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perspective

Causes and consequences of range size variation: the influence of traits, speciation, and extinction

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Abstract. The tremendous variation in species richness observed among related clades across the tree of life has long caught the imagination of biologists. Recently, there has been growing attention paid to the possible contribution of range size variation, either alone or in combination with putative key innovations, to these patterns. Here, we review three related topics relevant to range size evolution, speciation, and extinction. First, we provide a brief overview of the debate surrounding patterns and mechanisms for phylogenetic signal in range size. Second, we discuss some recent findings regarding the joint influence of traits and range size on diversification. Finally, we present the preliminary results of a study that suggests family range size is negatively correlated with contemporary extinction risk in flowering plant species.

Keywords. diversification, ecological limits, key innovations, phylogenetic signal, species richness, trait conservatism

The tremendous variation in species richness among clades has produced widespread support for species selection i.e., the idea that traits influence speciation and/or extinction rates (Heard and Hauser 1995). In plants, putative evolutionarily successful traits include, among other morphological attributes, floral traits involved in sexuality (self-incompatibility; Igić et al. 2008), pollinator guilds (biotic pollination vs. abiotic pollination; Ricklefs and Renner 1994) as well as more specific surrogates of specialization in pollination (floral asymmetry; Sargent 2004). However, from a macroevolutionary perspective, traits appear to play a secondary role to geography in terms of the amount of variation in diversification they explain (Vamosi and Vamosi 2011, Davies and Buckley 2012).

The low explanatory power of the majority of putative key innovations in determining tree imbalance has led some researchers to posit that much evolutionary success of any given lineage lies with idiosyncratic events early in its history (Ricklefs 2003), such as the appearance of a land bridge or uplift of a mountain range (Hughes and Eastwood 2006). One such critical extrinsic deter-

minant of evolutionary success that could be especially important is an early rise in geographical extent i.e., the amount of space occupied by a family (Ricklefs 2003, Davies et al. 2004, Jansson and Davies 2008). However, it is not well understood the degree to which, if at all, intrinsic biological traits influence early increases in geographical extent (Phillimore et al. 2006). It has been suggested that neither geographical nor biological traits influence diversification alone but that certain traits, or trait combinations, may facilitate/impede diversification within particular geographical contexts (Cracraft 1982, De Queiroz 2002).

Range size could be positively associated with net diversification in a number of different ways. For example, the probability of allopatric speciation is predicted to increase with geographical extent as the probability of reduced gene flow among populations increases (Owens et al. 1999, Losos and Schluter 2000). A “geographic potential for speciation” (Owens et al. 1999) may be increased with access to, and subsequent colonization of, new areas (Rosenzweig 1995). Admittedly, establishing a causal arrow has been difficult because one can also imagine that species rich

clades and/or those with high allopatric speciation rates will tend to occupy larger ranges than small clades and/or those with low allopatric speciation rates. We have argued (Vamosi and Vamosi 2010, 2011) that the predictive power of ecozone area and number of ecozones occupied provides evidence, at least in angiosperm families, for a “geographical potential for speciation” (sensu Owens et al. 1999). A finding of a minimum island size threshold for *in situ* speciation in *Anolis* lizards (Losos and Schluter 2000) is also rather direct evidence of a causal effect of geographical area on speciation, rather than the opposite. However, such clear-cut thresholds and resulting patterns are unlikely in most systems, and we encourage more work on these important questions.

Here, we discuss three areas relevant to range size and the origins, maintenance and potential loss of biodiversity. First, we discuss some of the literature relevant to whether there is a phylogenetic signal in the range size of closely related species. Second, we discuss some recent findings regarding the interactive effects of traits, especially putative key innovations, and range size on diversification. Finally, we present the results of a preliminary study investigating the potential benefits of family range size on contemporary extinction risk in flowering plant species.

Is there a phylogenetic signal in range size?

Although we are largely focused on “clade-level” questions related to diversification, the characteristics of ranges of sister species underlies many of the other inferences one would like to make. Two characteristics of ranges of related species have received growing attention to date: size and location/overlap. Focusing on the former, here we: (i) discuss some theoretical expectations that have been put forward regarding range size heritability under different macroevolutionary scenarios, (ii) present some of the (at times opposing) empirical data to date, and (iii) attempt to provide some suggestions for future work.

Arguments have been put forward supporting (e.g., Jablonski 1987, Roy et al. 2009) and rejecting (e.g., Webb and Gaston 2003) heritability of, or more strictly phylogenetic signal in (i.e., the

tendency for closely related species to be more similar to each other than expected by chance), range size. An expectation of more similar range sizes in sister species than expected by chance follows from the observation that sister species often demonstrate phylogenetic signal in various ecological, phenotypic, and behavioural traits. To the extent that organisms with similar body sizes, physiologies, resource requirements, etc. may interact with their environments in similar ways, such species may be predicted to have similar range sizes. Machac et al. (2011) formalized a variant of this notion: that closely related species are likely found in similar geographic regions and, therefore, may be subject to the same “spatiogeographic” constraints. These ideas echo those suggesting that available area may limit the species richness of higher clades (Ricklefs 2007, Rabosky 2009a,b, Vamosi and Vamosi 2010).

Conversely, none of the prevailing speciation scenarios easily leads to a null expectation of equal ranges of nascent species. For example, invoking allopatric speciation, it is not clear why the two descendant species should consistently ‘inherit’ the same range size as the ancestral species whether speciation follows from range splitting or founder dispersal. Although classic schematic representations of allopatric speciation following from barrier formation (i.e., vicariance) tend to split the range of the ancestral species in half, a 50:50 split is no more likely in nature than, say, a 78:22 split (Webb and Gaston 2003, Waldron 2007). An expectation of even ranges following vicariance is further complicated by possibly different competitors, predators, climate, etc. in the two ranges, which collectively should place different limits on the ranges of the focal sister species. Sympatric speciation may in fact (at least initially, and possibly for long time periods) be characterized by the descendant species having a smaller range than the parent species. For example, recent work suggests that the Arrow cichlid (*Amphilophus zaliosus*), endemic to the volcanic crater Lake Apoyo (surface area = 21.1 km²) in Nicaragua, may be the descendant of the more widespread Midas cichlid (*A. citrinellus*) via sympatric speciation (e.g., Barluenga et al. 2006,

Bunje et al. 2007; but see Schliewen et al. 2006). In addition to being present in Lake Apoyo, the Midas cichlid is found in at least four other lakes, including the very large Lake Nicaragua (8264 km²) and Lake Managua (1042 km²). Although there is some controversy regarding the origins of the Arrow cichlid (e.g., Schliewen et al. 2006) and evidence for a complicated evolutionary history for the Lake Apoyo complex (Geiger et al. 2010), what appears reasonably well established is the markedly different range sizes of the ancestral and descendant species. Finally, although they are the least supported modes, neither peripatric nor parapatric speciation scenarios easily lead to a null expectation of equal-sized ranges of the resulting species.

What is the evidence to date for phylogenetic signal, or lack thereof, in range size? Although an exhaustive review is beyond the scope of this article, we discuss a few key works that we hope will encourage the reader to delve deeper into this area of research. Recent interest in these questions was spurred by Jablonski's (1987) analysis of heritability of range sizes of Cretaceous molluscs. With $n = 77$ putative species pairs of fossil bivalves and $n = 95$ putative species pairs of fossil gastropods and borrowing methods developed for quantitative genetic analyses, strikingly high ($h^2 = 0.55$ and 0.63 , respectively) heritability estimates for range size were reported. The validity and generality of these findings were rebutted by Webb and Gaston (2003), who presented the results of a contemporary data set and promoted a different analytical approach for such data sets. For the former, Webb and Gaston (2003) researched range sizes for 103 pairs of contemporary avian sister species. For the latter, they advocated a range asymmetry approach over the standard linear regression used by Jablonski (1987), citing issues of non-normality, especially the high influence of a concentration of points near the origin, and the problem with assigning ancestor-descendant status to the members of contemporary sister pairs. Under their approach, heritability of range size would be reflected by more symmetric ranges than expected by chance; applied to the two data sets, the general trend was for more asymmetry in

range sizes than expected by chance. Furthermore, even when they applied Jablonski's (1987) approach to the contemporary avian data set, they obtained a much lower heritability estimate ($h^2 = 0.27$) than had been observed for fossil mollusks.

Although the generality of patterns and underlying mechanisms is poorly understood, the growing consensus appears to be that range size is heritable in a variety of groups (Waldron 2007). There appears to be an influence of analytical method used (Hunt et al. 2005, Machac et al. 2011) and taxonomic position of the focal species (Waldron 2007) on the degree to which heritability is observed. Birds, for example, may generally have relative low heritability in range size compared to other taxa (reviewed by Waldron 2007), although the underlying mechanism for this outcome appears unknown. Regardless of these findings, it is clear that more studies are needed. For example, in predaceous diving beetles, a group amenable to biogeography and phylogenetic community structure studies (Vamosi and Vamosi 2007, Vamosi et al. 2007), there is great variation in the range sizes of congeners in North America (Larson et al. 2000). A better understanding of range size evolution in this group, as in many others, will minimally require the construction of robust molecular phylogenies, and such efforts are currently underway. Going beyond simply confirming presence/absence of heritability, new approaches such as the Geographic State Speciation and Extinction model (GeoSSE ; Goldberg et al. 2011) hold the promise to further our understanding the influence of range on speciation and extinction.

Dispersal traits have emerged as most influential in determining range size in animal lineages (Böhning-Gaese et al. 2006, Roy et al. 2009). Associations between seed/fruit size and geographical extent in plants point to a common underlying mechanism (Morin and Chuine 2006, Kolb et al. 2007). Some indications also exist for relationships between large geographical extent and an outcrossing mating system (Lowry and Lester 2006). Similarly, even if range size itself is not strongly heritable, range size could still exhibit a phyloge-

netic signal because of the phylogenetic signal inherent in phylogeography i.e., related species tend to inhabit the same continents or ecozones and therefore tend to have similar abiotic limits exerted upon them (Machac et al. 2011). From a broad-scale macroecological perspective, these arguments are the subject of investigations of Rapoport's Rule (that temperate species have larger ranges on average than tropical species). The effect of range size could thus play a role in the latitudinal biodiversity gradient (Stevens 1989, Davies et al. 2004) although whether temperate species have generally larger ranges remains unresolved (Weiser et al. 2007). In general, the small ranges and more specialized niches of tropical species are thought to reduce competitive exclusion (Stevens 1989), thus fostering high alpha diversity observed in tropical communities, although others have postulated that small ranges may be the result of many speciation events in the past (Phillimore et al. 2006). Incorporating metrics of energy availability (UV, temperature, evapotranspiration) into models of latitude, range, and diversification rate for 86 angiosperm sister-families revealed that range and latitude were inextricably linked and had more influence on diversification rates than energy availability (Jansson and Davies 2008). Considering latitude was retained in the minimum adequate models, it suggests that other factors, potentially correlated with latitude, may play a role in driving diversification. These results indicate that complex interactions between key traits, latitude (or associated traits), and range are likely at play.

Interactive effects of range size and traits on diversification

Why should range size of a clade (e.g., a family) have any bearing on its species richness? Recent studies have found that lineages may reach something akin to a carrying capacity, with the majority of diversification occurring when a clade originates (Rabosky 2009 a,b, Vamosi and Vamosi 2010, 2011), as observed in the adaptive radiation of honeycreepers (Drepanididae) and *Drosophila* in Hawai'i following initial invasion and establishment. Rabosky (2009a) demonstrated a lack of a

significant relationship between clade age and clade richness in five groups, and modeling efforts showed that density-dependent processes best fit observed patterns in avian tribes. In an in-depth analysis of factors associated with diversification in angiosperms, Vamosi and Vamosi (2010) also observed a non-significant relationship between family age and species richness in 409 families. Furthermore, the two best-supported models explaining the variation among families in species richness included available area, such that families found in larger and/or more ecozones tended to contain more species than those found in smaller and/or fewer ecozones (see also Vamosi and Vamosi 2011). Admittedly, our metric for geographical potential for diversification was rather coarse, and one can envision that environmental heterogeneity could be another contributing factor. Remarkably high diversification rates in Andean *Lupinus* are consistent with a positive influence of habitat complexity (and opportunities for allopatric speciation) (Hughes and Eastwood 2006), although there is currently insufficient data from enough systems to make general statements about the relative importance of available area versus habitat complexity.

Available area and environmental heterogeneity may thus be factors that place limits on diversification (Ricklefs 2007, Rabosky 2009a), such that speciation declines as competition increases with the ever-increasing number of species within a particular clade (Phillimore and Price 2008). First, a trait may alter the ability of a lineage to expand its geographical extent, either by affecting life history (Morin and Chuine 2006) or dispersal capacity (Oakwood et al. 1993, Roy et al. 2009), which then in turn increases the carrying capacity of the lineage. Second, certain traits may appear to be key innovations by facilitating greater species packing upon a landscape (e.g., through increased specialization). Thus, ecological limits are present but the carrying capacity is set higher for some lineages over others for a given amount of space. Although not a key innovation in the same sense, an important contributor to this pattern might be if the bulk of diversification occurs within the tropics, as the tropics has long been acknowl-

edged for supporting more species per unit area (Pianka 1966, Currie and Paquin 1987). Teasing apart these effects, Vamosi and Vamosi (2011) found that certain traits do play a role upon this backdrop of range effects and can act as key innovations through two main mechanisms: by increasing speciation through increased specialization within a given area (e.g., zygomorphy), being associated with increases in the amount of area occupied (e.g., herbaceousness), or some combination of the two (e.g., tropicity).

Family range size and contemporary extinction risk in flowering plant species

There is general agreement that we are currently facing a biodiversity crisis of a magnitude rarely seen in the history of life (e.g., Koh et al. 2004). Undeniably, worrisome rates of species loss are being documented and/or projected in many groups, including amphibians (Sodhi et al. 2008), sharks (Myers et al. 2007), and angiosperms (Vamosi and Wilson 2008). However, our ability to predict extinction risk is still rather poor for most species. Large range size appears to have buffered some groups from past extinction, such as marine invertebrate genera (Payne and Finnegan 2007). It has been suggested that range size is the best predictor of extinction risk in angiosperms (Hubbell et al. 2008) whereas other evidence indicates that the location of a species range may be more important (Feeley and Silman 2009). At the family level, it originally was thought that species richness does not buffer extinction risk, based on the apparent finding that large families contain more locally rare species (Schwartz and Simberloff 2001). Conversely, a more recent global scale analysis found that species in small families are more often at risk of extinction than expected (Vamosi and Wilson 2008). Notably, none of the latter three analyses (i.e., Schwartz and Simberloff 2001, Vamosi and Wilson 2008, Feeley and Silman 2009) considered the possible influences of ecological/life history traits, yet clearly such traits such as woodiness, latitude, and breeding system have their own effects (Vamosi and Vamosi 2005, 2008, Sjöström and Gross 2006).

Here, we investigate the factors associated

with contemporary extinction risk in angiosperm families. Recent analyses of variation in diversification rate among angiosperm families concluded that family range was the best predictor, with relatively little influence of ecological or life history traits (Vamosi and Vamosi 2010, 2011). Thus, the reason why previous studies have found that species richness as an important predictor of extinction risk may simply have been examining the underlying covariation between species richness and range. Motivated by these findings, we sought to determine whether family range characteristics, species traits and/or species richness predicted extinction risk in angiosperms (see Box 1 for methods).

Extinction risk exhibited low, albeit statistically significant, phylogenetic signal ($\lambda = 0.046$, $P = 0.018$). Examination of AICc values revealed that model 11 (i.e., extinction risk $\sim$ range size + species richness + range size $\times$ species richness) was the best approximating model (Table 1). Considering families with below average species richness, log-odds of threatened species declined with increasing family range size (Figure 1). Proportion of threatened species tended to be lower overall for families with above average species richness, but there was no clear association with range size (Figure 1). With reference to Akaike weights, none of the other models were well supported by the data (all evidence ratios > 10), although those that included range size and/or species richness explained moderate amounts of variation in the response variable (Table 1). Explicitly considering several traits hypothesized to influence speciation and extinction rates increased the amount of unexplained variation to a very slight degree ($R^2 = 0.38$ vs. 0.32 for the full model vs. model 11, respectively).

Our results reveal a predominant interactive effect of range size and species richness on risk of extinction in angiosperm families. While species-poor families tend to have the greatest proportion of their species at risk overall, it is those with relatively small ranges that are most at risk of losing a significant proportion of their species. These results concur with, and extend those, of an earlier study that used a slightly different

Box 1: Methods for extinction risk analyses

Information on the number of threatened species per family—i.e., the sum of species having the IUCN threat categories (v3.1) of Vulnerable (VU), Endangered (EN), and Critically Endangered (CR)—was gathered from the IUCN Red List (see Vamosi and Wilson 2008 for detailed description of methods). We found 16,498 angiosperm species threatened (or 7.48% of the 246,317 described species). Data on growth form (woody, herbaceous, both), fruit type (fleshy, dry, both), breeding system (cosexual, dioecious, both), floral symmetry (actinomorphic, zygomorphic, both), range mid-latitude, range size, and species richness were taken from Vamosi & Vamosi (2010). Overall, we obtained data for all seven variables for 409 families, representing an estimated total of 231,583 species. Species richness was log-transformed, and range size was cube-root transformed prior to analyses. Traits were then mapped onto the fossil-calibrated angiosperm consensus tree, modified from Davies et al. (2004; see Vamosi and Vamosi 2010 for details). This tree collapses uncertain nodes (i.e., those with <80% bootstrap support) to polytomies making the phylogeny as insensitive to tree uncertainty as can be reasonably accomplished with a dataset of this size.

Associations between various trait combinations and proportion of species at risk were assessed within a phylogenetic generalized least squares (GLS) framework (Freckleton et al. 2002). The phylogenetic covariance matrix was multiplied by a phylogenetic signal value (λ), ranging from 0 (no phylogenetic autocorrelation) to 1 (maximum phylogenetic autocorrelation). We follow Freckleton et al. (2002) in formally reporting only the results of the phylogenetic GLS analyses, but note that non-phylogenetic GLM analyses produced highly congruent results (S.M. Vamosi unpublished), likely because of relatively weak phylogenetic signal for the traits and models (Table 1) considered.

We applied an information-theoretic approach to model selection, competing a limited number of models defined a priori based on inferences from previous literature (e.g., Verdú 2002, Vamosi and Vamosi 2004, 2005, 2008, 2010). We defined a set of 19 candidate models (Table 1). Model 1 was the highest-order “global” model that could be run without encountering singularities, and Model 2 was a reduced version of Model 1, including all seven main effects but no second-order interactions. Models 3–8 were largely “trait-based” models, 9–12 were models that focused on possible buffering effects of range size and species richness on extinction risk, and 13–19 considered each main effect on its own. The best approximating model was selected based on its AICc (i.e., small sample size AIC) score.

Because there is the possibility of some amount of circularity in our data (i.e., species have a higher probability of being Red-listed if they have restricted distributions and small-ranged families necessarily are composed of species with small ranges), we removed 50 families with ranges less than 58,1540 km² (i.e., approximate area of Madagascar) and reanalyzed the remaining subset. The results presented are qualitatively robust to the exclusion of these families (S.M. Vamosi unpublished). While wanting to account for this possible circularity, we did not expect that it had an undue influence because (i) with the exception of monotypic families, species are listed based on their characteristics rather than on those of higher taxonomic groupings (e.g., family) they belong to, and (ii) previous studies have found that large-ranged families often are composed of many species with small ranges (Vamosi and Vamosi 2010). Certainly, if family range size was a consideration, then one would not observe listed species from large-ranged families such as Rosaceae, Poaceae, or Cyperaceae. We suggest that future investigations of similar data consider applying structural equation models.

approach (Vamosi and Wilson 2008). Vamosi and Wilson (2008) used randomizations to show that species in small families, especially monotypic ones, were more likely to go extinct in the next

100 years than species in species-rich families, resulting in projected higher losses of phylogenetic diversity than expected by random chance.

It is striking how similar our findings are to

Figure 1. Relationship between range size and proportion of threatened species for 409 angiosperm families. For the graphic, families were grouped by species richness, with an equal number of families in the (a) low, (b) medium, and (c) high categories, to illustrate the interaction between range size and species richness on proportion of threatened species.

global patterns in amphibian extinction (see Sodhi et al. 2008) considering the differences in the biology of the two groups. In the analysis of amphibians, which also was conducted using an information-theoretic approach, the best model included geographic range and body size, although range alone explained nearly half of the variance deviance in threat risk. Furthermore, other traits such as habitat type and sexual system contributed little additional explanatory power, in contrast to recent finding of the vast importance of biological traits found in carnivores (Cardillo et al. 2004). While previous studies examining isolated traits or areas have found that angiosperm traits are predictive in terms of extinction risk (Sjostrom and Gross 2006), a global combined analysis indicates that their influences are likely to be localized and clade-specific, in comparison to the predominant influences of range and taxon size.

Finally, Sodhi et al. (2008) found very little phylogenetic signal to threat risk. We similarly found low phylogenetic signal for extinction risk in angiosperm families, which mirrors the moderate

signal for diversification rate and total lack of signal for species richness (Vamosi and Vamosi 2010). The low signal for extinction risk may be caused by where human disturbance is greatest, which may not have a predictable geographical signal but is instead influenced by species-specific exploitation and socio-political boundaries (Vamosi and Vamosi 2008). In contrast to a previous study that used the number of species at risk in countries (Vamosi and Vamosi 2008), the best model in our analysis did not include latitude, indicating that the influence of latitude is largely only of importance in non-phylogenetic analyses, where species belonging to species-poor and species-rich families are combined in a single analysis. Because speciation rates may be higher at tropical latitudes (Jansson and Davies 2008) tropical families are rarely species-poor (Vamosi and Vamosi 2010). In effect, the increased diversification in the tropics appears to mask the main effects of increased extinction risk caused by human-induced disturbance (Haskell and Adhikari 2009). Our analysis indicates that both temperate and

Table 1. Summary of a priori models of extinction risk in 409 angiosperm families.

Model	Terms	λ	$\log(L)$	K	AICc	Di	wi	R^2
1	All main effects and second-order interactions	<0.01	−619.74	29	1302.07	21.81	0	0.38
2	All main effects	0.01	−659.19	8	1334.74	54.48	0	0.24
3	G, F, Z	0.01	−708.02	4	1424.13	143.87	0	0.04
4	F, Z	0.03	−713.04	3	1432.14	151.88	0	0.02
5	G:F	0.02	−708.01	4	1424.11	143.85	0	0.04
6	G:B	0.02	−709.47	4	1427.04	146.78	0	0.03
7	F:B	0.04	−710.04	4	1428.17	147.91	0	0.03
8	Z:S	0.03	−658.97	4	1326.04	45.78	0	0.24
9	G, L, R, S	0.02	−658.84	5	1327.83	47.57	0	0.24
10	L, R, S	0.03	−659.26	4	1326.61	46.35	0	0.24
11	R:S	0.06	−636.08	4	1280.26	0	1	0.32
12	L:R	0.05	−670.51	4	1349.12	68.86	0	0.20
13	G	0.02	−709.46	2	1422.96	142.70	0	0.03
14	F	0.05	−715.84	2	1435.72	155.46	0	<0.01
15	B	0.05	−715.62	2	1435.26	155.00	0	<0.01
16	Z	0.03	−712.54	2	1429.11	148.85	0	0.01
17	R	0.04	−671.89	2	1347.80	67.54	0	0.19
18	S	0.03	−658.99	2	1322.01	41.75	0	0.24
19	L	0.06	−704.27	2	1412.57	132.31	0	<0.01

Variables: lambda statistic of model (λ), maximized log-likelihood ($\log(L)$), number of parameters (K), small sample Akaike's information criterion (AICc), AIC difference between model i and best model (Di), Akaike weight (wi), and adjusted R^2 values. Model terms: breeding system (B), fruit type (F), growth form (G), mid-latitude (L), cube root-transformed range size (R), log-transformed species richness (S), and floral symmetry (Z). The best model (i.e., AICmin) is indicated in bold.

tropical species belonging to small families with restricted ranges are at greater risk, supporting the call for the urgent targeting of species-poor, geographically restricted angiosperm families for conservation prioritization (Sodhi et al. 2008, Vamosi and Wilson 2008).

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