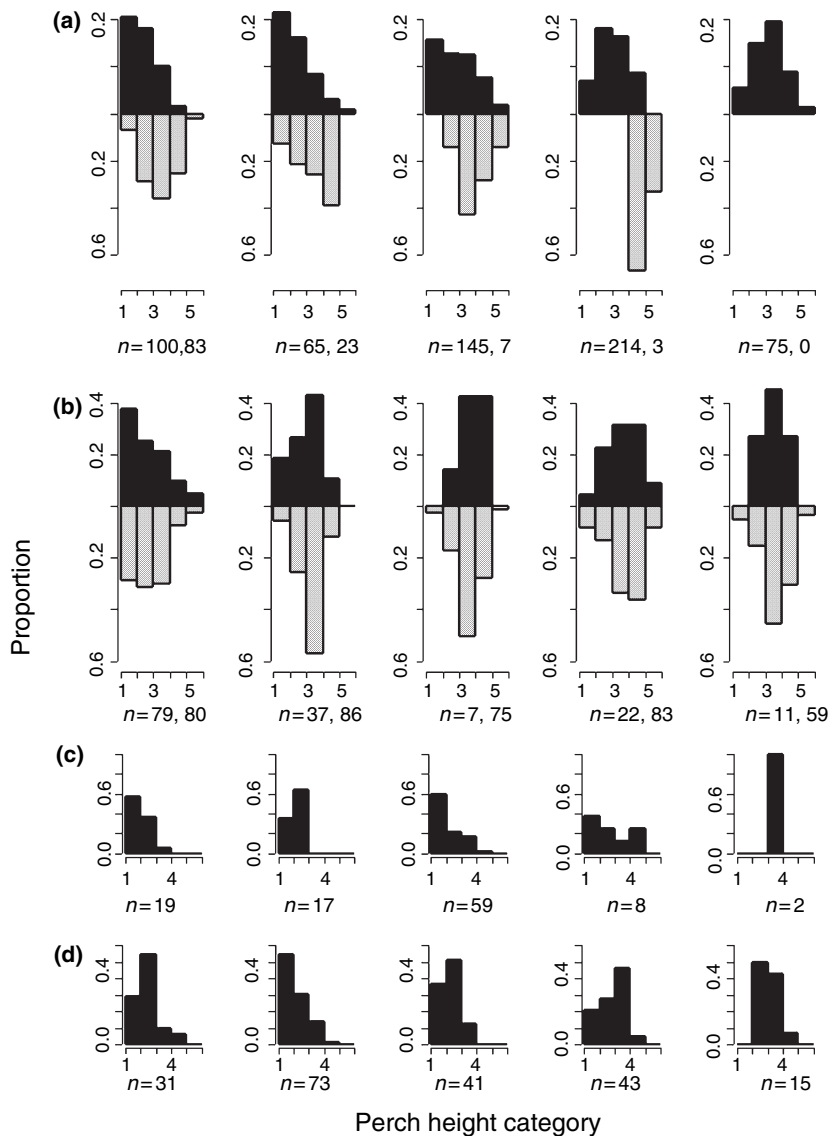


Figure 3 Density histograms of perch-height distributions for elevation classes (increasing left to right: 0–30 m, 30–150 m, 150–300 m, 300–450 m, 450–750 m) on (a) St Kitts (north two-species), (b) Grenada (south two-species), (c) Montserrat (north one-species), and (d) St Lucia (south one-species). The histograms indicate perch-height classes (1–5: 0–1.5 ft, 1.5–3 ft, 3–6 ft, 6–12 ft, and >12 ft). Bars for the smaller species extend upwards, while those for the larger species extend downwards. The *n* indicates the number of microclimate measurements for the smaller and larger species, respectively. Perch-height partitioning is restricted to areas of species overlap on the northern two-species island.

elevation ($F_{[4,100]} = 1.90$; $P = 0.12$; ANOVA; Fig. 3c). Those in the southern St Lucia do perch in higher perches with increasing elevation, and the magnitude of the elevation effect is similar to that on Grenada ($\eta^2 = 0.16$; $F_{[4,197]} = 9.19$; $P < 0.0001$; ANOVA; Fig. 3d).

DISCUSSION

Interaction of local and landscape scales

We demonstrate an interaction between local and landscape habitat partitioning along the elevation gradient. Shifts in both microclimate and perch-height use correspond to changes in relative species abundance at the landscape scale. Hence, considering the broader-scale context of local patterns of habitat use is important for understanding community assembly.

In the case of microclimate choice, interspecific differences in thermal physiology exist on the southern sympatric

island. However, the smaller, warm-adapted species only uses significantly warmer microclimates in high-elevation regions of species overlap (Schoener & Gorman, 1968; Buckley & Roughgarden, 2005). The species do not use distinct microclimates when solitarily occupying low-elevation sites, where the species are patchily distributed (Buckley & Roughgarden, 2005). Previous studies have consistently observed differential microclimate selection, as they were conducted in sites with both species present (Schoener & Gorman, 1968; Roughgarden *et al.*, 1981). What is the ecological significance of differential microhabitat use by sympatric southern species? The observation that intraspecific differences in microclimate use are restricted to areas containing both species provides only circumstantial evidence of competition. Adaptation of the smaller southern species to warmer conditions may or may not have resulted from past competition.

In the absence of different thermal physiologies, northern species partition local habitat along an additional spatial axis, namely perch height. The smaller species perches below the

larger species when both are abundant at low elevation. The smaller species shifts to perching higher as the abundance of the larger species declines along the landscape-scale elevation gradient. What is the ecological significance of this differential perch-height use by sympatric species? Little morphological adaptation to the use of different perch heights has occurred in the Lesser Antilles (Knox *et al.*, 2001; Glor *et al.*, 2003). All Lesser Antilles anoles are classified as trunk-ground 'ecomorphs' (classifications developed for the Greater Antilles; Williams, 1972). Hence, we would expect all species to prefer a similar mid-range perch height. Mid-range perch height is energetically optimal, as it enables both perspective and accessibility to ground insects, the primary prey (Roughgarden, 1995). The observation that intraspecific differences in perch-height use are restricted to areas containing both species provides only circumstantial evidence of competition. Field experiments are necessary to confirm competition, and have done so on two-species islands elsewhere in the Lesser Antilles (Pacala & Roughgarden, 1982, 1985; Roughgarden *et al.*, 1983b; but see also Rummel & Roughgarden, 1985).

Local-out or landscape-in?

How did the interaction between habitat partitioning at multiple scales develop? If differences in microclimate use between the southern sympatric species enable coexistence, did they initially do so at the local or landscape scale? One hypothesis for the interaction of habitat partitioning at local and landscape scales, which we term 'local-out', is that species will partition habitat along local axes within a site (α diversity) before spilling into adjacent habitats (β diversity). Under the alternative 'landscape-in' hypothesis, species spread out across a landscape (β diversity) and then partition within habitats to enable local coexistence (α diversity).

In the case of local-out habitat partitioning, all species will colonize the same region of optimal habitat. Alternatively, each species may colonize all available habitat, such as a small island. Only those colonizers that are able to coexist spatially with or displace existing occupants will be able to persist. As a community nears species saturation, the specialized traits that enable coexistence may enable species to spill out into adjacent habitat. Alternatively, species may spatially partition the space in which they formerly coexisted. Williams' (1972) hypotheses for community assembly on speciose islands in the Greater Antilles are consistent with local-out partitioning. He suggested that anole faunal buildup results when overlapping species use morphological and physiological differences to partition habitat.

In the case of landscape-in habitat partitioning, species are initially spread out along an environmental gradient. This spatial pattern results when an arriving species either colonizes empty habitat or causes range contraction of an existing species. Species may then specialize to their position along the gradient. Once they use habitat in a distinct manner from the adjacent species, range expansion can

result in species overlap. Diamond's (1973) hypotheses for community assembly among New Guinea birds are consistent with landscape-in habitat partitioning. He suggested that species at different elevations develop canopy-height specialization, which subsequently enables range expansion and local spatial coexistence.

What factors would favour one spatial community assembly model over the other? Initial colonization patterns, dispersal costs, and spatial patterns of carrying capacities combine to determine how community assembly occurs (Kirkpatrick & Barton, 1997; Case & Taper, 2000). If colonization is dispersed among random sites, species may develop overlapping distributions landscape-in from the sites of initial colonization. If colonization occurs in a common site and dispersal is costly, species may coexist and then spill out to adjacent sites from the region of initial colonization (i.e. local-out). The proximity of distinct habitat types (e.g. ecotones) may favour landscape-in habitat partitioning. Local-out habitat partitioning may be favoured when there are universal differences in habitat suitability.

What factors determined whether the thermal differences (through species sorting or coevolution) first enabled coexistence at the local or landscape scale on the southern island? Previous research has demonstrated that thermal adaptation may be selected for at either local (Freidenburg & Skelly, 2004) or landscape (Miller & Packard, 1977; Huey & Kingsolver, 1993; Gilchrist, 1995) scale (but see Huey *et al.*, 2003). In the Lesser Antilles, dispersal costs are probably relatively low between habitats on an island. Grenada's abundance of both low- and high-elevation habitat may have enabled thermal specialization along the landscape-scale gradient (Roughgarden *et al.*, 1983a), and ultimately landscape-in habitat partitioning. Spatially patchy abundance distributions at low elevation suggest spatial variation in competition. The smaller, warm-adapted species may have been able either to colonize unoccupied warm, low-elevation sites or to displace the cooler-adapted larger species, which may have been restricted to using the cooler microclimates within a site. The smaller species is only present at substantial abundances at low elevation. If local-out habitat partitioning occurred, the initial area of species overlap was probably at low elevation. However, differential microclimate use is not observed at low elevation. The absence of microclimate partitioning and patchy abundance distributions at low elevation lead us to speculate that coexistence developed landscape-in on the southern sympatric islands.

The observed interaction between habitat partitioning at local and landscape scales calls for further theoretical and empirical evaluation of whether habitat partitioning predominantly evolves local-out or landscape-in. Spatially explicit modelling examining how the ability to coexist and disperse influences community assembly is required in order to better understand the processes consistent with local-out and landscape-in habitat partitioning. Time series of spatial habitat data or a phylogeny may also resolve the local-out or landscape-in dichotomy. More broadly, considering how species resolve

environmental differences into habitats at multiple spatial scales is important to an understanding of how communities assemble.

ACKNOWLEDGEMENTS

This research was supported by a NSF Predoctoral Grant to LBB, the National Geographic Society Committee for Research and Exploration, and the Center for Evolutionary Studies and Field Studies Program at Stanford University. J. Eldon, H. Fienberg, E. Silva, and M. Thomas provided field assistance. P. Armsworth, L.J. Buckley, W. Cornwell, M. Frederickson, S. Lawler, R. Pringle, T. Root, and two anonymous referees provided helpful comments.

REFERENCES

- Buckley, L. B. & Roughgarden, J. (2005) Effect of species interactions on landscape abundance patterns. *Journal of Animal Ecology*, in press.
- Case, T. J. & Taper, M. L. (2000) Interspecific competition, environmental gradients, gene flow, and the coevolution of species' borders. *The American Naturalist*, **155**, 583–605.
- Case, T. J., Holt, R. D., McPeck, M. A. & Keitt, T. H. (2005) The community context of species' borders: ecological and evolutionary perspectives. *Oikos*, **108**, 28–46.
- Diamond, J. M. (1973) Distributional ecology of New Guinea birds. *Science*, **179**, 759–769.
- Diaz, J. A. (1997) Ecological correlates of the thermal quality of an ectotherm's habitat: a comparison between two temperate lizard populations. *Functional Ecology*, **11**, 79–89.
- Freidenburg, L. K. & Skelly, D. K. (2004) Microgeographical variation in thermal preference by an amphibian. *Ecology Letters*, **7**, 369–373.
- Gaston, K. J. (2003). *The structure and dynamics of geographic ranges*. Oxford University Press, Oxford.
- Gilchrist, G. W. (1995) Specialists and generalists in changing environments: fitness landscapes of thermal sensitivity. *The American Naturalist*, **146**, 252–270.
- Glor, R. E., Kolbe, J. J., Powell, R., Larson, A. & Losos, J. B. (2003) Phylogenetic analysis of ecological and morphological diversification in Hispaniolan trunk-ground anoles (*Anolis cybotes* group). *Evolution*, **57**, 2383–2397.
- Gurevitch, J., Morrow, L. L., Wallace, A. & Walsh, J. S. (1992) A metaanalysis of competition in field experiments. *The American Naturalist*, **140**, 539–572.
- Hochberg, Y. (1988) A sharper Bonferroni procedure for multiple tests of significance. *Biometrika*, **75**, 800–803.
- Holt, R. D., Keitt, T. H., Lewis, M. A., Maurer, B. A. & Taper, M. L. (2005) Theoretical models of species' borders: single species approaches. *Oikos*, **108**, 18–27.
- Hommel, G. (1988) A stagewise rejective multiple test procedure based on a modified Bonferroni test. *Biometrika*, **75**, 383–386.
- Huey, R. B. & Kingsolver, J. G. (1993) Evolution of resistance to high-temperature in ectotherms. *The American Naturalist*, **142**, S21–S46.
- Huey, R. B., Hertz, P. E. & Sinervo, B. (2003) Behavioral drive versus behavioral inertia in evolution: a null model approach. *The American Naturalist*, **161**, 357–366.
- Kirkpatrick, M. & Barton, N. H. (1997) Evolution of a species' range. *The American Naturalist*, **150**, 1–23.
- Knox, A. K., Losos, J. B. & Schneider, C. J. (2001) Adaptive radiation versus intraspecific differentiation: morphological variation in Caribbean *Anolis* lizards. *Journal of Evolutionary Biology*, **14**, 904–909.
- Kotliar, N. B. & Wiens, J. A. (1990) Multiple scales of patchiness and patch structure: a hierarchical framework for the study of heterogeneity. *Oikos*, **59**, 253–260.
- Miller, K. & Packard, G. C. (1977) An altitudinal cline in critical thermal maxima of chorus frogs *Pseudacris triseriata*. *The American Naturalist*, **111**, 267–277.
- Pacala, S. W. & Roughgarden, J. (1982) Resource partitioning and interspecific competition in two two-species insular *Anolis* lizard communities. *Science*, **217**, 444–446.
- Pacala, S. W. & Roughgarden, J. (1985) Population experiments with the *Anolis* lizards of St. Maarten and St. Eustatius. *Ecology*, **66**, 129–141.
- Parmesan, C., Gaines, S., Gonzalez, L., Kaufman, D. M., Kingsolver, J., Peterson, A. T. & Sagarin, R. (2005) Empirical perspectives on species borders: from traditional biogeography to global change. *Oikos*, **108**, 58–75.
- Poe, S. (2004) Phylogeny of anoles. *Herpetological Monographs*, **18**, 37–89.
- Rahbek, C. (2005) The role of spatial scale and the perception of large-scale species-richness patterns. *Ecology Letters*, **8**, 224–239.
- Ricklefs, R. E. & Schluter, D. (eds) (1993) Species diversity: regional and historical influences. *Species diversity in ecological communities*, pp. 350–364. University of Chicago Press, Chicago.
- Roughgarden, J. (1995). *Anolis lizards of the Caribbean*. Oxford University Press, Oxford.
- Roughgarden, J., Porter, W. & Heckel, D. (1981) Resource partitioning of space and its relationship to body-temperature in *Anolis* lizard populations. *Oecologia*, **50**, 256–264.
- Roughgarden, J., Heckel, D. & Fuentes, E. R. (1983a) Coevolutionary theory and the biogeography and community structure of *Anolis*. *Lizard ecology: studies of a model organism* (ed. by R. B. Huey, E. R. Pianka and T. W. Schoener), pp. 371–410. Harvard University Press, Cambridge.
- Roughgarden, J., Rummel, J. D. & Pacala, S. W. (1983b) Experimental evidence of strong present-day competition between the *Anolis* populations of the Anguilla Bank – a preliminary report. *Advances in herpetology and evolutionary biology – essays in honor of Ernest Williams* (ed. by A. Rhodin and K. Miyata), pp. 499–506. Museum of Comparative Zoology, Harvard University, Cambridge.

- Rummel, J. D. & Roughgarden, J. (1985) Effects of reduced perch-height separation on competition between two *Anolis* lizards. *Ecology*, **66**, 430–444.
- Schoener, T. W. (1970) Size patterns in West Indian *Anolis* lizards: correlations with sizes of particular sympatric species – displacement and convergence. *The American Naturalist*, **104**, 155–174.
- Schoener, T. W. & Gorman, G. C. (1968) Some niche differences in 3 Lesser Antillean lizards of genus *Anolis*. *Ecology*, **49**, 819–830.
- Sultan, S. E. & Spencer, H. G. (2002) Metapopulation structure favors plasticity over local adaptation. *The American Naturalist*, **160**, 271–283.
- VanBerkum, F. H. (1986) Evolutionary patterns of the thermal sensitivity of sprint speed in *Anolis* lizards. *Evolution*, **40**, 594–604.
- Williams, E. (1972) The origin of faunas. Evolution of lizard congeners in a complex fauna: a trial analysis. *Evolutionary Biology*, **6**, 47–88.
- Willis, K. J. & Whittaker, R. J. (2002) Species diversity – scale matters. *Science*, **295**, 1245–1248.

BIOSKETCHES

Lauren B. Buckley is a PhD Student in Ecology and Evolutionary Biology at Stanford University. Her dissertation couples bioenergetic models and field studies in order to understand how spatial distributions of Caribbean lizards form. Her research focuses on developing spatially explicit and process-based models of species distributions.

Joan Roughgarden is Professor of Biological Sciences and of Geophysics at Stanford University. She is a theoretical ecologist who has worked with *Anolis* lizards in the Caribbean and intertidal populations in California. Her most recent book, *Evolution's Rainbow*, received the Stonewall Prize for the best non-fiction work in 2004 from the American Library Association.

Editor: Bradford Hawkins