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Patterns in the diversity of the world's land vertebrate genera

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ABSTRACT

Background: The number of species of terrestrial vertebrate in one of the world's great zoological regions fits a linear combination of area (A) and one climatic variable – either annual actual evapotranspiration (AE) or mean annual temperature (T) – with an R^2 of 0.97. The same is true of species diversity in the four separate classes of terrestrial vertebrate; their R^2-values range from 0.90 to 0.95.

Goals: Determine whether the number of genera, G, fits the same or a similar pattern. Measure the relationship between G and S (the number of species). Estimate the effect of total breakdown of biogeographical barriers on G.

Data: The global terrestrial vertebrate data sets of the World Wildlife Fund. We used 755 of their 825 ecoregions and all 24,992 species in those 755 ecoregions. The WWF ecoregion data sets have names, locations, ID numbers, areas, and 102 climatic variables.

Results: The patterns for area, temperature, AE, and genera closely follow the patterns for species. Area, by itself, significantly fit the number of genera in the zoological regions. But a linear combination of log A and log AE significantly improved that fit. It closely and significantly fit log G ($R^2 = 0.972$). The same was true of a linear combination of log A and T ($R^2 = 0.964$). Each of the separate classes of vertebrate exhibited the same patterns as total G, although their R^2-values were slightly less. Neither climate variable was significant by itself in any case. G also fit the number of species very closely ($R^2 = 0.99$). The fit is a power function with a coefficient of 0.77, so that there are more species per genus in provinces with high than low diversity. The Neotropics (most diverse) have 5.22 species per genus; Hawaii (least diverse) has 1.74 species per genus. The advent of the Homogocene (complete homogenization of the world's zoological regions) would cause the extinction of 49% of her terrestrial vertebrate genera, leaving sustainable only 2239 of the 4416 now sustainable. In addition, loss of natural terrestrial area would further reduce sustainable G. For example, loss of 80% of the area (the

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currently sanctioned international hope is to protect 20%) would lead to the extinction of 54% more genera, leaving only 1021.

Keywords: global generic diversity, conservation biology, New Pangaea, World Wildlife Fund.

INTRODUCTION

The number of species, S, in a zoological region is determined largely by that region's area and climate (Rosenzweig *et al.*, 2012). For the world's land vertebrates, the relationship accounts for more than 97% of the variance. Moreover, to a great extent, evolutionary ecology understands the mechanisms behind the correlation of S with area (Rosenzweig, 1995), although not that with climate.

In contrast, very little is known about the variable(s) that might account for the number of genera in a zoological region. Flessa (1975) did ask how the number of mammal genera varies with area, but we know of no other investigation of the question until now.

In this work, we study the same database that produced the species results cited above, but we search for patterns relating to the number of genera. Somewhat to our surprise, we show that the genus patterns are much the same as the species patterns: the number of genera in a zoological region is determined largely by that region's area and climate. Also, the genus patterns – like the species patterns – account for 97% of the variance in generic diversity among zoological regions. The equations that fit the two taxonomic levels do differ in one important detail: the relationship of species diversity to area is closer to linear than is the relationship of generic diversity to area.

We shall discuss the considerable importance of the genus patterns for conservation biology. In particular, our results suggest that breakdown of biogeographical borders and homogenization of the world's biota pose a more serious threat to generic diversity than to species diversity. We also set out some fascinating questions about the origin and maintenance of genera, questions suggested by the patterns themselves. At this point, we do not understand why the genus patterns echo the species patterns. But we will show that the number of genera might as well be thought of as a deterministic function of the number of species; the regression of the first on the second leaves very little variance unaccounted for ($R^2 = 0.99$).

METHODS

We used three terrestrial data sets of the World Wildlife Fund as they existed in mid-2006 (evolutionary-ecology.com/data/2771Wildfinder.pdf). The basis of these data sets is WWF's division of the world's land into ecoregions. Ecoregions are biological entities; they ignore political borders of any sort. Each ecoregion is intended to contain a small, related set of habitats whose variation is about the same as the variation of habitats in any other ecoregion. The borders of a given ecoregion depend on the expert ecological opinions of WWF scientists – as such, they may not be perfect, but they represent a vast improvement over the arbitrary borders of states and nations.

One WWF ecoregional data set contains the physical characteristics of all ecoregions – their areas, etc. It also registers their code name and the zoological region to which WWF assigned them. The second ecoregional data set contains 102 climatological characteristics of each ecoregion. From these we chose the same subset used by Rosenzweig *et al.* (2012): mean annual temperature (T, °C) and mean annual actual evapotranspiration (AE, mm). AE is a surrogate for net plant productivity, as shown in Rosenzweig *et al.* (2012).

The third data set lists each ecoregion and all the land vertebrate species that each one contains.

Data reduction

Each ecoregion was assigned to the same zoological region as it had been in Rosenzweig *et al.* (2012). Most of the nine regions correspond to traditional ones as designated in the WWF data set. However, we split out three smaller ones because of their high endemicity: Madagascar, Hawaii, and New Zealand. We redrew (slightly) the border (in Mexico) between the Nearctic and Neotropics. Again, we did this based on endemicity. And again, what we used for this study repeated exactly what we had used for its predecessor.

We wished to search for generic patterns among the zoological regions, i.e. those areas that obtain new species from endemic speciation. Many islands, however, contain a mixture of endemic and immigrant species, which might mask the signal of endemic dynamics. Such islands were deleted from the study just as they had been from the previous one. (For a list of the ecoregions used in this study, as well as the zoological region each ecoregion was assigned to, see evolutionary-ecology.com/data/2771RegionList.txt.)

We reused the data sets that were used for species except that we added four columns to register the number of genera in each class (Amphibia, Reptilia, Mammalia, Aves) region-by-region. To obtain these numbers, we wrote a script using Rfi statistical analysis software (R Development Core Team, 2007) to query the data sets and output the totals.

Table 1 shows the reduced data ready for analysis.

Data manipulation

From Table 1, we generated eight new variables: total number of genera (all four classes combined); common logarithms of the five genus diversities; log AE; and log A.

Table 1. The reduced data from which we generated the derived and composite variables and then performed the analyses

Province	Area (km^2)	Temperature (°C)	AE (mm)	Amphibia	Aves	Mammalia	Reptilia
Palearctic	52 935 176	8.07	281.13	65	447	275	172
Nearctic	21 138 284	5.76	444.53	48	312	130	133
Africa (sub-S)	20 897 996	24.25	768.86	88	465	274	213
Neotropics	19 189 404	21.88	1039.22	165	964	316	316
Australasia	8 928 949	21.97	525.78	59	475	184	194
Indo-Malaysia	8 197 050	24.26	945.31	79	472	249	269
Madagascar	591 548	22.12	939.44	20	152	57	54
New Zealand	265 601	10.32	397.08	1	51	2	5
Hawaii	16 712	22.00	902.99	0	49	1	0

Note: AE = actual evapotranspiration; sub-S = sub-Sahara.

Data analysis

We performed single-variable and two-variable least-squares linear regressions on the data of Table 1, both class-by-class and for all classes combined. The two-variable studies used either log A and T, or log A and log AE. Note that because Hawaii has no native Amphibia or Reptilia, all separate regressions for these two classes used only eight points.

RESULTS

Single-variable regressions

Area (A) – All regressions use log A.

All land vertebrate genera: $\log G = -0.347 + 0.46 \log A$ ($P = 0.0003$; $R^2 = 0.86$)
Reptilia: $\log G = -2.28 + 0.63 \log A$ ($P = 0.007$; $R^2 = 0.73$)
Amphibia: $\log G = -3.43 + 0.73 \log A$ ($P = 0.007$; $R^2 = 0.72$)
Mammalia: $\log G = -3.36 + 0.79 \log A$ ($P = 0.0002$; $R^2 = 0.87$)
Aves: $\log G = 0.04 + 0.36 \log A$ ($P = 0.0007$; $R^2 = 0.83$)

The regression between area and number of genera was significant in every case.

Actual evapotranspiration (AE) – All regressions use log AE.

All land vertebrate genera: not significant ($P = 0.87$)
Reptilia: not significant ($P = 0.39$)
Amphibia: not significant ($P = 0.35$)
Mammalia: not significant ($P = 0.98$)
Aves: not significant ($P = 0.82$)

The regression between actual evapotranspiration and number of genera was not significant in any case.

Temperature (T) – All regressions use mean temperature, T.

All land vertebrate genera: not significant ($P = 0.69$)
Reptilia: not significant ($P = 0.32$)
Amphibia: not significant ($P = 0.33$)
Mammalia: not significant ($P = 0.78$)
Aves: not significant ($P = 0.66$)

The regression between temperature and number of genera was not significant in any case.

Two-variable regressions

Area and actual evapotranspiration

All land vertebrate genera: $\log G = -3.37 + 0.508 \log A + 0.968 \log AE$ ($P < 0.00001$; $R^2 = 0.972$)
Reptilia: $\log G = -6.03 + 0.667 \log A + 1.27 \log AE$ ($P = 0.001$; $R^2 = 0.930$)
Amphibia: $\log G = -8.02 + 0.775 \log A + 1.55 \log AE$ ($P = 0.0007$; $R^2 = 0.944$)
Mammalia: $\log G = -7.68 + 0.858 \log A + 1.38 \log AE$ ($P = 0.0001$; $R^2 = 0.952$)
Aves: $\log G = -2.53 + 0.404 \log A + 0.823 \log AE$ ($P = 0.00011$; $R^2 = 0.952$)

In all five cases, a linear combination of log A and log AE closely and significantly fit the number of genera in zoological regions. Both independent variables were significant. Figure 1a graphically displays the accuracy of the fit.

Area and temperature

All land vertebrate genera: log $G = -0.97 + 0.488$ log $A + 0.025\ T$ ($P < 0.00001$; $R^2 = 0.964$)
Reptilia: log $G = -2.88 + 0.641$ log $A + 0.032\ T$ ($P = 0.002$; $R^2 = 0.912$)
Amphibia: log $G = -4.12 + 0.742$ log $A + 0.037\ T$ ($P = 0.003$; $R^2 = 0.898$)
Mammalia: log $G = -4.26 + 0.830$ log $A + 0.036\ T$ ($P = 0.0001$; $R^2 = 0.948$)
Aves: log $G = -0.481 + 0.389$ log $A + 0.021\ T$ ($P = 0.0002$; $R^2 = 0.939$)

In all five cases, a linear combination of log A and T closely and significantly fit the number of genera in the zoological regions. Both independent variables were significant. Figure 1b graphically displays the accuracy of the fit.

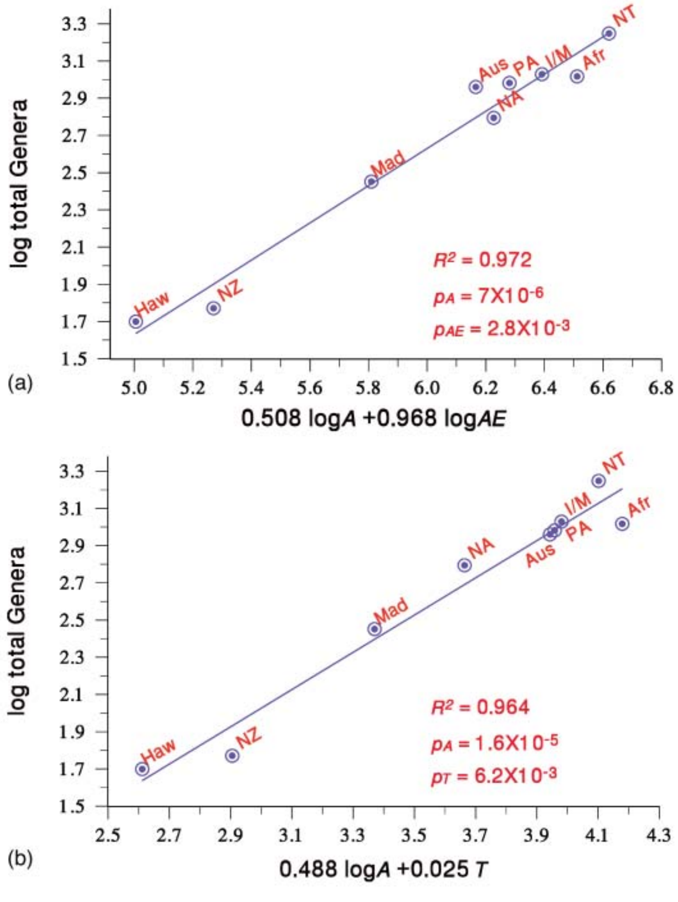

Fig. 1. The number of genera in a biogeographical province is closely fit by a linear combination of area and a climatic variable. (a) Area and annual actual evapotranspiration (mm). (b) Area and mean annual temperature (°C). See Table 1 for the list of provinces.

DISCUSSION

In every case, area, by itself, fit generic diversity significantly. That was not true of either temperature alone or actual evapotranspiration alone. Neither climatic variable fit significantly in even a single case. However, both climatic variables proved significant in reducing the residual variance of the area regressions. The result was a remarkably good fit in all cases: all but one returned an R^2-value greater than 0.91, and that one exception had $R^2 = 0.898$.

Although area was the variable of first choice in every case, we found no statistical evidence that would lead us to prefer either temperature or actual evapotranspiration as the second variable. Each did an excellent job of providing a signal to represent the climate. But the fact that both area and a climatic signal are required to account successfully for taxonomic diversity at the regional scale is no surprise (Rosenzweig *et al.*, 2012).

Comparison with the results for species

Except for the value of the regression coefficients, our results for generic diversity closely mirror those obtained for species diversity (Table 2). All the genus regression coefficients are smaller than those for species. As you will soon agree, it could not be otherwise.

All species belong to precisely one genus. But many genera have more than one species. As species are added to a region, they may belong to an already established genus or constitute a new one. If the latter case were always true, then the genus coefficients would be identical to the species coefficients. But because some new species belong to established genera, the genus coefficients must be less than the species coefficients. The species versus genus differences of the log *A* coefficients have profound conservation implications and we discuss them below in a separate section.

However, we can imagine an alternative mathematical possibility, albeit perhaps a remote one. Suppose, over low diversities, new species do contribute fewer than a single genus, as we

Table 2. Species-level and genus-level regression summaries (slope coefficients; R^2) for area and annual actual evapotranspiration as well as area and mean annual temperature

	Total	Amphibia	Reptilia	Mammalia	Aves
Species level					
log *A*, log *AE*	0.66, 1.4	0.922, 2.19	0.612, 1.43	1.07, 1.74	0.551, 1.14
	(0.973)	(0.931)	(0.931)	(0.952)	(0.934)
log *A*, *T*	0.635, 0.033	0.887, 0.048	0.594, 0.036	1.04, 0.041	0.534, 0.030
	(0.970)	(0.869)	(0.937)	(0.943)	(0.947)
Genus level					
log *A*, log *AE*	0.508, 0.968	0.775, 1.55	0.667, 1.27	0.858, 1.38	0.404, 0.823
	(0.972)	(0.944)	(0.930)	(0.952)	(0.952)
log *A*, *T*	0.488, 0.025	0.742, 0.037	0.641, 0.032	0.830, 0.036	0.389, 0.021
	(0.964)	(0.898)	(0.912)	(0.948)	(0.939)

Note: All coefficients are significant, as are all R^2-values. The single systematic difference is that genus-level regression coefficients, though no less significant, are smaller except in the case of area/temperature/reptilian genera.

argue in the previous paragraph. But then suppose that once a large enough pool of species has accumulated, new species somehow promote the splitting up of established genera. Then, a new species could result in more than one new genus! The result would be a non-linear coefficient – low over low G but rising over high G until it actually exceeded its parallel S-coefficient. We hasten to add that although such non-linearity is mathematically possible, we have no evidence for it whatsoever.

Number of genera closely follows the number of species

The similarity of the genus and species results suggests a close correlation between these two measures of diversity. In fact, the correlation is very tight. Knowing how many species exist in a region is tantamount to knowing how many genera live there. The power regression (Fig. 2) is $G = 1.59\ S^{0.77}$ ($P = 2.7^{-10}$; $R^2 = 0.99$). We did not perform this regression for separate classes, although the reader will find all the numbers needed to do it in Table 1.

We were actually astonished at the precision of the pattern. If genera are so arbitrarily assigned, then how is it that taxonomists did it so predictably? Figure 2 does not look very random to us.

Our result is hardly the first to observe a good correlation between the numbers of species and genera. Among others, Kelly and Bowler's (2005, Fig. 4a) pattern is rather striking because it studies woody plants all over the world using Gentry's database. It also shows that the pattern is maintained within several of the world's continents. But Gentry's data came from 100 m^2 quadrats. We believe our study is the first to enumerate all species in almost all the world's terrestrial area.

Only a statistical pattern

Despite the similarity between the species and genus results, they are far from being equals in intellectual merit. The species patterns began with a theory of provincial diversity (Rosenzweig, 1975), which identified the area of species' ranges as likely to be a variable that

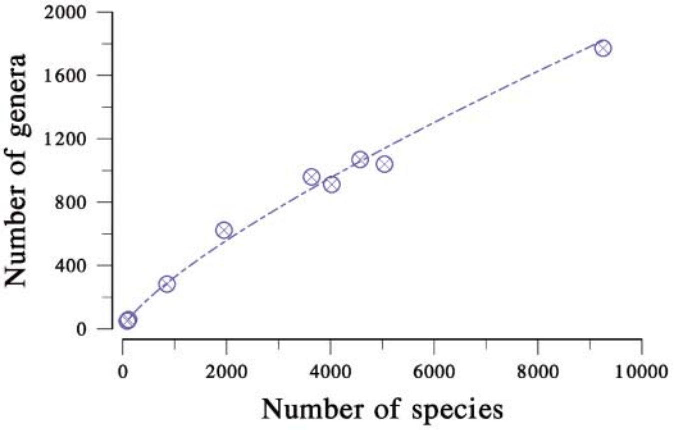

Fig. 2. The number of genera in a biogeographical province is a power function of the number of species $G = 1.59\ S^{0.77}$ ($P = 2.7^{-10}$; $R^2 = 0.99$). Hawaii, with the fewest species, has 1.74 species per genus, whereas the Neotropics, with the most species, has 5.22 species per genus.

produces negative feedback and steady states of *S*. This theory has been reinforced over the years (Rosenzweig, 1995) and so provided the impetus for studying *S* versus *A*. No similar theory of climate and *S* exists (although many attempts have been made to generate one). Given the failure of area to account fully for large-scale differences in *S* (Rosenzweig, 1995), and the immense number of species in the tropics combined with the very few in polar regions, it would have been foolhardy not to include climate in the study of *S*. The data demanded it.

However, the genus pattern investigations simply followed the lead of the species pattern investigations. We had no theory to provide hypotheses, so we did not know what to expect. Yes, we certainly knew that the number of genera is correlated with the number of species; it has to be. But we were quite surprised at the strength of the correlation. Bottom line: when it comes to generic diversity, we confess to having conducted a statistical fishing expedition. Had we come home with only minnows we would have had no reason to complain. But instead of minnows, we seem to have caught a blue-fin tuna. Why were we so lucky?

What is a genus and what causes them to originate?

Stebbins (1956, p. 235) put it very well: 'Do the evolutionary principles underlying the origin of genera differ materially from those which operate in the origin of species?' If there is no difference, then what we found was to be expected.

As with *S*, the answer to Stebbins' question must lie in feedback dynamics, in our case, the feedback dynamics of generic origination and extinction. What are these dynamic processes and what is the nature of negative feedback in them?

In a sense, extinction is easy. A genus becomes extinct when its last species does. So genus extinction rates will follow species extinction rates. They should also follow the ratio 'species-per-genus'; other things being equal, systems with high ratios should have lower genus extinction rates.

Origination rates for genera are a much more complicated issue. A new genus is born when a taxonomist splits an old one in two. Clearly, there is an upper limit to the rate of this process. No species belongs to more than one genus, so, as the ratio 'species-per-genus' declines, so will the rate of genus origination.

Is that all? Are genera merely the result of the collective but arbitrary decisions of thousands of professional taxonomists? Is the growth rate of named genera controlled by negative feedback merely because taxonomists grow more and more reluctant to approve and adopt further generic splitting as fewer and fewer species remain in recognized genera? We think not.

First, it would seem that if generic distinctions are simply arbitrary we could not have expected such regularity in our comparisons of generic results to species results. Second, if generic distinctions are simply arbitrary, we would not have observed the very tight pattern in the relationship between the number of genera and the number of species (Fig. 2). Consider the two extreme cases. The Neotropics have the most species, 9251, and have 5.22 species per genus. Hawaii has the fewest species, 87, and only 1.74 species per genus. The ratios that fit the power equation are quite similar: 5.09 and 1.75 species per genus, a straightforward reflection of the very high R^2 of the power model.

Examining the long discussion of the meaning of the word 'genus' (e.g. Stebbins, 1956; Inger, 1958), we are encouraged to believe that taxonomists have recognized something real and of ecological consequence. As a graduate student, the (very) senior author learned simply that a genus is a set of related species that are difficult to distinguish in the field. That definition had some merit because it dealt with the need for different species in a genus to be closely related. Stebbins (1956) viewed genera this way, i.e. easy to distinguish if separated for a long time, much more difficult if separated only recently, but genera in both cases because of phylogenetic relationship. Jablonski and Finarelli (2009) strongly support the agreement of generic distinctions with molecular phylogenies.

But Inger (1958) saw more than evolutionary relationship. He also saw ecological function and advocated an ‘adaptive approach to genera’. He wanted taxonomic work to transcend the morphological by considering the relation of morphology to adaptation. Given modern tools of phylogenetic reconstruction (see PD below), we might express that today as considering not only relatedness but also ecological similarity. To Kelly (in litt.), the similarity parallels what some term functional groups of species, and what we suspect has previously been meant by the ecological guild (Root, 1967) and the *G*-function (Brown and Vincent, 1987). In any case, we agree and consequently think of the genus as a group of species that share an evolutionary ancestor and a set of similar ecological niches. To the extent that taxonomists use such a genus concept, it is little wonder that they have produced meaningful groups.

Yet the concept is far from precise. It still relies on a great deal of professional judgement, and is somewhat unstable from scientific generation to generation (Mares, 1992). For example, Inger (1958) notes that in three separate lists from 1923 to 1958, the number of genera in Cyprinidae (a North American fish family) varied from 23 to 63 to 34. And Mares (in litt.), reflecting on his own experience with rodents, notes that ‘in the complex world of South American sigmodontine systematics, a single species may end up being moved to more than 5 (or) 6 genera over time’.

One possible way to improve the stability of genera is to incorporate both modern techniques of phylogenetic reconstruction (see PD below) and modern concepts of niche relationships such as the *G*-function of Brown and Vincent (1987). The latter, in particular, may resolve the question of how far down we should cut the tree to lop off our genus – we lop off enough species to include all the members of one *G*-function and we exclude any species in the branch that have diverged to explore a new *G*-function. For now, this is but a dream. Yet, however imprecisely, it is likely that the scholarship of taxonomists has roughly approximated it. And that would mean that the conservation of generic diversity may be of extraordinary significance to ecological functioning.

Implications of the patterns for conservation biology

Conservationists have long been aware of and concerned by the probable negative effects on diversity of both natural area losses, and the promiscuous intermingling of the species of different biogeographical regions (Mooney and Cleland, 2001). Faced with the reality of limited resources, both Vane-Wright *et al.* (1991) and Faith (1992) struggled with the need to prioritize conservation efforts, explicitly acknowledging that not all species can be represented in the reserve system. And Mares (1992) explicitly questioned excluding all but the number of species from biodiversity conservation considerations. There are higher taxonomic levels to think about, and sometimes they may not have many species, he opined. Genus is one of those levels.

If genera truly represent functional groups, their component species may be somewhat redundant (Rosenzweig, 1990). That is to say, the realized niches of different species in the same genus may be constrained largely by competitive interactions within the genus.

Thus when redundant species become extinct, the realized niches of the residual species of the genus could expand and help to maintain the ecosystem processes that would otherwise be jeopardized (Schwinning *et al.*, 2013). Of course, that implies the desirability of prioritizing the conservation of genera.

We can use the equations we have fitted to develop a better quantitative understanding of conservation challenges. But we must do so rather carefully because of the many species and genera found in more than one region. Having no equation for predicting the proportion of these taxa in any circumstance (except for the trivial case of total intermingling), these taxa prevent us from simply substituting various geographical properties into the equations and then solving them.

As an example, consider the number of genera in the data. We found 4416 distinct genera in the nine regions. But if we had looked at regions separately, counted the number of genera in each one, and then summed the nine numbers, we would have reached a total of 6767 genera. The higher number exceeds 4416 owing to genera that occur in more than a single region. They got counted once for every region in which they occur.

However, the instant that New Pangaea arrives, no genus can be counted more than once. So we decided to compensate for the multi-counted taxa by comparing 4416, the results of the empirical current count (stripped of its records of second, third, etc., occurrences), with the projected count after union. That is not a perfect answer because the projected count will come from an equation that was fitted using both endemic genera and multi-counted genera. The projection therefore might be too high. Or maybe not! After all, those multi-counted genera are present and if there is anything like a steady state in the number of genera in a region, then the multi-counted genera should matter ecologically wherever they are found. In sum, we do not yet know whether the projection is too high but it is the best estimate we can currently manage.

So we approach the conservation question in two stages. First, we estimate the reduced diversities of New Pangaea. If our statistical equations overestimate endemic, sustainable, generic diversity in a region today because of immigration from other regions, then the projection for New Pangaea would be too high and the estimate of extinction too low. The same may be said of species diversity estimates. Thus our estimates of extinction will be conservative.

In step two, we turn our attention to the loss of area. Using several sample values, we shrink the area available to the single region of New Pangaea produced by the union of the nine regions. Because the projections for diversities in New Pangaea have no multi-counted genera, results that derive from shrinking its area should produce good estimates of the area-connected, proportional losses of diversity (although they may still overestimate the actual number of taxa that will be left if step one yields an overestimate of the number of taxa).

Step one: the advent of New Pangaea

Rosenzweig (2001) used interprovincial relationships to address the question of the Homogocene: what happens to species diversity if human actions eliminate the biogeographical boundaries between provinces? He showed that if the coefficient of log A for all species is 1.0, the total intermingling of all provinces would not change sustainable, global S. However, if the coefficient is less than 1, the Homogocene would depress sustainable diversity.

In fact, Rosenzweig *et al.* (2012), having now incorporated climate into the vertebrate species diversity equation, find that the coefficient of log A is considerably less than 1.0 for Aves and Reptilia. So the species diversity of these two classes is indeed threatened by the loss of biogeographical distinctness. And we may now predict that those losses will result in a severe depletion of the sustainable species diversity of vertebrates. To calculate the S of New Pangaea, we use $T = 14.2782$°C (the current terrestrial average temperature), then apply the equation $\log S = -1.50 + 0.631 \log A + 0.033\ T$, and discover that New Pangaea would sustain only 13,309 species versus the 24,992 species that are now present in the nine regions. That amounts to a mass extinction of 47%.

Much of the world's sustainable generic vertebrate diversity would also disappear. Applying the equation $\log G = -0.97 + 0.488 \log A + 0.025\ T$, we estimate that New Pangaea would sustain only 2239 genera as opposed to the 4416 genera that are now present in the nine separate regions. So the world's sustainable terrestrial vertebrate generic diversity would decline by 49%.

Notice that the proportional loss of G exceeds that of S. That will happen because New Pangaea, containing all of today's nine zoological regions, will be larger than any of them. Thus, following the equation of Fig. 2, it will have more species per genus than any of them. In evolutionary time, those genera that survive will flourish.

Although homogenization does not appear to threaten the number of species of amphibians or mammals, even Mammalia (generic coefficient of log $A \approx 0.83$) and Amphibia (generic coefficient of log $A \approx 0.74$) do stand to lose genera. Mammals would lose 6%, amphibia 38%.

The losses of specific and generic diversity that we calculate here depend on the assumption of complete and utter homogenization of the Earth's zoological regions. Anything less would diminish the consequences accordingly. Moreover, because people move relatively few vertebrate species between zoological regions, the homogenization threat is no doubt vastly outweighed by the consequences of area losses that we are about to calculate.

Step two: loss of area

Just as for species diversity, conserving generic diversity depends upon conserving natural area – or else reconciling our use of the land with the needs of native species (Rosenzweig, 2003). But the consequences of not doing either of those things are less serious for genera than species. The difference emanates from a difference in the curvatures of their diversity–area relationship. For example, the coefficient of log A for all species is about 0.65, whereas the coefficient of log A for all genera is about 0.5. The coefficient of log A in the relationship signifies its curvature. A coefficient of 1.00 means linearity, whereas coefficients between 0 and 1 signal curvature, i.e. diminishing returns of sustainable diversity as area is added. As the coefficient declines from 1, curvature becomes more and more extreme. So smaller coefficients mean less log-diversity loss for equivalent log-area loss.

Table 3 projects the results of the A–T relationship, again keeping the climate variable constant ($T = 14.2782$°C). We predicted the remaining diversities after losses of several proportions of natural land area (50%, 80%, and 95%). For comparison, we added the calculation for species. Despite the increased curvature of the generic relationship, there is little comfort in Table 3's predictions, i.e. losses of 29% to 77% of sustainable G. Because we have no way to predict endemicities yet, even this global estimate of generic loss may

Table 3. Global loss of natural area will lead to heavy losses of both species and genera

	Area loss			
	0%	50%	80%	95%
Number of species	13 309	8593	4820	2010
Species loss		*35%*	*64%*	*85%*
Number of genera	2 239	1596	1021	519
Generic loss		*29%*	*54%*	*77%*

Note: Cells in Roman font report sustainable diversities after various % losses of natural area (after first considering losses engendered by the total admixture of separate regions into a New Pangaea). Cells in *italic* font report the associated % loss of diversity.

somewhat understate the losses. And remember, too, these losses will come in addition to those caused by the intermingling of the zoological regions.

Using the tools provided by island biogeography, many conservation biologists have warned that we must protect about 20% of the land. That is proving difficult enough to do. But Table 3 shows that even that laudable goal will not prevent a mass extinction of 64% of species and 54% of genera. If we hope to prevent such losses, we must add the tactics of reconciliation ecology to those of reservation ecology (Rosenzweig, 2003).

Usefulness of the genus concept

Does the concept of a genus retain significance in our molecular age? Based on their masterly reconstruction of the phylogenetic tree of South Africa's Cape flora, Forest *et al.* (2007) suggest that conservationists might be better to consider the phylogenetic distance (PD) within a group of genera rather than the number of genera included. They advise, 'PD protection is the best strategy for preserving feature diversity in the Cape'. Let us evaluate that bold suggestion in the light of our results.

Forest and colleagues begin with a list of 735 genera and analyse *rbcL* – the plastid ribulose-1,5-biphosphate carboxylase/oxygenase large subunit – of one species in each genus. Assuming that the difference in *rbcL* between species is a good indicator of the time since they diverged, they build the phylogenetic tree. Implicitly, branch lengths of the tree are proportional to evolutionary time. So, a subset of genera connected by the relevant subset of the branch lengths indicates the amount of evolutionary time experienced by that subset. ('Relevant', here, means only the branches needed to connect each taxon in the subset to the root of the tree.) Forest and colleagues then show that increasing PD by adding area is better accomplished by basing the addition on the amount of PD added rather than the number of genera added. Finally, they illustrate with a sub-sample containing only the 'useful' plant genera: selection of areas to incorporate all three types of uses requires 15 units if it is based on genera but only 13 if it is based on PD.

Although their suggestion is quite interesting, we believe it to be premature to replace the use of generic diversity with PD in selecting areas for conservation. First, these PD analyses are based on genera; how could they have done them without taxonomy to the genus level?

Second, many now question the basic assumption of PD, i.e. that the difference in a gene between species is an entirely reliable indicator of the phenotypic change since they diverged. Davies and Savolainen (2006) found that when evolutionary time was measured by neutral genes and compared with actual phenotypic change, the correlation between them was only 3% to 11%. Third, Forest *et al.* define a good outcome as one of PD conservation; to a certain extent that definition dictates the results in advance. Suppose it had assumed that genus conservation were the best outcome? We suggest in fact that many conservationists would prefer conserving plant species that are functionally diverse rather than merely temporally diverse. Forest and colleagues would seem to agree implicitly because they illustrate their idea with an examination of useful genera. But we remind the reader that *rbcL* is so useful as a timekeeper in part because it is so functionally neutral. Furthermore, mere time ignores the phenomenon of punctuated equilibrium. If species spend most of their evolutionary time merely drifting, and change function significantly in fits and starts, then the superdiverse Western Cape flora is where the functional action must have been despite the relative short times these species took to evolve. Wisheu *et al.* (2000) explain the rapid speciation rates as a consequence of the short plant generation times that accompany the need for most Western Cape species to germinate from seed after a wildfire.

Finally, we tip our hats to the many generations of botanists who have painstakingly grouped species into genera. The close relationship of generic diversity to species diversity shows that they have largely succeeded in creating a consistent and useful entity, even in South Africa's Western Cape where, apparently, so many genera have been recognized among so many recently diverged species. Conservation biology would be remiss were it to ignore the results of such success.

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