Lizard community structure along environmental gradients

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Summary

1. How the total number of individuals in a community is divided among its species is governed by both the distribution of species along landscape-scale environmental gradients and by local resource partitioning. In vertebrate ectotherms, abiotic environmental conditions may constrain geographic distributions more strongly than local population densities due to thermal constraints on resource acquisition and due to behavioural thermoregulation.

2. We investigate whether local density and species richness are decoupled for lizard communities within the Southwest US by comparing 18 species-abundance distributions.

3. While species richness decreases strongly with decreasing temperature, there is no significant relationship between temperature or resource availability (net primary productivity) and the total number of individuals within a community. Consequently, in more species-rich communities species have lower mean abundances.

4. This suggestion that lizard species richness is not a function of an area's capacity to support more individuals questions for this group species diversity theories based on this assumption.

Key-words: more individuals hypothesis, rank-abundance distribution, species-abundance distribution, species–energy theory, thermal constraints

Introduction

The variation of population abundance and species richness across assemblages is at the very heart of community ecology. Species-abundance distributions (SADs) – plots of the number of individuals observed for each species within a community – unite both aspects in one representation and offer an effective way to study them in conjunction. SADs exhibit a similar shape, as communities consistently contain a few very abundant species and many rare species (McGill *et al.* 2007). SADs have long been hypothesized to be influenced by the partitioning of local resources between species (MacArthur 1960). However, local abundances are also a function of species' distributions along landscape-scale environmental gradients. Whittaker's (1965) classic plots depict how the change in one species' abundance along an environmental gradient interacts with that of other species to determine the composition of individuals at any given site. Central to this presumed interaction is that species' densities are often highest in the centre of species distributions (but see Sagarin & Gaines

2002) and that environmental gradients constrain total number of individuals (Whittaker 1965).

Many theories attempting to explain the shapes of SADs are based on resource partitioning within communities. If each species sequentially uses a fixed fraction of the available resources in a competitive dominance hierarchy, the number of individuals per species may form a geometric series (Motomura 1932; Whittaker 1965). Alternatively, a lognormal distribution can result from relative species importance being determined by numerous partitioning axes, yielding a normal distribution (Whittaker 1965). Geometric series are common in communities with low richness as the number of axes for resource partitioning tends to increase with species richness and communities tend to lognormal distributions (McGill *et al.* 2007).

It follows that local species richness and its variation across communities may be an important co-determinant of SADs, and we here set out to explicitly consider this effect. Several prominent theories of species richness contend that species richness is a consequence of the number of individuals in a community. For example, the characteristic shape of abundance distributions forms the basis of Preston's (1962) species–area theory. According to this theory, the area

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(assuming a constant density of individuals per unit area) and thus number of individuals sampled will consistently predict the number of species in a sample (Preston 1962). Wright (1983) generalized this concept as the more individuals hypothesis (MIH), suggesting that the total resources available in an area constrains the number of individuals. He hypothesized that more species can persist in a community with more individuals as larger population sizes can reduce extinction risk. The related species–energy theory invokes resource availability as a driver of population size (Wright 1983). This perspective based on population size suggests a secondary role for climatic tolerances determining distributions along environmental gradients (physiological tolerance hypothesis, Currie *et al.* 2004). The MIH has been repeatedly invoked as a potential explanation for the ubiquitous positive species–energy (and –area) associations (Evans, Warren & Gaston 2005b). Studies that have examined the MIH for several groups by relating resource availability to total abundance or richness have found mixed support (Srivastava & Lawton 1998; Currie *et al.* 2004; Evans, Greenwood & Gaston 2005a). However, despite long history (Whittaker 1960) empirical investigations of species-abundance patterns along broad-scale environmental gradients and thus MIH remain limited (Hubbell 1979; Cotgreave & Harvey 1994; Kaspari, O'Donnell & Kercher 2000b; Hurlbert 2004, 2006). To our knowledge, none exist for ectotherm terrestrial vertebrates. Yet, ectotherms represent an important test case, as environmental temperatures may set hard direct limits in addition to affecting energy availability (Kaspari, Alonso & O'Donnell 2000a; Kaspari *et al.* 2000b).

Here, we set out to jointly assess the variation of SADs and species richness across landscapes for an ectotherm vertebrate group whose distributions are known to be sharply constrained by environmental conditions – lizards (Schall & Pianka 1978). We are specifically interested in the way temperature – via direct and indirect effects – may differently affect species richness and total abundance of lizard communities. Our analysis provides a first broad-scale test of the MIH in this group. We aim to investigate the following hypotheses:

First, we note that for lizards as vertebrate ectotherms environmental temperatures strongly constrain the ability to acquire resources (Huey 1982). Temperatures below a lizard's thermal tolerance zone prevent activity. This imposes a direct constraint on geographic distributions as lizards are unable to live in areas where temperatures rarely warm sufficiently for them to initiate activity. We hypothesize that such a direct thermal constraint will primarily act on species richness rather than abundance as, along a gradient from warm to cold environments, special adaptations are required for survival and fewer and fewer species may have evolved appropriate thermal tolerances (Schall & Pianka 1978).

Second, one would expect temperature to also have an indirect effect on ectotherm taxa. Outside regions where cold climate may constraint survival, temperature may still exert a soft constraint, as it affects the time available for activity and thus restricts energetic intake and population growth rates (Kearney & Porter 2004; Buckley 2008). However, where the environment is sufficiently warm for activity, lizards can often behaviourally thermoregulate to their preferred temperature. Therefore, thermoregulation reduces the influence of environmental temperatures on metabolic rates and performance (Huey, Hertz & Sinervo 2003). We thus expect temperature differences between sites to have little influence on demography and ultimately abundance if they do not influence foraging times (i.e. temperatures fall within the temperature range for activity) and thermoregulation is effective. Recent analyses of lizard density found little evidence for thermal constraints on global patterns of lizard population density, suggesting that effective behavioural thermoregulation is widespread if one assumes energetic equivalence between species (Buckley, Rodda & Jetz 2008). This release from thermal constraints on density suggests a potential decoupling of abundance and diversity that questions the dependence of species richness on the number of individuals in a community in general and the MIH in particular.

Third, we note that compared to similar-sized endotherm vertebrates lizards have much lower energy requirements (Pough 1980). This is likely to weaken the relationship between local net primary productivity (NPP) and the number of individuals in a community commonly observed for endotherms. More specifically, for lizards the relative importance of thermal habitat quality on resource acquisition and thus demographic parameters (Diaz 1997) is likely much greater, and productivity may only play a secondary role. Abundance is expected to be at most weakly related to temperature or productivity.

To address these hypotheses, we compare the SADs of 18 lizard communities in National Parks within the Southwest US. In addition to testing the respective effects of ambient temperature and species richness on SADs, we also consider energy flow by examining the primary productivity required (PPR) by species and communities. We test the following three predictions for these lizard communities: (I) *Species richness*: Lizard species richness is constrained by environmental temperature consistent with sensitivity to thermal constraints. Environmental productivity is a weaker constraint on total number of individuals and species richness than has been observed for endothermic groups (as lizards' ectothermy leads to limited energy requirements). (II) *Abundance*: The ability of lizards to thermoregulate and thus buffer the energetic implications of environmental temperature will weaken the relationship between environmental temperature and the total number of individuals in a community. Temperature may have a weak influence on abundance via alterations in the activity time available for foraging. (III) *Community evenness*: If these empirically-based predictions hold then it follows that the stronger constraint of environmental temperatures on distribution than on population density will likely result in communities with greater species richness (located in high-temperature environments) more evenly dividing resources among species. We thus predict that this effect will be revealed in greater evenness in communities with higher species richness.

Materials and methods

LIZARD COMMUNITY AND ENVIRONMENTAL DATA

Lizard community data were collected as part of the National Park Service Inventory and Monitoring Program (science.nature.nps.gov/im/). Recognizing the severe data limitations for ectotherm vertebrates at regional scales we here assume that each park represents one community. Data was accessed through the NPSpecies portal and through requesting reports from individual park units. Inventories were initiated within all national park units identified as containing significant natural resources with goals including documenting at least 90% of the species present and establishing a monitoring baseline. We focused on the data collected within the Southern Colorado Plateau Inventory & Monitoring Network (SCPN) between 2001 and 2003 as the parks were consistently intensively surveyed with robust methods.

We assessed both quantitative and qualitative quality control measures for data from an initial set of 54 parks. We then selected only those parks that had at least 50 person hours of survey efforts, had areas of at least 2 km², and were qualitatively considered to have utilized consistent, repeatable methods. Further, we excluded parks without representative and complete coverage of all habitats. This resulted in a final set of 18 national parks, recreation areas and monuments (including park codes) as follows (Drost, Persons & Nowak 2001; Persons & Nowak 2004, 2006a,b, 2007; Prival & Goode 2005; Persons, Nowak & Hillard 2006): Amistad (AIMS), Bandelier (BAND), Big Bend (BIBE), Carlsbad Caverns (CAVE), Chaco Culture (CHCU), Death Valley (DEVA), El Malpais (ELMA), Fort Davis (FODA), Glen Canyon (GLCA), Guadalupe Mountains (GUMO), Hovenweep (HOVE), Manzanar (MANZ), Mojave, (MOJA), Petrified Forest (PEFO), Petroglyph (PETR), Salinas Pueblo Missions (SAPU), White Sands (WHSA) and Wupatki (WUPA). The primary sampling method that we included in our analysis was time–area constrained search, where both the time spent searching and area covered are standardized (Crump & Scott 1994). These searches were generally constrained for 1 h within 1 ha plots. For the larger parks (i.e. BAND, CHCU, ELMA, PETR, SUCR, WACA and WUPA), plots were randomly allocated within the park boundaries. The survey effort per park averaged 290 person hours (median: 141; range: 52–940). Species richness averaged 10·2 with a median of 9·5 (range: 5–18). The number of individuals sampled per park averaged 779 with a median of 556 (range: 124–2074). Abundances were normalized by search effort (lizards/person hour) throughout. Our findings are robust to sampling biases induced by differential detectability of species (Appendix S1, Supporting information).

We used park boundary polygons to extract mean environmental data (temperature, precipitation and elevation) for each park (data from 1961 to 1990 with 10′ latitude/longitude resolution; New *et al.* 2002). To estimate energy availability, we use consensus mean annual NPP estimates compiled from numerous models by the Potsdam institute (g C m⁻², 30′ resolution, Cramer *et al.* 1999).

ANALYSIS OF ABUNDANCE DISTRIBUTIONS

We constructed rank-abundance distributions (RADs) by plotting logarithmic abundances against the abundance ranks of species. Distributions were fit by maximum likelihood estimation using the suite of radfit commands in the ʀ package vegan. We consider the geometric series, also known as the niche pre-emption model (Motomura 1932; Whittaker 1965), which assumes that each species sequentially uses a fixed fraction of the available resources. The geometric series is a straight line on a RAD plot and takes the form, $a_r = N\alpha\,(1-\alpha)^{r-1}$, where a_r is the expected abundance of species at rank r, N is the number individuals in the community and α is the single fitted parameter representing proportional energy use (Wilson 1991). We additionally fit the log-normal series as $a_r = \exp[\log(\mu) + \log(\sigma)\Phi]$, where μ and Φ are the fitted parameters. The slope of the geometric fit to the RAD, α, indicates the evenness of species' abundances, but is influenced by species richness. We thus use an additional metric that accounts for species richness; we calculate the probability of intraspecific encounter (PIE), an unbiased measure of community evenness (Hurlbert 1971) as

$$\mathrm{PIE} = \sum_{i=1}^{S} \frac{N_i}{N}\frac{N - N_i}{N - 1},$$

where N_i is the number of individuals of the ith species, N is the total number of individuals in the community and S is the number of species in the community. We also use rarefaction to examine the number of species contained in random subsets of the total number of individuals in communities (Hurlbert 2004).

Unaccounted for similarities between the parks due to spatial proximity have the potential to influence regressions for richness and abundance. We used Moran's I and spatially autoregressive linear models (Haining 2003) to confirm that spatial autocorrelation did not significantly influence our results (Appendix S2, Supporting information).

ANALYSIS OF THE DISTRIBUTION OF ENERGY REQUIREMENTS

In addition to considering the number of individuals, we examine the amount of energy in the form of primary production required by each individual (PPR$_{individual}$, Jetz & Wilman manuscript). For the case of an insectivorous lizard, PPR$_{individual}$ is

$$\mathrm{PPR}_{individual}(\mathrm{KJ\,day^{-1}}) = \mathrm{FMR}_{liz} \times A_{liz}P_{insect}A_{insect},$$

where FMR is individual field metabolic rate, and A_x and P_x are the taxon specific assimilation and production efficiencies respectively. The two latter terms are omitted for herbivorous lizards as they refer to the efficiencies of insects eating plants. We used a lizard assimilation efficiency (A_{liz}) of 75% (Derickson 1976) regardless of diet as assimilation efficiency data was not available for herbivorous lizards. We assume a P_{insect} of 44% (Wiegert & Petersen 1983) and an A_{insect} of 0·97% (Humphreys 1979). We use an empirically derived regression to estimate lizard FMR [FMR(KJ day⁻¹) = 0·196$M^{0.889}$, $n = 55$ species, $r^2 = 0.94$, Nagy 2005]. Lizard body sizes (Snout-vent length, SVL) were assembled primarily from regional guides (Table S2, Supporting information). We used a well-established relationship for lizards to convert mean adult SVL (mm) to mass (g): $M = 3.25 \times 10^{-5}$ SVL$^{2.98}$ (Pough 1980). Data from the literature was used to assign an herbivorous or insectivorous (including omnivores) diet (references including Cooper & Vitt 2002; Metzger & Herrel 2005; Pough 1973; Perry & Garland 2002). We then multiply an individual's PPR$_{individual}$ by the observed number of individuals to estimate a species' total PPR in a community. Our rank-PPR plots are similar to the rank-energy plots of Thibault, White & Ernest (2004), but additionally account for the efficiency of energy transfer across trophic ranks.

Results

SPECIES RICHNESS

We first consider how environmental conditions constrain species richness and abundance. We find that lizard community richness is strongly constrained by environmental temperature (Fig. 1a, slope $\pm$ CI $= 0\cdot84 \pm 0\cdot30$, $F_{[1,16]} = 28\cdot7$, $r^2 = 0\cdot64$, AIC $= 84\cdot84$, $P < 10^{-4}$). The model fit improves slightly when additionally accounting for precipitation ($F_{2,15} = 15\cdot9$, $r^2 = 0\cdot68$, AIC $= 84\cdot8$, $P < 10^{-3}$). Temperature is a much stronger predictor of species richness than NPP ($F_{1,16} = 0\cdot1$, $r^2 = 0\cdot0$, AIC $= 111\cdot1$, $P = 0\cdot8$) which is consistent with the limited energy requirements of lizards due to their ectothermy. An alternative potential constraint on species richness is park area. As larger parks might have greater habitat and topographic diversity, we test for a species–area relationship. We do find a weakly significant increase in species richness with park area (ln(SR)~ln(Area), slope $\pm$ CI $= 0\cdot071 \pm 0\cdot054$, $F_{1,16} = 6\cdot2$, $r^2 = 0\cdot28$, $P < 0\cdot05$). However, temperature is a much stronger predictor of species richness than area, and area is no longer significant when both are included in the model (ln(SR)~ln(Area) + ln(Temp), Area: $t = 1\cdot7$, $P = 0\cdot11$; Temp: $t = 3\cdot9$, $P < 0\cdot001$, $F_{2,15} = 13\cdot6$, $r^2 = 0\cdot64$, $P < 0\cdot001$).

ABUNDANCE

In contrast to the influence of temperature on richness, the total individuals in the community are not related to environmental temperature (Fig. 1b, $F_{1,16} = 0\cdot1$, $r^2 = 0\cdot00$, $P = 0\cdot8$). Nor is NPP a predictor of total individuals ($F_{1,16} = 0\cdot1$, $r^2 = 0\cdot0$, $P = 0\cdot7$). Finally, no clear relationship exists between total individuals and species richness in a community (Fig. 1c, slope $\pm$ CI $= -0\cdot13 \pm 0\cdot16$, $F_{1,16} = 2\cdot7$, $r^2 = 0\cdot14$, $P = 0\cdot1$). Abundance per species shows a weak decrease with increasing richness (Fig. S1, Supporting infor-

mation, slope $\pm$ CI $= -0\cdot03 \pm 0\cdot02$, $F_{1,182} = 15\cdot9$, $r^2 = 0\cdot08$, $P < 10^{-4}$).

COMMUNITY EVENNESS

We next consider the repercussions of there being more species, but equivalent total individuals in warmer environments for community structure. We find that individuals are more evenly partitioned among species in warmer environments. When dividing the RADs into three quantiles of increasing mean annual environmental temperature (Fig. 2), we find that the more species-rich lizard communities characteristic of warmer environments tend to have individuals more evenly partitioned into species. The geometric series fit (by AIC) the observed RADs for the eighteen park units better than a lognormal series (11 of 17 cases with one case indistinguishable, Table S1, Fig. S2, Supporting information). Among all plots, the median difference in AIC values (AIC$_{geometric}$–AIC$_{lognormal}$) is $-7\cdot3$ (Mean difference in AIC $= -22\cdot4$). In a plot of geometric series fits of (proportional) abundances per species versus species rank for all communities together (Fig. 3), the most abundant species in communities with lower richness is proportionally more abundant. Interestingly, we find that all lines intersect at a similar species rank. When examining the RAD slopes of the geometric series fits (i.e. the alpha term) as a function of species richness (Fig. 4a), the steepness of the RAD slope declines consistently with increasing species richness (slope $\pm$ CI $= -0\cdot025 \pm 0\cdot009$, $F_{1,16} = 30\cdot6$, $r^2 = 0\cdot66$, $P < 10^{-4}$). Using the RAD slope (alpha) to assess evenness does not control for the effects of species richness, and we therefore also consider the PIE, an unbiased measure of evenness (Hurlbert 1971; Fig. 4b). The observation of increasing evenness with increasing species richness persists when using the PIE metric (slope $\pm$ CI $= 0\cdot019 \pm 0\cdot009$, $F_{1,16} = 18\cdot5$, $r^2 = 0\cdot54$, $P < 10^{-4}$). Alpha decreases (slope $\pm$ CI $= -0\cdot018 \pm 0\cdot01$, $F_{1,16} = 7\cdot3$, $r^2 = 0\cdot27$, $P < 0\cdot01$) and PIE increases (slope $\pm$ CI $= 0\cdot013 \pm 0\cdot01$, $F_{1,16} = 4\cdot9$,
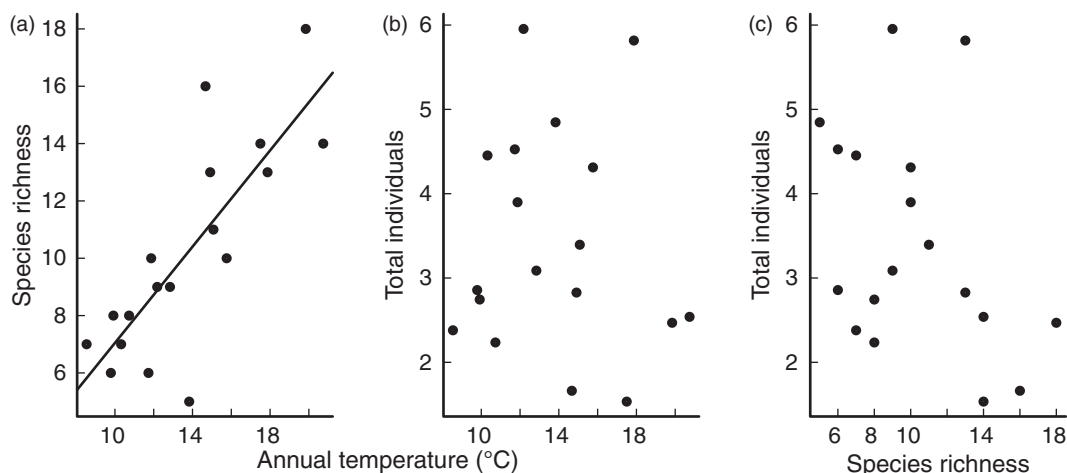

Fig. 1. The relationship between mean annual temperature (°C), lizard community species richness and total individuals per community (lizards/person hours).
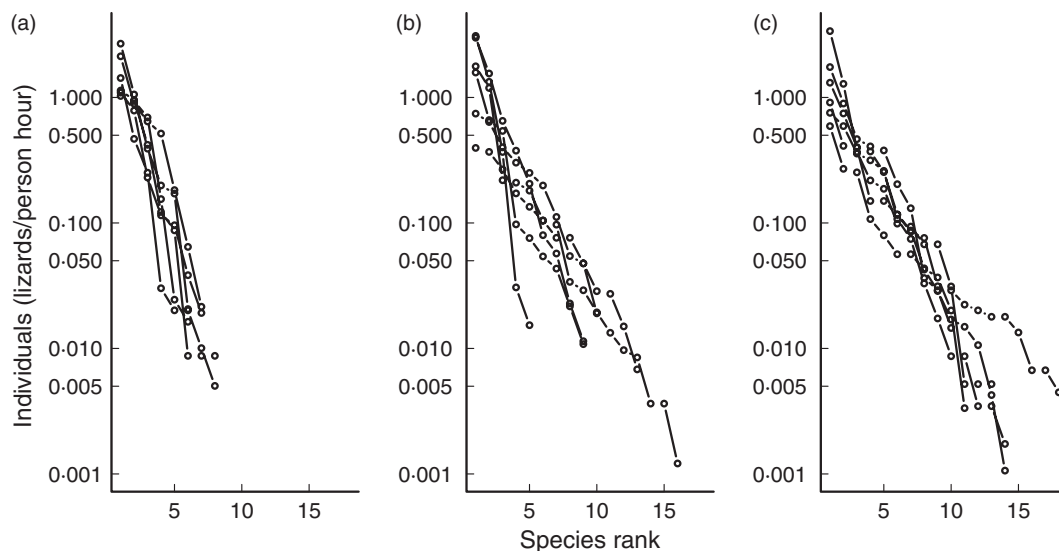
Fig. 2. The number of individuals (lizards/person hour) as a function of species rank for the 18 parks divided into three quantiles of mean annual temperature (a: coldest – c: warmest).
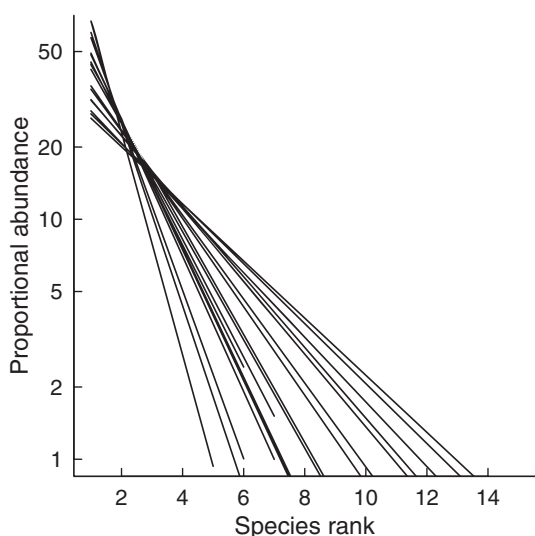

Fig. 3. Geometric series fits of proportional abundance by species rank show that in communities with more species, individuals are more evenly partitioned into species.

$r^2 = 0.18$, $P < 0.05$) with temperature also, but the relationship is weaker than that with species richness. We use rarefaction curves to account for differential numbers of individuals sampled between communities. Differences in expected species richness between communities persist when controlling for the number of individuals sampled in opposition to the MIH (Fig. S3, Supporting information).

Species abundance is often used as a proxy of energy use by a community but does not account for actually observed body sizes and trophic level differences in energy needs (Thibault *et al.* 2004). We therefore additionally consider energy flow directly by assessing the PPR by all observed individuals of a species. Plotting each species' PPR against rank reveals similar community patterns as those observed in RADs

(Fig. S4, Supporting information). Analogous to the patterns for individuals, we find little relationship between total community PPR (PPR summed across all species) and NPP ($F_{1,16} = 0.1$, $r^2 = 0.0$, $P = 0.8$). We also find little relationship with temperature (Fig. S5a, Supporting information; $F_{1,16} = 0.3$, $r^2 = 0.0$, $P = 0.6$) and species richness (Fig. S5b, Supporting information; slope ± CI = -0.018 ± 0.03, $F_{1,16} = 1.3$, $r^2 = 0.08$, $P = 0.3$). This supports our claim that resources are more evenly distributed among species in communities with higher species richness. When plotting proportional PPR use by each species in a community versus rank for all communities together (Fig. 5a), we find that the most abundant species in communities with lower richness use a greater proportion of the community's energy use. As with individuals, all lines intersect at a similar species rank, suggesting that RAD slopes shift consistently with increased richness. When examining the slope of this relationship (α term) as a function of species richness (Fig. 5b), we find that the steepness of the RAD slope declines consistently with increasing species richness (slope ± CI = -0.025 ± 0.011, $F_{1,16} = 18.0$, $r^2 = 0.53$, $P < 10^{-3}$).

Discussion

Is the occurrence of a lizard species at a given location in the southwestern US primarily determined by the species' environmental tolerance or are ecological interactions with the other species present also important (MacArthur 1972)? Our analysis suggests the primacy of environmental constraints on distribution in structuring the analysed lizard communities. Thermal constraints on activity limit survival and resource acquisition and have been demonstrated to constrain lizard ranges (Kearney & Porter 2004; Buckley & Rougharden 2006; Buckley 2008). We find supporting evidence for this constraint as the species richness of lizards
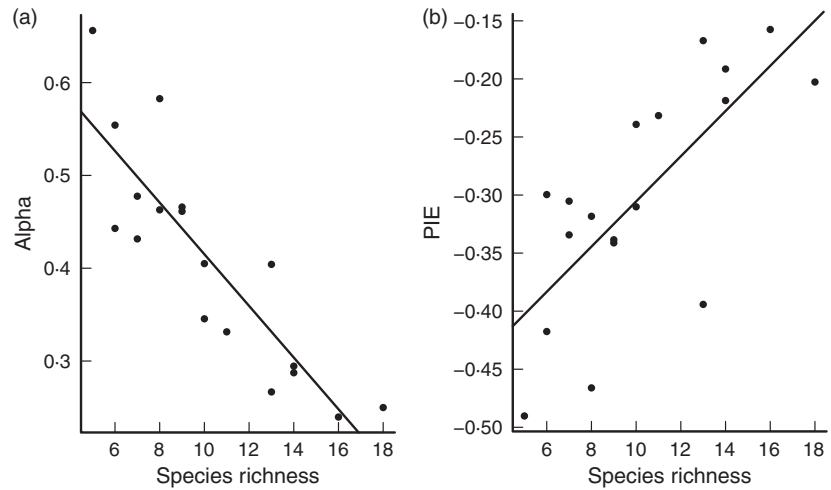
Fig. 4. Increasing community richness corresponds to (a) shallower rank-abundance distribution slopes (based on geometric series fit, alpha) and (b) a higher probability of intraspecific encounter (PIE).
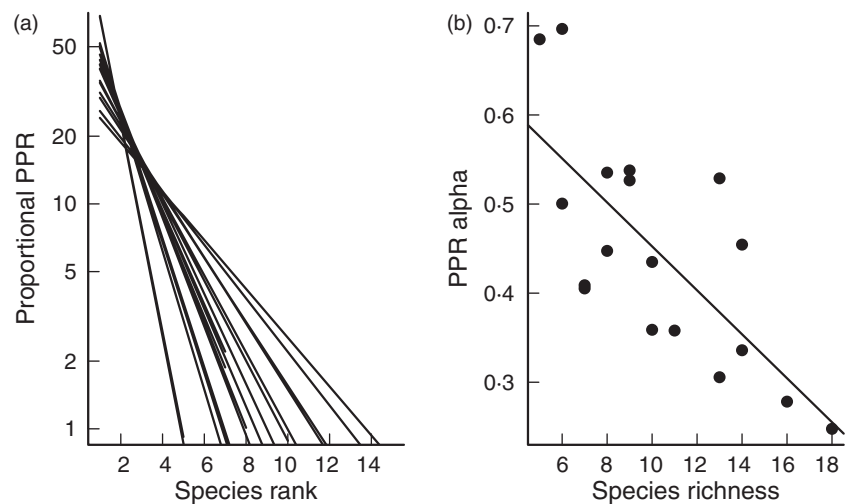

Fig. 5. Geometric series fits of species' primary productivity required (PPR) by rank show that in communities with more species, individuals are more evenly partitioned into species (a). This increasing evenness is also revealed by examining the shallowing of rank-PPR slopes with increasing community richness (alpha, b).

in the southwestern parks increases with increasing environmental temperatures. While many researchers have correlated energy estimates against species richness, few have actually examined the link with number of individuals (but see Hurlbert 2004, 2006; Evans, James & Gaston 2006; Yee & Juliano 2007; Srivastava & Lawton 1998; Currie *et al.* 2004). In the case of southwestern lizards, one might falsely infer a role of abundance from the positive relationship between temperature and species richness.

However, we find little evidence for total individuals in a community mediating the relationship between temperature or resource availability and richness. This initial result for vertebrate ectotherms corresponds to findings in other systems (Srivastava & Lawton 1998; Currie *et al.* 2004). Body temperature exerts an exponential effect on the metabolic rates of ectotherms, with individuals with higher body temperatures, e.g. as a consequence of living in warmer environments, requiring disproportionately more energy per unit of mass (Gillooly *et al.* 2001). However, behavioural thermoregulation buffers the influence of environmental temperature on body temperatures and thus the energetic implications of environmental temperature

(Hertz, Huey & Stevenson 1993). Accordingly, neither this analysis nor a global scale study of lizard population densities found thermal constraints on lizard population densities (Buckley *et al.* 2008). Among southwest parks, we further found that total number of individuals in a community does not correlate with environmental productivity or even species richness. While the global scale study did find increasing per-species abundance with increasing NPP, the relationship did not persist when considering entire communities potentially due to other ecological constraints (Buckley *et al.* 2008). We therefore conclude that the low energetic costs of ectotherms, which can be up to ten times lower than those of endotherms (Pough 1980), may limit the influence of productivity on the number of individuals in lizard communities and limit the relevancy of the MIH for reptiles. Productivity has been observed to have a more pronounced influence on the number of individuals and subsequently species richness for some endothermic taxa (Hurlbert 2004; Monkkonen, Forsman & Bokma 2006). It follows that the processes governing vertebrate community structure likely vary substantially between ectotherms and endotherms.

Environmental temperature appears to exert a stronger constraint on species richness than densities. As a consequence, we find that individual lizards are more evenly partitioned into species in more species-rich communities in warm environments. This finding holds when controlling for sampling biases using an unbiased evenness metric and rarefaction. In contrast, some other taxa exhibit a structure that is similar across communities when controlling for resource availability and species richness (Hurlbert 2004, 2006). The ability of lizards to partition resources along multiple niche axes may be central to determining densities. Pianka (1975) found among three continental desert lizard systems that lizard species density increased with the diversity of resources (e.g. microclimate, time of activity) utilized. The primacy of thermal constraints on lizard distributions was also suggested by Buckley & Rougharden (2006), who found that superimposing competition on the abundance patterns predicted by energetic constraints along an elevation gradient accounted for observed abundances.

Mounting evidence questions the role of abundance and resources in constraining ectotherm diversity along environmental gradients. Thus, integrating evolutionary and ecological approaches may be essential to understanding diversity gradients (Harrison & Cornell 2007). Developing a more mechanistic understanding of constraints on density, distribution, and ultimately community structure that addresses the role of life history and organismal characteristics such as ectothermy or endothermy is central to this goal. One promising approach is to place an increasing emphasis on organismal traits – and the functional implications of these traits – in community ecology (McGill *et al*. 2006). Organismal traits evolve to enable both local niche differentiation and adaptation to landscape-scale environmental conditions. Whether climatic suitability evolved before or after niche differentiation is central to understanding SADs (Ackerly, Schwilk & Webb 2006). As our analysis demonstrates, examining the broader context of environmental tolerances among species may be essential to understanding the community ecology of ectotherms.

Acknowledgements

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Supporting Information

Additional supporting information may be found in the online version of this article.

Fig. S1. The number of individuals per species (lizards/person hour) declines weakly with increasing species richness.

Fig. S2. Rank-abundance distributions normalized by search effort (lizards/person hour×1000) for park communities (with abbreviations) ordered by increasing mean annual temperature from left to right (°C).

Fig. S3. Rarefaction curves showing how species richness accumulates with the number of individuals sampled within each park community.

Fig. S4. Primary productivity required (PPR) by all observed individuals of each species (KJ day^{-1} search hour^{-1}) as a function of rank for park communities (with abbreviations) ordered by increasing mean annual temperature (°C).

Fig. S5. Total primary productivity required (KJ day^{-1} search hour^{-1}) by each lizard community is not strongly related to either (a) mean annual temperature (°C) or (b) species richness.

Table S1. The species richness (Spec), total number of individuals (Ind), and AIC values corresponding to geometric series (Geo) and lognormal (Log) rank-abundance distribution fits for each park.

Table S2. Species listed by park with diet (herbivore, insectivore or omnivore), snout-vent length (SVL in cm), and the body-size reference (Ref).

Appendix S1. Supplementary methods and results controlling for species detectability

Appendix S2. Supplementary methods and results controlling for spatial autocorrelation

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