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Acknowledgements We thank I. Proctor and A. M. Kellerer for their essential support of this project. We also thank S. Fujita and K. Shizuma for providing copper samples for this study. We thank the following organizations for supporting this work: the US Department of Energy, the US National Academy of Sciences, the European Commission, the German Federal Ministry of Environment, Nature Conservation and Nuclear Safety.

Competing interests statement The authors declare that they have no competing financial interests.

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Niche lability in the evolution of a Caribbean lizard community

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Niche conservatism—the tendency for closely related species to be ecologically similar—is widespread^{1–3}. However, most studies compare closely related taxa that occur in allopatry³; in sympatry, the stabilizing forces that promote niche conservatism^{4,5}, and thus inhibit niche shifts, may be countered by natural selection favouring ecological divergence to minimize the intensity of interspecific interactions^{6,7}. Consequently, the relative importance of niche conservatism versus niche divergence in determining community structure has received little attention⁷. Here, we examine a tropical lizard community in which species have a long evolutionary history of ecological interaction. We find that evolutionary divergence overcomes niche conservatism: closely related species are no more ecologically similar than expected by

random divergence and some distantly related species are ecologically similar, leading to a community in which the relationship between ecological similarity and phylogenetic relatedness is very weak. Despite this lack of niche conservatism, the ecological structuring of the community has a phylogenetic component: niche complementarity only occurs among distantly related species, which suggests that the strength of ecological interactions among species may be related to phylogeny, but it is not necessarily the most closely related species that interact most strongly.

Anolis lizards are a dominant component of Caribbean ecosystems (reviewed in refs 8 and 9) and are well suited for studies of the evolution of community structure because the species on individual islands have a long history of interaction and coevolution. For example, 55 of 58 species on Cuba are endemic (the remaining three have colonized other Caribbean islands from Cuba), and most are members of large clades that have diversified on Cuba¹⁰. Species on many islands attain extremely high densities^{11,12}, and many species—differing in ecology, morphology, and behaviour—coexist locally⁸. Interactions among sympatric species can be strong^{8,9,13,14}, usually as a result of interspecific competition, although intra-guild predation may sometimes be important¹⁵.

We studied the community structure of anoles at Soroa, Biosphere Preserve Sierra del Rosario, in the Pinar del Río province of western Cuba. Eleven anole species occur sympatrically at Soroa, the highest anole diversity known from any island or continental site. Of these species, ten are either widely distributed in Cuba or are members of island-wide clades of ecologically similar species (for example, the *Anolis equestris* group, to which *A. luteogularis* belongs, occurs throughout Cuba and is composed of six primarily allopatric species similar in morphology and ecology). Because the clades of Cuban anoles to which the Soroa species belong are widespread and arose within a relatively short period in the distant past¹⁰ (Fig. 1), the sympatric clades at Soroa have probably coexisted for a long time and over a large spatial scale. Thus, these *Anolis* species probably evolved in the presence of the same clades with which they currently coexist, a necessary prerequisite for community coevolution.

We examined ecological relationships among these species to investigate whether the community exhibited nonrandom ecological or phylogenetic structure. We measured ecological variables relevant to the three resource axes that sympatric *Anolis* generally partition: structural habitat, thermal habitat, and prey size¹⁶. Principal components analysis reveals three significant axes of ecological differentiation (Table 1; results below are qualitatively unchanged if another, nearly significant, axis is also retained). Examination of the position of species in multivariate ecological space reveals both that niche use has not been conserved and that the community is nonrandomly structured (Fig. 2).

The minimal extent of niche conservatism is indicated by the weak association between phylogenetic relationship and position in multivariate ecological space: phylogenetic similarity explains less than 4% of the variation in ecological similarity among species (Mantel test, $P = 0.11–0.30$ depending on phylogenetic topology and mode of character evolution used in the analysis; all variables but one exhibit similarly low correlations with phylogenetic relationships (Table 1); P -values in Mantel tests based on 5,000 simulations). The molecular data strongly reject alternative phylogenetic topologies in which ecologically similar species are grouped phylogenetically (see Supplementary Information).

Although some closely related species differ little ecologically, many distantly related species are just as ecologically similar, and some closely related species are ecologically dissimilar (Fig. 2). Moreover, although members of the *sagrei* and *porcatus* clades form clusters in ecological space (Fig. 2; multivariate analysis of variance, MANOVA, Wilks' $\lambda = 0.013$, $F_{12,10} = 3.79$, $P = 0.018$), they are no more ecologically similar than would be expected for

Table 1 Principal components analysis

Component loadings	Principal component axes				Variation explained by phylogenetic relationships*
	1	2	3	4	
Activity time	0.793	-0.111	0.286	0.256	0-3%†
Body temperature	0.688	0.151	0.400	0.455	0-12%†
Perch height	0.791	0.396	-0.294	-0.275	3-5%
Perch diameter	-0.204	0.900	0.298	-0.152	0-3%†
Use of rocks	-0.852	-0.069	0.049	0.455	2-5%
Snout-vent length	0.141	0.514	-0.715	0.442	12-42%
Diameter of surfaces used during locomotion	-0.310	0.893	0.214	0.012	3-10%†
Variance explained by components	1	2	3	4	
	2.612	2.069	0.977	0.773	
Percentage of total variance explained‡	1	2	3	4	
	37.3	29.6	14.0	11.0	
	(37.0)	(22.8)	(15.6)	(10.9)	

Activity time was the weighted average of eight evenly spaced categories (given values of 1-8) corresponding to the times of activity transects (for example, category 1 = 07:00-08:30, category 2 = 08:30-10:00). For perch height, perch diameter, diameter of substrates used during locomotion, and body temperature, mean values were used for each species. These variables, as well as snout-vent length, were natural-log-transformed before analysis. *Use of rocks* was the proportion of all animals observed on or within 1 m of a rocky surface and was arcsine square-root-transformed. Snout-vent length values for adult males were taken from ref. 27; when ranges were provided, the value closest to our measurements of specimens from Soroa was used.

†Proportion of similarity among species in these traits explained by phylogenetic similarity. Ranges indicate results using different phylogenetic topologies and branch lengths.

‡Negative correlations between trait and phylogenetic similarity.

‡Expected by chance according to Broken Stick model in parentheses; thus, axes 1, 2 and 4 are statistically significant.

clades of their age (phylogenetic simulations: *sagrei* clade, $P = 0.49-0.76$ (ranges represent results from analyses using different phylogenies, branch lengths and modes of character evolution); *porcatus* clade, $P = 0.60-0.80$; average for both clades, $P = 0.52-0.73$). Taken together, these results indicate that recently diverged species are ecologically similar, but their divergence is not constrained and thus niches are conserved no more than would be expected if they were diverging randomly. Moreover, the data indicate that ecologi-

cal divergence is occurring at a sufficiently rapid rate that only the ecological similarities among relatively closely related species have a significant component attributable to common ancestry; overall comparisons that include distantly related species reveal no correlation between phylogenetic relatedness and ecological similarity.

Nonrandom community structure is evident in the pattern of similarity of species along different ecological axes. The niche complementarity hypothesis¹⁶ predicts that species similar along one niche axis will differ along others. The positions of species along the three significant principal components (PC) axes indicate that niche complementarity occurs at Soroa (Table 2). For all three pairwise combinations of the three axes, the distance separating species in ecological space along one axis is negatively correlated with the corresponding distance along the second axis. The probability that all three pairwise correlations should have as strong a negative relationship as that observed is extremely low ($P \leq 0.002$; Table 2).

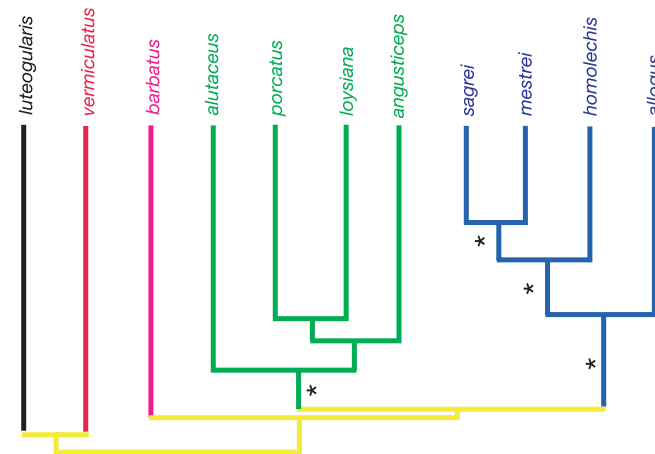


Figure 1 Phylogenetic relationships of the 11 anole species at Soroa. The phylogeny is a subset of a phylogeny for 129 species of anoles with non-Soroa species removed. Branch lengths are proportional to time since divergence (illustrated here is the maximum-likelihood tree with branch lengths fitted by non-parametric rate smoothing). Asterisks indicate clades that are strongly supported on both the maximum likelihood (>90% bootstrap support) and bayesian (100%) trees in analyses including the 11 Soroa species. The same nodes are recovered on the maximum parsimony tree, all but the *porcatus* clade (green) with high (>94% bootstrap) support. In addition, both the *porcatus* and the *sagrei* (blue) clades were originally described on the basis of morphological data. Maximum Tamura-Nei corrected distance observed between species is 0.31, which corresponds to a divergence time of approximately 24 Myr ago²⁸. This is in accordance with dates for anole divergence based on immunological differences²⁹ and fossil amber specimens³⁰. Of the Soroa species, all are endemic to Cuba except *A. sagrei*, which has colonized the Bahamas and a number of other islands in the western Caribbean, and all are either widespread or members of widespread clades of ecologically similar species except *A. vermiculatus*, which is only found in western Cuba.

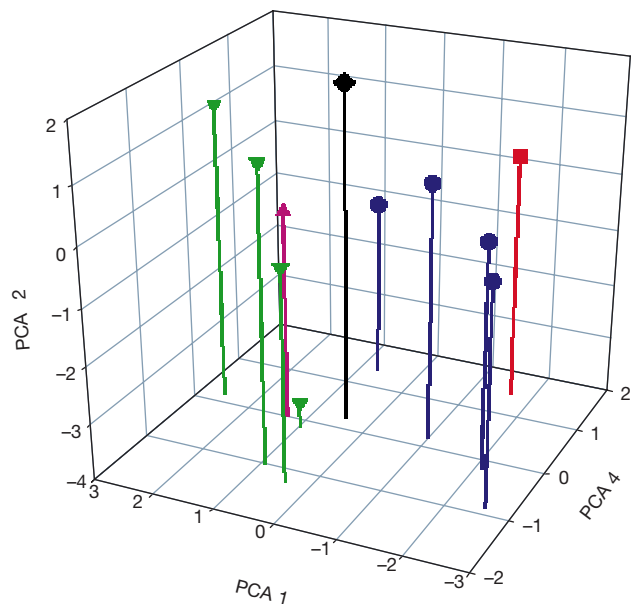


Figure 2 Dispersion of species in multivariate ecological space. Colours and symbols correspond to the five clades in Fig. 1. PCA, principal components analysis.

Table 2 Niche complementarity

	PC 1 versus 2	PC 1 versus 4	PC 2 versus 4	Probability*
All species	-0.19	-0.18	-0.23	0-2/1,000
Within <i>sagrei</i> clade	0.40	0.90	0.34	1,000/1,000†
Between <i>sagrei</i> clade species and other species	-0.21	-0.26	-0.24	1-16/1,000
Within <i>porcatus</i> clade	-0.41	0.38	-0.37	175-191/1,000
Between <i>porcatus</i> clade species and other species	-0.11	-0.23	-0.22	3-16/1,000

*Statistical significance was judged using the number of simulations out of 1,000 in which the number of negative pairwise correlations with an absolute value greater than that for the smallest negative pairwise correlation in the real data was as great as the number of negative pairwise correlations in the real data. Numbers indicate the range of results using the different phylogenies and branch-length estimations. Thus, for 'all species', in no more than 2/1,000 simulations did all three pairwise comparisons have correlations less than -0.18, whereas for the *porcatus* clade, 17.5-19.1% of simulations produced at least two correlations less than -0.37.

† Given that all pairwise correlations are positive for the within-*sagrei* clade analysis, no evidence exists for niche complementarity. Indeed, in only 4.5-7.3% of simulations were all three correlations positive with a correlation greater than 0.34.

In all cases, the results are the same if PC 3, which does not explain a statistically significant proportion of the variance (Table 1), is included. For example, for those cases in which all three comparisons are in the same direction (that is, have the same sign), the three comparisons involving PC 3 are also in that direction and the statistical significance is qualitatively unchanged. For the comparison of *porcatus* group species to other species, two of three comparisons involving PC 3 have a negative sign.

Consideration of niche dissimilarity in a phylogenetic context provides insight to the evolution of community structure. Niche complementarity is not evident within either the *porcatus* or *sagrei* clades; indeed, in the *sagrei* clade, all pairwise correlations are positive, implying that degree of ecological differentiation among species is positively related among ecological axes (Table 2). By contrast, examination of distances separating members of each clade from other members of the community reveals significant niche complementarity for both clades (Table 2). Thus, although community structure shows little evidence of phylogenetic effects among distantly related species, interactions among these species appear to be responsible for the nonrandom dispersion of species in ecological space.

These results have important implications for studies of community ecology. The increasing availability of detailed phylogenetic information at last permits explicit examination of the role of evolutionary divergence in community assembly⁷. In the case of the anoles of Soroa, and in contrast to the many studies that have documented niche conservatism³, the limited extent of phylogenetic structuring in this community implies that niche divergence, rather than conservatism, has had primacy in shaping community evolution. Although the community is not structured phylogenetically, it is structured ecologically: the nonrandom distribution of species in multivariate ecological space suggests that interspecific interactions have shaped community structure, a hypothesis that is supported by the extensive evidence that indicates that ecologically similar anole species interact strongly^{8,9,13,14}.

This ecological structuring, in turn, reveals an unexpected phylogenetic aspect. Since Darwin's time, ecologists have suggested that interspecific interactions may be strongest among closely related species^{17,18}. However, when such strong interspecific interactions occur in a system dominated by niche divergence, species may diverge from near relatives to the extent that they interact just as strongly with less related species. Consequently, the evolutionary outcome may be that ecological interactions among distantly related species play an important role in structuring communities⁶, a prediction which is supported by our discovery that the non-random structure of the Soroa community results from the ecological spacing of distant relatives.

Our findings are particularly relevant to the study of adaptive radiation, a topic of considerable recent interest⁶. A classic model of adaptive radiation postulates that interspecific interactions play an important role in driving evolutionary divergence⁶. Although adaptive radiations have been studied from both community ecological and evolutionary perspectives, integration of these approaches is just beginning⁶. Consequently, investigation of the generality of the patterns exhibited by anoles will provide insight into how adaptive radiation leads to the evolution of diverse communities.

Quantitative analyses of the relationship between ecological and phylogenetic similarity do not yet exist for other evolutionarily

assembled communities, but qualitative examination suggests both that substantial variation may exist among adaptive radiations and that the evolutionary age of the radiation may be related to this variation. For example, relatively young evolutionary radiations of Darwin's finches¹⁹ and Lake Malawi cichlids²⁰ have produced communities in which closely related species are ecologically similar; by contrast, in a community of Old World leaf warblers, which like anoles are the result of a more ancient (>10 Myr ago) radiation, ecological and phylogenetic similarity do not appear to be related²¹, as is also the case in anoles. These differences suggest that community evolution may occur in fundamentally different ways; the length of time community members have been coevolving may be important, but other factors such as prevalence of sexual selection or geographic setting also should be investigated. Future study of ecological relationships in a phylogenetic context will permit testing of these hypotheses and will enrich our understanding of both adaptive radiation and the evolutionary genesis of community structure. □

Methods

Ecological data collection

Habitat-use data were collected by walking transects in the forest in May 1997 and noting perch height, type, and diameter for each undisturbed adult lizard observed. Data were also collected for *A. sagrei*, an edge- and open-habitat species, in areas surrounding the forest. Diameter of substrates used during locomotion was recorded by observing adult lizards from a distance >5 m for 5-257 min and noting the diameter of every woody surface used; multiple measurements were taken when lizards moved along surfaces that varied greatly in diameter. Observations (made 07:00-18:00 when rain was not falling or imminent) were conducted only on males for species in which sex could be determined from a distance. For each individual, we calculated the mean of all substrate diameters.

Body temperature and activity time were measured in a pre-arranged regimen in which sampling effort was constant throughout the day. Lizards were captured and cloacal temperature quickly recorded by inserting a thermocouple using standard methods. Activity time was measured by walking transects at 1.5 h intervals throughout two days and noting every lizard observed. For rare species, data were augmented by measurements taken whenever individuals were observed. Because of Soroa's protected status, we did not collect the large sample of specimens necessary for diet analyses. Instead, we used snout-vent length, which correlates strongly with prey size in *Anolis*⁸. Except where noted, data were collected for both males and females. Although anoles are sexually dimorphic in habitat use²², dimorphism in Soroa species was minor relative to interspecific differences.

Phylogenetic analysis

We used PAUP* v4.0b10 (ref. 23) and MrBayes v3.0b3 (ref. 24) to generate phylogenies from mitochondrial DNA haplotypes representing 129 anole species using parsimony, maximum-likelihood and bayesian approaches. DNA extraction, amplification and sequence alignment were conducted as described in ref. 10, which presented 53 of these sequences. We sequenced approximately 1,500 base pairs, including ND2, five transfer RNAs, the origin of light-strand replication, and part of CO1. The HKY model (transition/transversion ratio = 3, proportion of invariable sites = 0.2, shape parameter = 0.7), selected for maximum-likelihood analyses using Modeltest 3.0 (ref. 25), resulted in a single tree with a likelihood score of -ln(66946.90). For the bayesian analysis, four chains were run for 1,000,000 generations. Following a burn-in period of 50,000 generations, the mean likelihood score for sampled trees was -ln(66917.60) (s.d. = 11.99). Relative dates of divergence of the species present at Soroa were estimated on both trees by transforming branch lengths with the Langley-Fitch method²⁶ and non-parametric rate smoothing using the program 'r8s' version 1.01b (<http://ginger.ucdavis.edu/r8s/>).

Statistical analysis

All analyses were conducted on four ultrametric trees (Langley–Fitch and NPRS branch lengths for both the maximum-likelihood and bayesian phylogenies); further analyses were run assuming both a speciation and a gradual mode of character evolution. Results from these analyses were qualitatively nearly identical.

To examine whether distances between species in ecological space was related to phylogenetic proximity, we conducted a Mantel test comparing matrices of ecological and phylogenetic distance. Ecological distance was the euclidean distance between species in a multidimensional space determined by the axes of a PC analysis. Phylogenetic distances were the branch lengths separating species (that is, their patristic distance). To examine whether niche position of the species in the two species-rich clades (Fig. 1) was conserved, we examined whether members of these clades occupied a nonrandomly small part of ecological space relative to the other species by conducting a MANOVA with PC axis scores as variables and five groups (the two clades and the other three species).

Then, to assess whether members of these clades were more similar to each other than would be expected by random evolutionary divergence, we calculated for each clade the ratio of the mean distance between species within the clade and the mean distance of species within the clade to other species. To assess whether these ratios were unusually small, we conducted phylogenetic simulations. For each significant PC axis, trait evolution was simulated on the phylogeny assuming either gradual or speciation models of character evolution; variance in trait value among species in the simulations was adjusted to that observed in the real data. Using these simulations, we then assessed whether the ratios for each clade separately or for the average of the two clades was significantly smaller than expected by chance.

To determine whether species were nonrandomly dispersed in ecological space, we examined whether the pairwise euclidean distance between species on one PC axis was negatively related to the distance along a second axis ('niche complementarity'). Because the three pairwise comparisons among the three PC axes are not independent, an experiment-wise *P*-value cannot be calculated. We investigated the statistical significance of these findings using phylogenetic simulation as above. For both the real and simulated values, correlations were calculated between euclidean distances on each possible pairwise combination of PC axis scores.

Received 29 January; accepted 29 May 2003; doi:10.1038/nature01814.

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Supplementary Information accompanies the paper on www.nature.com/nature.

Acknowledgements We thank J. Chase, R. Ricklefs and T. Schoener for comments, and V. Rivalta González, A. Daniel Alvarez, and A. Torres Barboza for assistance in the field. We thank the National Geographic Society, the David and Lucile Packard Foundation, the National Science Foundation and Barnard College for support.

Competing interests statement The authors declare that they have no competing financial interests.

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Constrained circulation at Endeavour ridge facilitates colonization by vent larvae

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Understanding how larvae from extant hydrothermal vent fields colonize neighbouring regions of the mid-ocean ridge system remains a major challenge in oceanic research^{1,2}. Among the factors considered important in the recruitment of deep-sea larvae are metabolic lifespan, the connectivity of the seafloor topography, and the characteristics of the currents³. Here we use current velocity measurements from Endeavour ridge to examine the role of topographically constrained circulation on larval transport along-ridge. We show that the dominant tidal and wind-generated currents in the region are strongly attenuated within the rift valley that splits the ridge crest, and that hydrothermal plumes rising from vent fields in the valley drive a steady near-bottom inflow within the valley. Extrapolation of these findings suggests that the suppression of oscillatory currents within rift valleys of mid-ocean ridges shields larvae from cross-axis dispersal into the inhospitable deep ocean. This effect, augmented by plume-driven circulation within rift valleys having active hydrothermal venting, helps retain larvae near their source. Larvae are then exported preferentially down-ridge during regional flow events that intermittently over-ride the currents within the valley.

The Endeavour segment of Juan de Fuca ridge (Endeavour ridge) is a hydrothermally active, intermediate-rate spreading centre located in 2,500 m of water roughly 300 km seaward of British Columbia and Washington State in the northeast Pacific (Fig. 1). Hydrothermal venting from this segment is concentrated within a 1-km-wide, 10-km-long rift valley located along the ridge crest. Water depths within the axial valley shoal from 2,300 m in the south to 2,170 m in the north. Valley relief ranges from 100 to 150 m. A 25-km-wide, 50-km-long depression links the southern end of the Endeavour segment to the main portion of Juan de Fuca ridge.