

The decoupling of abundance and species richness in lizard communities

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Summary

1. Patterns of species richness often correlate strongly with measures of energy. The more individuals hypothesis (MIH) proposes that this relationship is facilitated by greater resources supporting larger populations, which are less likely to become extinct. Hence, the MIH predicts that community abundance and species richness will be positively related.

2. Recently, Buckley & Jetz (2010, *Journal of Animal Ecology*, **79**, 358–365) documented a decoupling of community abundance and species richness in lizard communities in south-west United States, such that richer communities did not contain more individuals. They predicted, as a consequence of the mechanisms driving the decoupling, a more even distribution of species abundances in species-rich communities, evidenced by a positive relationship between species evenness and species richness.

3. We found a similar decoupling of the relationship between abundance and species richness for lizard communities in semi-arid south-eastern Australia. However, we note that a positive relationship between evenness and richness is expected because of the nature of the indices used. We illustrate this mathematically and empirically using data from both sets of lizard communities. When we used a measure of evenness, which is robust to species richness, there was no relationship between evenness and richness in either data set.

4. For lizard communities in both Australia and the United States, species dominance decreased as species richness increased. Further, with the iterative removal of the first, second and third most dominant species from each community, the relationship between abundance and species richness became increasingly more positive.

5. Our data support the contention that species richness in lizard communities is not directly related to the number of individuals an environment can support. We propose an alternative hypothesis regarding how the decoupling of abundance and richness is accommodated; namely, an inverse relationship between species dominance and species richness, possibly because of ecological release.

Key-words: ecological release, lizard communities, more individuals hypothesis, probability of interspecific encounters, species dominance, species evenness

Introduction

Broad-scale patterns of species richness often correlate positively with measures of energy (Gaston 2000). The more individuals hypothesis (MIH) (Wright 1983) proposes that energy drives richness by providing more resources that support larger populations which are less likely to suffer extinctions. Thus, the MIH predicts a positive relationship between community abundance and species richness.

Recently, Buckley & Jetz (2010) examined community abundance and species richness of lizards in 18 study areas that spanned a broad environmental gradient across south-west USA. In contrast to predictions from the MIH, they documented a decoupling of abundance and richness; communities with greater richness did not contain more individuals. They hypothesized that this was a consequence of differential constraints on species richness and abundance from abiotic conditions, notably temperature. A predicted consequence was that instead, communities with greater richness would divide resources and species' abundances more

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evenly, allowing more species to coexist (Buckley & Jetz 2010). They used two measures of evenness to test this latter prediction: (i) the slope of decay ('alpha') from a geometric model fitted to the rank abundances of each community; and (ii) Hurlbert's (1971) probability of interspecific encounters (PIE). They noted that alpha is influenced by species richness, but considered PIE to be unbiased in relation to species richness.

Here, we test the prediction that species richness and community abundance are decoupled in lizard communities across broad environmental gradients, and consider whether this decoupling is associated with a more even distribution of abundances in species-rich communities relative to species-poor communities. First, we show that PIE is not robust to the influence of species richness. Second, using an additional evenness metric that is robust to the influence of species richness, we test the relationship between evenness and species richness in two large-scale data sets; one from semi-arid south-east Australia; and the other from south-west United States used by Buckley & Jetz (2010). We highlight differences obtained using alternative measures of evenness, thus illustrating the problems associated with evenness metrics that are influenced by species richness. Finally, we propose an alternative hypothesis for allowing the decoupling of abundance and richness in lizard communities: namely, an inverse relationship between species dominance and species richness, possibly due to ecological release.

Materials and methods

DATA SETS ON LIZARD COMMUNITIES

South-east Australia

We surveyed lizards using pitfall trap-lines in each of 28 landscapes (each 12.6 km²) across a 104 000 km² study region within the Murray Mallee bioregion of south-east Australia. This region, characterized by multistemmed 'mallee' eucalypts, experiences a semi-arid climate with a mean annual rainfall of between 200 and 350 mm (Australian Bureau of Meteorology; <http://www.bom.gov.au>). We established 10 trap-lines within each of the 28 landscapes (i.e. $n = 280$ trap-lines overall). Trap-lines were comprised of a 50-m drift-fence connecting ten 20-L pitfall traps spaced at 5-m intervals. All landscapes were separated by a minimum of 2 km and were located within large (>8000 ha) conservation reserves. Trap-lines were surveyed for 20 nights (10 during spring and 10 during summer) during four trapping sessions over 2 years (2006–2007 and 2007–2008). This trapping effort (56 000 trap nights) resulted in >6800 captures of lizards (excluding recaptures) from 44 species. We pooled the data from trap-lines in each landscape to measure abundance and richness for 28 communities.

South-west United States

We used the data set on lizard communities in south-west United States described by Buckley & Jetz (2010). This data set spans a broad environmental gradient and includes data on abundance and richness of 18 lizard communities from national parks, recreation areas and monuments. Data were collected using time and area-con-

strained searches, and therefore, the measurement of abundance was normalized to account for differences between parks in the amount of time spent searching for lizards (see Buckley & Jetz 2010). Abundance is therefore represented as lizards/person hour.

SPECIES EVENNESS METRICS

First, we illustrate mathematically the relationship between PIE and species richness, highlighting the nonindependence of these two measures of biodiversity.

Consider a set of communities in which individuals are partitioned equally but which range in species richness from 2 to 10. Assuming a definition of evenness as the 'equitability of abundances between species' (Alatalo 1981), an evenness index that is unbiased by species richness should return the same value for each community (Smith & Wilson 1996). The equation for the PIE is

$$\text{PIE} = \sum_{i=1}^R \frac{N_i(N - N_i)}{N(N - 1)}$$

where N_i is the abundance of the i -th species, R is species richness and N is the number of individuals. Calculating PIE for the above communities, we observe that PIE increases as species richness increases (Fig. S1, Supporting Information). This is because, in the case of a perfectly even community,

$$N_i = N \frac{1}{R}, \forall i$$

Substituting into PIE gives,

$$\begin{aligned} \text{PIE} &= R \left(\frac{N \frac{1}{R} (N - N \frac{1}{R})}{N(N - 1)} \right) \\ &= \frac{N(1 - \frac{1}{R})}{N - 1} \end{aligned}$$

This indicates that PIE can be predicted from species richness in a perfectly even community; communities with more species receive higher PIE values (Fig. S1, Supporting Information). Hurlbert (1971) noted the influence of species richness on PIE in his original article, stating 'three communities consisting, respectively, of 2, 10 and 100 equally abundant species yield A_1 [i.e. PIE]...values of .50, .90 and .99'. Despite this, the interpretation of PIE remains variable (Gosselin 2006) and Buckley & Jetz (2010) are not alone in using PIE as an evenness index (e.g. Lepori, Palm & Malmqvist 2005).

Other evenness metrics that do satisfy the assumption of independence from species richness are available and thus are suitable for investigating relationships between richness and evenness. One such metric, Smith & Wilson's (1996) E_{var} , is based on the variance in abundance of species. Smith & Wilson (1996) found E_{var} values to remain constant for equally even communities when species richness varied between 1 and 75, highlighting the independence of E_{var} from species richness across this range. For this reason, E_{var} has been used in research on the relationship between species evenness and richness (e.g. Ma 2005; Symonds & Johnson 2008).

E_{var} can be expressed as,

$$E_{\text{var}} = 1 - \frac{2}{\pi} \arctan \left\{ \frac{1}{R} \sum_{i=1}^R \left(\ln(p_i) - \frac{1}{R} \sum_{j=1}^R \ln(p_j) \right)^2 \right\}$$

where p_i and p_j are the abundance of the i -th and j -th species, respectively.

To illustrate the differences in interpretation when using alternative measures of species evenness, we calculated the same measures of

evenness as Buckley & Jetz (2010) for our data on lizard communities in south-east Australia. This involved: (i) fitting a geometric model to the rank abundance of each community and extracting alpha; and (ii) calculating PIE for each community. The geometric model was fitted with the use of the *vegan* package in R Version 2.10.1 (Oksanen *et al.* 2009). Additionally, to examine whether a positive relationship between evenness and richness persists when using an evenness measure robust to the influence of species richness, we calculated E_{var} for lizard communities in each data set.

SPECIES DOMINANCE METRICS

Buckley & Jetz (2010) noted that the proportional abundance of the most common species decreased as species richness increased. Their observation was based on rank abundance distributions that showed a higher y -intercept for communities with low species richness relative to those with high species richness. Although not elaborated further, this provides another potential explanation for the decoupling of abundance and richness. The y -intercept of a rank abundance distribution based on proportional abundance and fitted by the geometric series is conceptually similar to the Berger Parker Index (d) (Berger & Parker 1970; also see Magurran & Phillip 2001); a simple measure of species dominance. This index is calculated as $d = N_{\text{max}}/N_{\text{total}}$, where N_{max} and N_{total} represent the abundance of the most abundant species and the total abundance of all species in the community, respectively. Increased dominance in species-poor sites relative to species-rich sites would modify the relationship between abundance and richness and represents an alternative hypothesis for how decoupling between community richness and abundance might be accommodated.

To investigate the role of dominance in each data set, we calculated d for all communities. However, note that in the range of species richness values considered here, d is low for species-rich communities and hence is not robust to the influence of species richness (Magurran & Phillip 2001). Thus, we propose a modified form of the Berger Parker Index, d_m , which is independent of species richness: $d_m = (d - N_{\text{even}})/(1 - N_{\text{even}})$, where N_{even} is the line of perfect evenness for each value of R (i.e. the dashed line in Fig 3a). This simple measure removes the bias associated with species richness by scaling d to the unit interval. We calculated d_m for all communities in each data set.

STATISTICAL ANALYSIS

All statistical analyses were undertaken in R version 2.10.1 (R Development Core Team 2009).

We initially explored all relationships between predictor and response variables for nonlinearity using Generalized Additive Models, but found that all were linear. As such, we fitted simple linear models for analysing the relationship between species richness and PIE, alpha and E_{var} . Following model fitting, we inspected model residuals for normality and assessed spatial autocorrelation using bubble plots and semi-variograms (Zuur *et al.* 2009). When model residuals were not normally distributed, we applied a log transformation to the response variable and reran the model. In some instances, the residuals of these models were not homogenous. We then refitted the models using generalized least squares (GLS) equations specifying variance structures. GLS models returned similar results, so we present only the results from the original models allowing a direct comparison between our results and those of Buckley & Jetz (2010).

We investigated how d and d_m change with species richness using generalized linear mixed models (GLMMs), with species richness specified as a fixed factor, and location (i.e. south-east

Australia or south-west United States) as a random factor. GLMMs were generated in the *MASS* package version 7.3-7 (Venables & Ripley 2002). As d is a proportion, we specified d as having a binomial distribution relating to the number of dominant and nondominant individuals within the community, where each dominant individual represents a 'success' and each nondominant individual a 'failure' in a discrete number of Bernoulli trials based on the total number of individuals in a community. Therefore, the predicted values of the GLMM represent the probability that a randomly selected individual belongs to the dominant species (Caruso & Migliorini 2007). A logit link function was used for this analysis, and thus, the relationship between d and species richness is linear on a logit scale (Zuur *et al.* 2009). As d_m rescales to the unit interval, it is not a proportion and therefore was fitted with a Gaussian distribution and an identity link function.

Results

For the Australian data set, our results were consistent with Buckley & Jetz (2010), in that we found: (i) no significant relationship between total abundance and species richness (slope \pm CI = 2.534 ± 7.23 , $F_{1,26} = 0.47$, $R^2 = 0.02$, $P > 0.05$); (ii) that alpha was significantly and negatively associated with species richness (slope \pm CI = -0.01 ± 0.00 , $F_{1,26} = 26.27$, $R^2 = 0.50$, $P < 0.01$); and (iii) that PIE was significantly and positively associated with species richness (slope \pm CI = 0.007 ± 0.003 , $F_{1,26} = 22.69$, $R^2 = 0.47$, $P < 0.01$) (Fig. 1). In contrast, the index E_{var} was not significantly associated with species richness in either data set (Australia: slope \pm CI = -0.00 ± 0.00 , $F_{1,26} = 1.26$, $R^2 = 0.05$, $P > 0.05$; United States: $\ln(E_{\text{var}}) \sim \text{SR}$, slope \pm CI = -0.00 ± 0.03 , $F_{1,16} = 0.03$, $R^2 = 0.00$, $P > 0.05$) (Fig. 1e,f).

In a mixed model, in which location (i.e. data set) was specified as a random effect, dominance (d) decreased with increasing species richness (slope \pm CI = -0.09 ± 0.02 , $t = -7.94$, $P < 0.05$; Fig. 2a). This relationship also persisted when d_m was used to measure dominance (slope \pm CI = -0.02 ± 0.00 , $t = -8.70$, $P < 0.05$; Fig. 2b), indicating that dominance declines even when the bias imposed by species richness is considered. In addition, we found that for each data set, the decoupling of abundance and species richness progressively disappeared with the iterative removal of the 1st, 2nd and 3rd most dominant species. After the removal of the top three species in each community, a significant and positive relationship between total abundance and species richness was observed for lizard communities in both south-east Australia and south-west USA (Fig. 3a,b).

Discussion

A positive relationship between the evenness and richness of lizard communities has been postulated for several decades (see Heatwole & Taylor 1987), but with few empirical tests. Here, we found that a positive relationship between evenness and richness in lizard communities does not persist when using an evenness measure robust to the influence of species

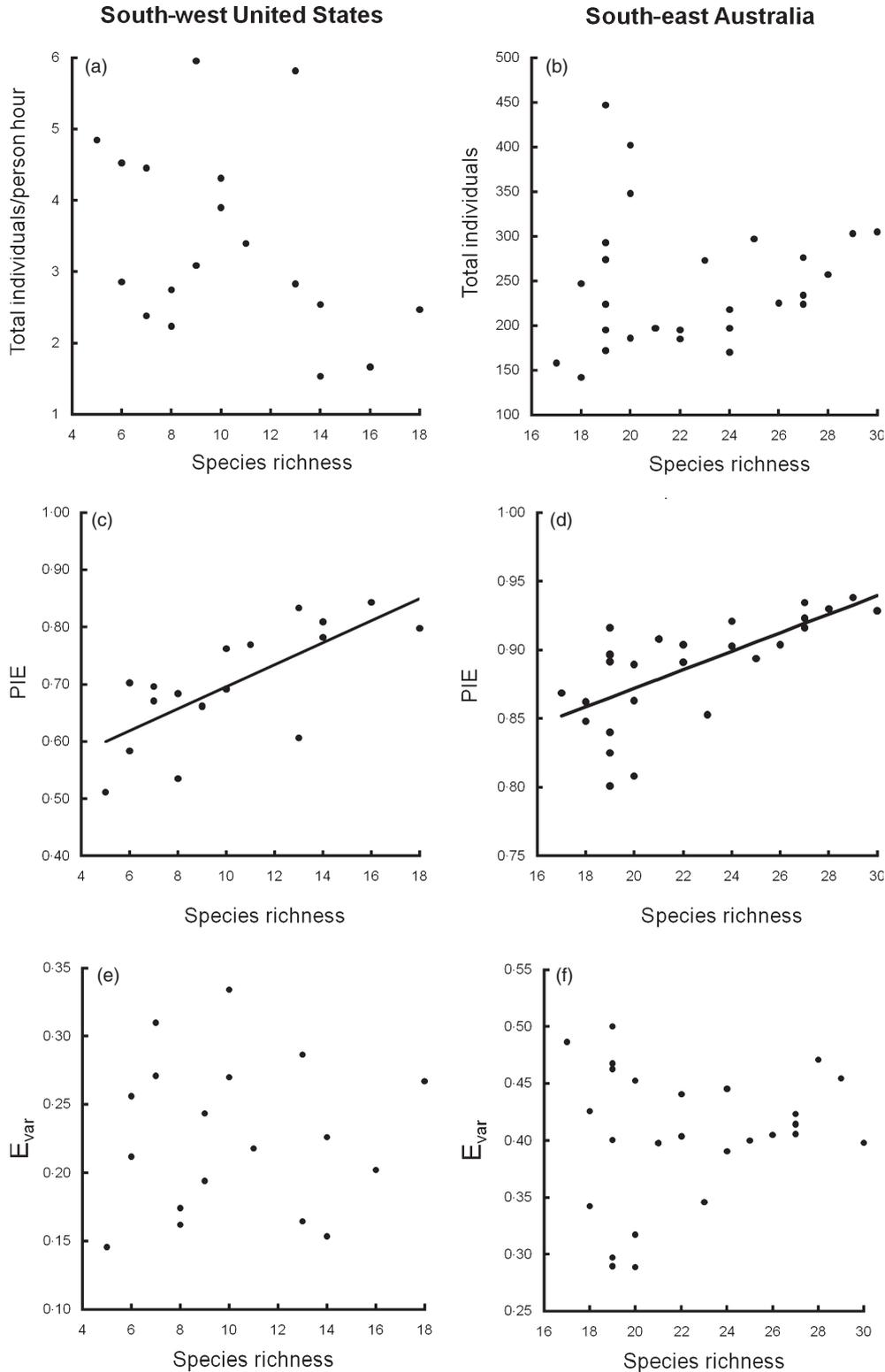


Fig. 1. Relationship between species richness of lizards in south-west United States and south-east Australia and: (a, b) total abundance of all lizards; (c, d) Hurlbert's (1971) probability of interspecific encounter; and (e, f) Smith & Wilson's (1996) E_{var} .

richness. Thus, greater evenness in species-rich communities, as a predicted consequence of mechanisms determining the decoupling of abundance and richness in lizard communities, is not supported by our data from Australia or that of Buckley & Jetz (2010) from the USA.

The absence of a relationship between evenness and richness raises an obvious question; if decoupling is not afforded by a more even distribution of abundances in more species-rich communities, then how *does* this decoupling persist? We propose that a decline in the abundance of dominant

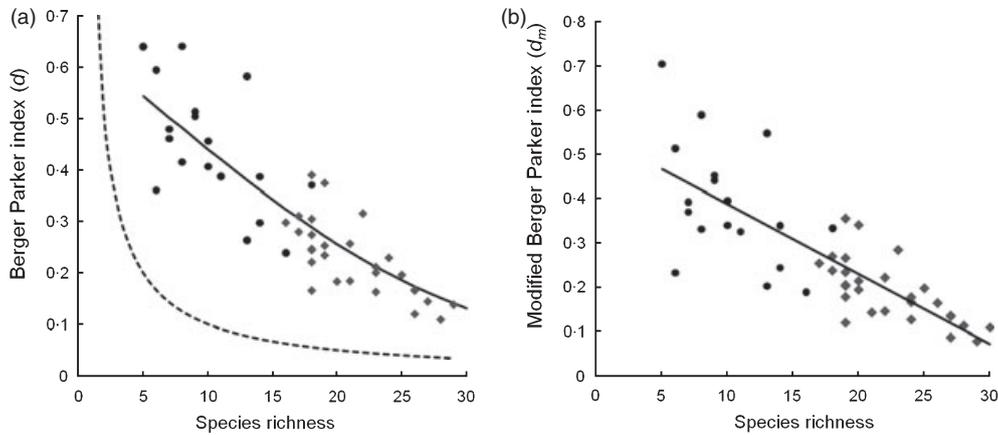


Fig. 2. The relationship between species dominance and species richness in lizard communities in south-east Australia (diamonds) and south-west United States (circles). (a) Dominance expressed as the Berger Parker index, where fitted values of d represent the probability that a randomly selected individual belongs to the dominant species in a community. The dashed line represents dominance in a perfectly even community (Magurran & Phillip 2001). (b) Dominance expressed as the modified Berger Parker Index (d_m) (see text). Solid line for both figures represents model predictions from a generalized linear mixed model.

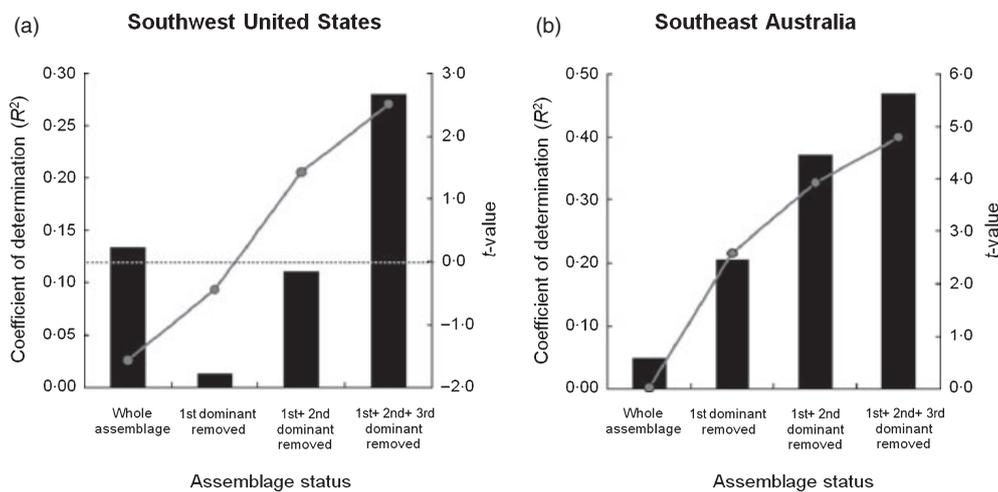


Fig. 3. The relationship between abundance and species richness of lizards with the removal of the 1st, 2nd and 3rd most dominant species, respectively, as indicated by changes in the coefficient of determination (R^2) (solid bars) and t value (i.e. coefficient divided by standard error: grey circles) for lizard communities in (a) south-west United States and (b) south-east Australia. For Fig. 3a, the dashed line highlights where t -values change from being negative (below dashed line) to positive (above dashed line), hence indicating the sign of the variable's coefficient.

species with increasing species richness could also accommodate a decoupling between abundance and richness and thus represents an alternative hypothesis. Decreasing dominance with increasing species richness has been observed in North American bird communities (e.g. Wiens & Dyer 1975), but to our knowledge has not been documented for reptiles. When considering both lizard data sets in a mixed model, with location as a random factor, there was a strong negative relationship between the modified Berger Parker Index of dominance and species richness, indicating that dominance decreases as species richness increases. Furthermore, as dominant species were removed iteratively from each data set, the relationship between abundance and richness became progressively more positive.

The effect of the removal of dominant species was stronger in the Australian data than for that from the

United States. The relationship between abundance and richness became significant in the Australian data following the removal of the single most dominant species in each community; whereas it took the removal of the three most dominant species to reveal a significant relationship in the data from USA. However, the initial relationship between abundance and richness for the latter data set had a negative coefficient, whereas that for Australia had a positive coefficient. The actual change in R^2 , as relationships became progressively more positive with the iterative removal of the n th dominant species, was comparable across data sets.

What causes dominance to decrease as species richness increases, and why might dominant species mask underlying patterns in abundance-richness relationships? We propose ecological release as a possible mechanism leading to the

observed patterns. Ecological release is the expansion of niche space by a species owing to some change in biotic conditions, such as competition or predation (Crowell 1962). Although research on ecological release has been focused mainly in areas characterized by sharp boundaries to species distributions, such as oceanic islands (Case 1975; Cox & Ricklefs 1977; Buckley & Jetz 2007), there is also evidence for ecological release along gradients that impose more gradual constraints on the distributions of species, such as elevation gradients (Noon 1981).

Ambient energy (i.e. solar radiation or temperature) is emerging as a strong driver of reptile richness at regional (Rodríguez, Belmontes & Hawkins 2005; Buckley & Jetz 2010), continental (Powney *et al.* 2010) and global scales (Qian 2010) and strongly influences the richness of lizards in both locations considered here (Buckley & Jetz 2010; D.G. Nimmo, unpublished data). Because ambient energy limits the geographical ranges of reptile species (Guisan & Hofer 2003), local richness varies considerably across climatic gradients. This variability in local species richness is a possible mechanism allowing ecological release across environmental gradients. Species that have adapted thermal tolerances to survive in cooler environments may reach higher abundances in species-poor communities, because of the smaller number of interspecific competitors and hence a greater access to resources. Such species may occupy vacant niche space that is progressively filled as local richness increases (e.g. with increasing temperature), leading to a negative relationship between dominance and species richness. Such locally abundant species may obscure relationships in the underlying community structure.

Conclusions

Our results concur with Buckley & Jetz (2010) with regard to the decoupling of abundance and richness in lizard communities. Together, these two data sets from different continents strongly question the role of the MIH (Wright 1983) as an explanation for richness patterns of lizard species across broad environmental gradients. However, the conclusion that decoupling is associated with a more even distribution of individuals in species-rich communities is not supported by either data set. We propose that a decline in dominance with increasing richness accommodates the decoupling and that ecological release is a mechanism by which such a pattern could arise. Further work on the structure of lizard communities across environmental gradients will help determine whether decoupling of abundance and richness is a general occurrence, and, if so, the mechanisms that best explain and accommodate this pattern.

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References

- Alatalo, R.V. (1981) Problems in the measurement of evenness in ecology. *Oikos*, **37**, 199–204.
- Berger, W.H. & Parker, F.L. (1970) Diversity of planktonic foraminifera in deep-sea sediments. *Science*, **168**, 1345–1347.
- Buckley, L.B. & Jetz, W. (2007) Insularity and the determinants of lizard population density. *Ecology Letters*, **10**, 481–489.
- Buckley, L.B. & Jetz, W. (2010) Lizard community structure along environmental gradients. *Journal of Animal Ecology*, **79**, 358–365.
- Caruso, T. & Migliorini, M. (2007) Statistical notes to “The Berger–Parker index as an effective tool for monitoring the biodiversity of disturbed soils: a case study on Mediterranean oribatid (Acari: Oribatida) assemblages”. *Biodiversity and Conservation*, **16**, 3933–3934.
- Case, T.J. (1975) Species numbers, density compensation, and colonizing ability of lizards on islands in the Gulf of California. *Ecology*, **56**, 3–18.
- Cox, G.W. & Ricklefs, R.E. (1977) Species diversity and ecological release in Caribbean land bird faunas. *Oikos*, **28**, 113–122.
- Crowell, K.L. (1962) Reduced interspecific competition among the birds of Bermuda. *Ecology*, **43**, 75–88.
- Gaston, K.J. (2000) Global patterns in biodiversity. *Nature*, **405**, 220–227.
- Gosselin, F. (2006) An assessment of the dependence of evenness indices on species richness. *Journal of Theoretical Biology*, **242**, 591–597.
- Guisan, A. & Hofer, U. (2003) Predicting reptile distributions at the mesoscale: relation to climate and topography. *Journal of Biogeography*, **30**, 1233–1243.
- Heatwole, H.F. & Taylor, J. (1987) *Ecology of Reptiles*. Surrey Beatty and Sons Pty Ltd, Chipping Norton, NSW.
- Hurlbert, S.H. (1971) The nonconcept of species diversity: a critique and alternative parameters. *Ecology*, **52**, 577–586.
- Lepori, F., Palm, D. & Malmqvist, B. (2005) Effects of stream restoration on ecosystem functioning: detritus retention and decomposition. *Journal of Applied Ecology*, **42**, 228–238.
- Ma, M. (2005) Species richness vs evenness: independent relationship and different responses to edaphic factors. *Oikos*, **111**, 192–198.
- Magurran, A.E. & Phillip, D.A.T. (2001) Implications of species loss in freshwater fish assemblages. *Ecography*, **24**, 645–650.
- Noon, B.R. (1981) The distribution of an avian guild along a temperate elevational gradient: the importance and expression of competition. *Ecological Monographs*, **51**, 105–124.
- Oksanen, J., Kindt, R., Legendre, P., O'Hara, B., Simpson, G.L., Solymos, P., Stevens, M.H.H. & Wagner, H. (2009) *Vegan: Community Ecology Package*. R package version 1.15-4.
- Powney, G.D., Grenyer, R., Orme, C.D.L., Owens, I.P.F. & Meiri, S. (2010) Hot, dry and different: Australian lizard richness is unlike that of mammals, amphibians and birds. *Global Ecology and Biogeography*, **19**, 386–396.
- Qian, H. (2010) Environment–richness relationships for mammals, birds, reptiles, and amphibians at global and regional scales. *Ecological Research*, **25**, 629–637.
- R Development Core Team (2009) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna.
- Rodríguez, M.A., Belmontes, J.A. & Hawkins, B.A. (2005) Energy, water and large-scale patterns of reptile and amphibian species richness in Europe. *Acta Oecologica*, **28**, 65–70.
- Smith, B. & Wilson, J.B. (1996) A consumer's guide to evenness indices. *Oikos*, **76**, 70–82.
- Symonds, M.R.E. & Johnson, C.N. (2008) Species richness and evenness in Australian birds. *The American Naturalist*, **171**, 480–490.
- Venables, W.N. & Ripley, B.D. (2002) *Modern Applied Statistics with S*, 4th edn. Springer, New York.
- Wiens, J.A. & Dyer, M.I. (1975) Rangeland avifaunas: their composition, energetics, and role in the ecosystem. *USDA Forest Service General Technical Report WO-1*, 146–181.
- Wright, D.H. (1983) Species-energy theory: an extension of species-area theory. *Oikos*, **41**, 496–506.

Zuur, A., Leno, F.E., Walker, N.N., Saveliev, A.A. & Smith, G.M. (2009). *Mixed Effects Models and Extensions in Ecology with R*. Springer-Verlag, New York.

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Fig. S1. Relationship between species richness and the probability of interspecific encounters (PIE; Hurlbert 1971) assuming perfectly 'even' communities.

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