

An ecological telescope to view future terrestrial vertebrate diversity

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ABSTRACT

Background: Some regions of the Earth sustain their own diversities through the processes of speciation and extinction. Theory predicts and data support the conclusion that the number of species (S) in such regions should attain a steady state whose value correlates with their areas (extents). Other data strongly suggest that climate plays a significant role in determining S .

Aim: Combine the influences of area and climate in a mathematical model that fits known global terrestrial vertebrate species diversities.

Data: The *WildFinder* terrestrial vertebrate data set of the World Wildlife Fund as it stood in January 2006 (less some data associated with islands). Each of *WildFinder*'s 825 ecoregions is accompanied by a set of abiotic variables (area and values of climate variables), as well as a list of the resident vertebrate species it contains.

Methods: Assign each ecoregion to a zoological region (*sensu* Sclater, 1858). Compile a list of all species that reside in each zoological region. Calculate the area of each region (A), the number of species in it (separated into the four vertebrate classes: Amphibia, Reptilia, Aves, Mammalia). Find a suitable variable to represent annual energy flow (i.e. ecological productivity). Determine the number of species endemic to each zoological region. Calculate the mean annual temperature (T) and actual evapotranspiration (AE) in each zoological region. Find the regression equations that best fit the numbers of species.

Results: The land has nine zoological regions (in order of area): Palearctic, Nearctic, Sub-Saharan Africa, Neotropics, Australasia, Indo-Malaysia, Madagascar, New Zealand, and Hawaii. The number of species, S , fits area ($R^2 = 0.84$; $P = 6 \times 10^{-4}$). Neither T by itself nor AE by itself is significantly correlated with S . However, adding either T or AE as the second variable in the regression does increase R^2 significantly. Their statistical effects on R^2 are virtually identical: using $\log A$ and $\log AE$ as independent variables yields $R^2 = 0.974$; using $\log A$ and T yields $R^2 = 0.973$. The results for the diversities of the four separate classes are quite similar to those of the total S , except that their four z -values vary from 0.53 to 1.07.

Conclusion: The Earth's terrestrial vertebrates face a mass extinction of 30–96%.

Keywords: climate, ecoregions, endemism, mass extinction, realms, species–area relationships, species diversity, steady states, zoological regions.

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INTRODUCTION

Astronomers use telescopes to see things that are far away and long ago. In contrast, ecologists need a telescope to see far into the future. This paper's task is to build one to view the number of sustainable terrestrial vertebrate species on the Earth.

We proceed by analysing the extensive terrestrial vertebrate data set of the World Wildlife Fund (WWF). But we do not enter this data set blindly. Instead, we build our analyses with available theory. Then we develop a global statistical model of species diversity in terrestrial zoological regions. It is within these evolutionarily significant regions that species are born and species die. It is within these regions that the term 'sustainability' finds its ultimate meaning.

In analysing diversity, one cannot over-emphasize the importance of specifying and adhering to the scale appropriate to testing a hypothesis or theory. Different mechanisms are at work in determining diversity at different scales (Rosenzweig, 1995; Turner and Tjørve, 2005; Jetz and Fine, 2012). Causes at one scale can even be effects at another. Combining data that arise from different scales is likely to overwhelm the analyses with noise. That is why we devoted so much of our pre-analysis efforts to extracting data packets from the WWF data set that would best reflect zoological regions.

The model uses only two independent variables, regional area and regional climate. Yet the result leaves surprisingly little variance behind: its R^2 is greater than 0.97.

We chose regional area as a variable because theoretical work implicates it. Regional area is the only parameter known to set up a negative feedback relationship between the number of species S and its associated rates of origination and extinction (Rosenzweig, 2011). We also chose it because empirical evidence has supported that theory: Beginning with the seminal works of Findley and Wilson (1983) and Fleming *et al.* (1987), S has been shown to correlate well with regional area. In fact, the studies suggest tentatively that the correlation approaches linearity ($\log S \propto 1 \times \log A$) (Rosenzweig, 2001, 2003a).

But area cannot be the entire story. Climate is impossible to ignore. It shouts out from decades of data collection. In fact, the signal of climate is so obvious that many investigators study one or more climate-related variable to the exclusion of the area signal. They do so without being as careful before excluding area (Rosenzweig, 2003b) as one must be before excluding climate. They see that the principal repositories of diversity on the planet are its four large, wet tropical areas. But they largely ignore the low diversities of the world's several small, wet tropical engines of evolutionary novelty such as Hawaii and Madagascar.

We do not favour eliminating either area or climate from consideration. And so we set out to study them both as two pieces of the same puzzle. Is there a quantitative rule that combines their influence? Having achieved an R^2 of 0.97, we are delighted to answer, 'yes'. Recently, Jetz and Fine (2012) asked a similar question. We shall compare our two approaches in the Discussion but are pleased to note here that they too achieved substantial success.

Because civilization is shrinking the habitat and reducing the energy flow available to wild species – as well as changing their climates – the telescope affords a view of future steady states in vertebrate diversity. It reinforces the concern that life is undergoing a mass extinction of species and even suggests that estimates of that extinction are troubling underestimates.

The telescope is hardly definitive, as the reader will see. Focused as it is on the grand evolutionary scale, it cannot resolve important fine-scale variation within zoological regions

[e.g. hot spots (Myers *et al.*, 2000; Mittermeier *et al.*, 2003)]. It also cannot resolve a crucial ambiguity in its climatic section, i.e. whether temperature or energy flow is the causal factor in climate's effect; a major advance in theory is required to help with that. And it is not designed to estimate speciation or extinction rates – in particular, the rate of relaxation to steady state. It is an instrument for viewing the steady states themselves. Finally, it cannot reveal any future decisions society might make to change the result. Nonetheless, the model suggests what we can do to make those changes follow the direction most people would probably prefer.

THE DATA SET

The WWF data set is embedded in its online program *WildFinder* (Olson *et al.*, 2001). Scientists at the WWF provided us with a complete copy dated 17 January 2006. That is the copy we studied, although new species have been added since. The reader will see that our results are so clear-cut that trying to keep up with *WildFinder* changes could have had very little impact on those results.

WildFinder's data are organized into 825 terrestrial ecoregions, each of which is defined using climatic and biological (rather than political) information. As WWF reports: 'Ecoregions are defined as "relatively large units of land that contain a distinct assemblage of natural communities and species, with boundaries that approximate the original extent of the natural communities prior to major land use change"' (Olson *et al.*, 2001). Thus the definitions do not rely on strict algorithms to set borders. But we believe all biologists would agree that the flexible judgements of those setting the borders of the ecoregions have resulted in defensible decisions that vastly improve upon rigid political boundaries, which rarely have any biological meaning whatsoever.

WildFinder omits the species of nine small ecoregions but their area amounts to only 0.175% of the 134,735,751 km² land-area of the world's ecoregions. The interior sections of both Greenland and Antarctica are also not included as ecoregions because most of their area contains no terrestrial vertebrates (World Wildlife Fund, 2006). More information about the data may be found in Olson *et al.* (2001), Lamoreux *et al.* (2006), and WWF's own explanation, published contemporaneously with the January 2006 version of *WildFinder* (evolutionary-ecology.com/data/2771Wildfinder.pdf), which we archived when obtaining the data set and now make available digitally in case changes confound attempts to duplicate our results.

The WWF data set reports the area of each ecoregion. Except for all species that are introduced, present as human commensals, vagrants or passage migrants, it also lists each ecoregion's vertebrate species (some 30,744 different species of amphibians, reptiles, birds, and mammals). A species is listed in every ecoregion in which it occurs. Extinct species are not listed.

WWF scientists also provided us with a table of 102 climatic variables compiled for each ecoregion. We cursorily tested a number of these for usefulness but in the end settled on two that have been the most prominent in ecological discussions about diversity for decades: a measure of temperature (i.e. its annual average) and a measure of annual energy flow (i.e. productivity).

WWF assigns each ecoregion to a zoological region, which they call a realm. It defines them as 'continental-scale biogeographic regions which contain distinct assemblages of plants and animals, particularly at higher taxonomic levels.' These regions derive ultimately

from the insight and investigations of nineteenth-century zoologists, especially Philip Lutley Sclater (1858), who conceived them, and Alfred Russel Wallace (1876), who popularized them. But WWF used the ‘biogeographic regions’ of Elizabeth Pielou (1979) and modified them somewhat. A necessary part of our work was to modify them once more (see below). But we did not modify Sclater’s term for them – ‘zoological regions’.

METHODS

Preparing the data set

We did not collect the data set and, except for sorting ecoregions into their zoological regions, we used it exactly as we got it. By resisting the temptation to ‘improve’ it, we avoided colouring it with our biases.

We also did not mine the data for previously unsuspected patterns. In other words, we did not intend, nor have we executed, a statistical fishing expedition. Instead, our job was to address the effects of area and climate on the number of species in the world’s separate, self-sustaining zoological regions, i.e. sections of the globe that depend on themselves for their animal diversity. Ideally, we would have been able to use totally isolated zoological regions, i.e. those lacking any immigrant species at all. Of course, none of those exist [except in mathematics, where they make illuminating objects of theoretical study (Rosenzweig, 1995)]. So we tried our best to use pieces of the Earth that others have recognized as evolutionarily distinct at the species level and whose endemities largely support their distinctiveness.

True biogeographic islands are, by definition, not zoological regions. The ideal island gets its species from a donor, a fixed species pool often called the ‘mainland’. We included islands that can reasonably be viewed as zoological pieces of their mainlands, just as we included the various parts of those mainlands. But some islands present complications and we excluded them from the analysis in advance. We removed many islands that have mixed sources of origination, many species coming from immigration perhaps but many also from speciation on the island. We felt that their mixed status would be likely to confuse the analyses. Following that protocol, we eliminated the entire Caribbean and New Caledonia. We also eliminated the Philippines because they are so biogeographically complex that they probably contain more than one zoological region for at least one class [i.e. mammals (Heaney, 1993)], whereas they are islands for one or more others (i.e. Aves). Finally, except for Hawaii, we excluded the islands of Oceania; they have lost too high a proportion of their species and are unlikely to be near steady state (Steadman, 1995). Altogether we used 755 of *Wildfinder*’s ecoregions and 24,992 of its species.

All data set preparation described in the preceding section was done before the analyses.

Delimiting the zoogeographic regions

Wallace (1876, pp. 59–61) reports that soon after their proposal by Sclater, investigators like T.H. Huxley were debating the regions. Huxley suggested and Sclater agreed that New Zealand ought to be singled out as a separate region. Blyth thought Madagascar deserved regional rank, too. Wallace objected, in part because he thought them both too small and in part because knowledge of their faunas was still quite incomplete. He was also focused on the family level rather than the species level. We decided that Huxley and Blyth were right.

We note that Wallace rejected New Zealand's separate status because it is so much smaller and has so much less diversity than the six regions he recognized. He felt the same about Madagascar. He also pointed out that their taxa are closely related to the larger regions. But in this, he focused on familial and generic relationships. Thus he missed the point of endemism, i.e. where did the *species* evolve? For an instant Wallace had lost sight of Sclater's fundamental motive: delimit regions that were evolutionarily separate. Clearly, New Zealand has enough endemism to qualify. Madagascar does, too. And so does Hawaii, a region suggested by no one in the nineteenth century as far as we know. If they are very small compared with the Neotropics, so be it. Besides, Wallace's extra filter of similar size creates a statistical obstacle: it minimizes the variance of area and hobbles one's ability to investigate its influence. It is similar to setting out equal-area samples and then asking what effect area has on the data.

In fact, the realms (i.e. zoological regions) of the WWF data set include only two that we adopted exactly: Indo-Malaysia and the Palearctic. Of the others, we did not use their Antarctic zoological region at all; it is empty. As we said, we separated the Afrotropics into Sub-Saharan Africa and Madagascar (because each has considerable endemism). For the same reason, we pulled New Zealand's ecoregions out of Australasia into a separate zoological region. And we extracted Hawaii from Oceania and discarded the remainder of that zoological region (for the reason mentioned above). Finally, we found that we could raise the endemism of the Neotropics by transferring a single ecoregion (NT0904) from the Neotropics to the Nearctic.

The discerning reader will suspect that we also did a lot of trial-and-error region adjustment that failed to produce zoological regions with substantial endemisms. We did indeed. For example, we divided the Palearctic into arid and mesic pieces – but the endemism of the arid piece was negligible (12.7% or about one-third the endemism of the least endemic zoological region). And we tried uniting the cold ecoregions of the Palearctic with the cold ecoregions of the Nearctic to produce a circumpolar Holarctic – another of Blyth's suggestions but a failure nonetheless. Perhaps our most remarkable failure was the attempt to extract a Neotemperate zoological region from the Neotropics. Despite the impressive number of Gondwanan plant species in southern South America, its vertebrate endemism was zero species!

Before doing the analyses, we settled on nine zoological regions (Fig. 1). Table 1 lists them and reports their diversities and endemisms, class by class. An Appendix (evolutionary-ecology.com/data/2771RegionList.txt) records the list of the constituent ecoregions of each of the nine zoological regions that we used.

We conformed to Sclater's term, 'zoological region'. We did so because Sclater invented the concept, giving him the right to name it. Also, Sclater's term was good enough for Alfred Russel Wallace. Thus we defer to long-established tradition. In fact, Charles Sanders Peirce (1903), in discussing scientific terminology, declared that it is actually unethical for a scientist to coin a new name for an already established one (see also Oliver, 1963). Peirce, one of the great philosophers of science, had good reason to proscribe renaming. It leads to confusion. Consider that zoological regions have been called biogeographical provinces, realms, biogeographic realms, ecozones, biogeographic regions, bioregions, and perhaps other terms as well. It is true that the terms ecozones and biogeographic regions attempt to expand zoological regions to include plants, but the large-scale biogeographical units of plants often conflict with those of animals. Moreover, botanists have been more disciplined in conforming to 'floristic kingdom', their term for a large-scale, plant

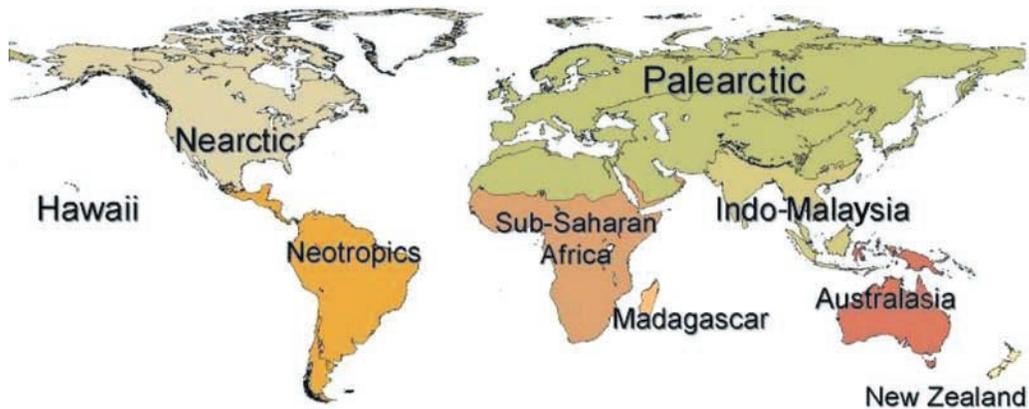


Fig. 1. The world's nine zoological regions. See details in text and Appendix.

biogeographical unit. So we work in zoological regions, although we do occasionally use the abbreviation 'region'.

The climate variables

We know of two hypotheses to relate species diversity to climate. The temperature hypothesis claims that higher temperatures lead to higher mutation rates, thus to higher speciation rates, and thus to higher species diversities (Rohde, 1978). The energy flow hypothesis claims that enhanced productivity leads to higher species diversities because more productivity yields larger population sizes (at any given diversity) and thus lower extinction rates. Note that we know of other hypotheses to relate productivity to species diversity but they do not add a new candidate variable and we know of no reason to prefer them.

Hence we need two climate variables, temperature and one to represent energy flow.

The data set supplies the average annual temperature of each ecoregion. We calculated the average annual temperature of a zoological region as the weighted average of the temperatures of its ecoregions. That is, we multiplied each ecoregional temperature by the proportion of its region's area that it occupies, before summing the results of all ecoregions in the zoological region to get the weighted average.

Energy flow is more difficult (see Huston and Wolverton, 2009). But the data set had entries for net annual primary productivity (*NPP*) in most ecoregions (calculated by measuring chlorophyll-a remotely and generating the *NDVI* – normalized difference vegetation index), and for actual evapotranspiration (*AE*) in millimetres per year. Unfortunately, there were no entries for Hawaii's *NPP* and we were unwilling to exclude Hawaii's data. However, as Fig. 2 indicates, *AE* is an excellent surrogate for *NPP* (Rosenzweig, 1968). So we used *AE*.

As with temperature, we computed the weighted average of the *AE* values of its ecoregions. Table 2 shows the values of the variables for all nine zoological regions.

Computing the number of species in a zoological region

Most species occur in more than one ecoregion. We obtained *S*, the number of species in a zoological region, by reducing multiple occurrences in the region to one. If a species

Table 1. Number of species and zoogeographical endemics in the nine zoological regions (endemicities are the ratios of endemics to total species)

	All classes	Amphibian	Bird	Mammal	Reptile
Totals					
Madagascar	853	143	240	136	334
Hawaii	87	0	86	1	0
New Zealand	122	3	82	2	35
Australasia	4015	526	1610	674	1205
Sub-Saharan	5043	629	2046	1038	1330
Indo-Malaysia	4572	710	1780	830	1252
Neotropics	9259	2168	3687	1229	2175
Palaearctic	3638	376	1568	905	789
Nearctic	1950	267	728	481	474
Endemics					
Madagascar	709	140	122	126	321
Hawaii	36	0	36	0	0
New Zealand	80	3	40	2	35
Australasia	3532	515	1285	607	1125
Sub-Saharan	4277	618	1536	919	1204
Indo-Malaysia	2497	565	555	438	939
Neotropics	8127	2092	3110	1023	1902
Palaearctic	1353	231	211	471	440
Nearctic	758	192	95	258	213
Ratios					
Madagascar	0.83	0.98	0.51	0.93	0.96
Hawaii	0.41	–	0.42	0.00	–
New Zealand	0.66	1.00	0.49	1.00	1.00
Australasia	0.88	0.98	0.80	0.90	0.93
Sub-Saharan	0.85	0.98	0.75	0.89	0.91
Indo-Malaysia	0.55	0.80	0.31	0.53	0.75
Neotropics	0.88	0.96	0.84	0.83	0.87
Palaearctic	0.37	0.61	0.13	0.52	0.56
Nearctic	0.39	0.72	0.13	0.54	0.45

occurs in more than one zoological region, we count it as present in each region in which it lives.

Statistical methods

We transformed the variables S and AE to common logarithms. Then we performed univariate and bivariate linear regressions and calculated the usual statistics: intercepts, coefficients, probabilities, and R^2 -values. We excluded Hawaii from the regression analyses for Amphibia and Reptilia because these classes are not found in that zoological region.

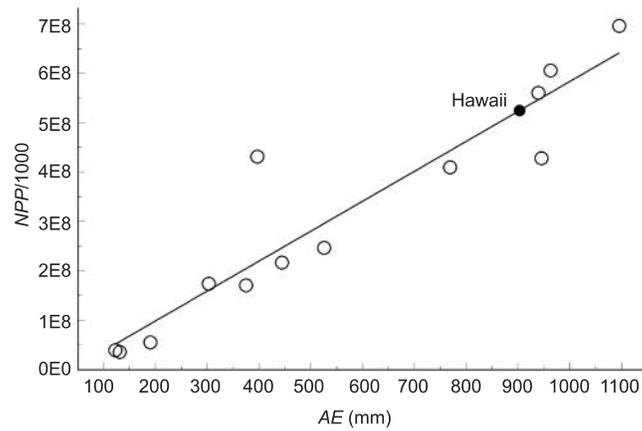


Fig. 2. Net primary production (*NPP*) closely follows annual actual evapotranspiration (*AE*). Hawaii's *NPP* was missing from the data set. We used *AE* as a surrogate for *NPP*, which allowed us to include Hawaii in the analyses

Table 2. Values of area ($\log \text{km}^2$), annual actual evapotranspiration ($\log \text{mm}$), and mean temperature ($^{\circ}\text{C}$) used in the analyses.

Zoological region	$\log A$	$\log AE$	Temperature
Australasia	6.95	2.72	22.05
Neotropics	7.28	3.02	22.00
New Zealand	5.43	2.60	10.32
Sub-Saharan Africa	7.32	2.89	24.25
Madagascar	5.77	2.97	22.12
Palaearctic	7.72	2.43	6.98
Indo-Malaysia	6.91	2.98	24.26
Nearctic	7.33	2.57	2.03
Hawaii	4.22	2.96	22.00

RESULTS

Univariate linear regressions

S , the number of species in a zoological region, fits A , regional area, significantly (Fig. 3):

$$\log S = -0.59 + 0.58 \log A \quad (R^2 = 0.84; P = 0.0006)$$

S also fits A when we analyse separately the number of species in the four classes:

$$\textit{Amphibia}: \quad \log S_{\text{amph}} = -3.26 + 0.83 \log A \quad (R^2 = 0.62; P = 0.02)$$

$$\textit{Reptilia}: \quad \log S_{\text{rept}} = -0.99 + 0.55 \log A \quad (R^2 = 0.63; P = 0.019)$$

$$\textit{Aves}: \quad \log S_{\text{aves}} = -0.30 + 0.48 \log A \quad (R^2 = 0.80; P = 0.001)$$

$$\textit{Mammalia}: \quad \log S_{\text{mamm}} = -4.135 + 0.97 \log A \quad (R^2 = 0.86; P = 0.0003)$$

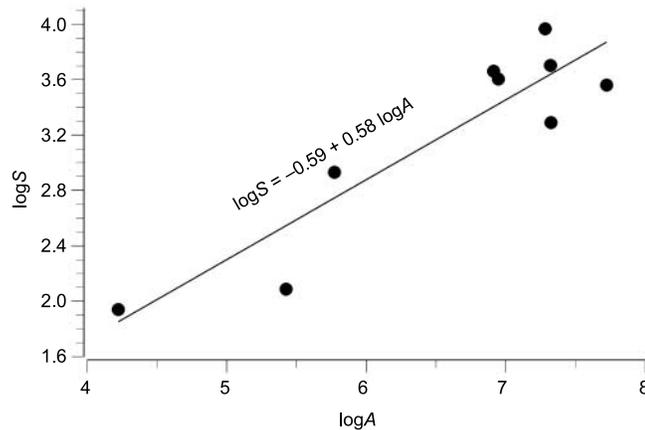


Fig. 3. The number of vertebrate species of the world's zoological regions fits the area of those regions significantly. See text for statistics.

But S does not fit either climatic variable, mean annual temperature (T) or $\log AE$ (log annual actual evapotranspiration). Polynomial regressions did not help. However, the residuals from the $\log A$ relationship did fit climate well. So we proceeded to calculate bivariate linear regressions.

Bivariate linear regressions

When both $\log A$ and one of the two climatic variables (T or AE) are used to fit $\log S$, both climatic variables attain significance and the regressions are significant:

$$\log S = -4.79 + 0.654 \log A + 1.32 \log AE \quad (R^2 = 0.974; P_A = 5 \times 10^{-6}; P_{AE} = 0.00127)$$

$$\log S = -1.50 + 0.631 \log A + 0.033 T \quad (R^2 = 0.973; P_A = 7 \times 10^{-6}; P_T = 0.0016)$$

Separating the classes yields similar results to those for total S . And, as before, the regressions and separate variables are significant for each class.

Amphibia:

$$\log S_{\text{amph}} = -9.96 + 0.92 \log A + 2.19 \log AE \quad (R^2 = 0.931; P_A = 0.0007; P_{AE} = 0.005)$$

$$\log S_{\text{amph}} = -4.46 + 0.89 \log A + 0.05 T \quad (R^2 = 0.869; P_A = 0.004; P_T = 0.027)$$

Reptilia:

$$\log S_{\text{rept}} = -5.36 + 0.61 \log A + 1.43 \log AE \quad (R^2 = 0.931; P_A = 0.0007; P_{AE} = 0.0054)$$

$$\log S_{\text{rept}} = -1.88 + 0.59 \log A + 0.04 T \quad (R^2 = 0.937; P_A = 0.0006; P_T = 0.004)$$

Aves:

$$\log S_{\text{aves}} = -3.80 + 0.54 \log A + 1.11 \log AE \quad (R^2 = 0.934; P_A = 8 \times 10^{-5}; P_{AE} = 0.012)$$

$$\log S_{\text{aves}} = -1.11 + 0.53 \log A + 0.03 T \quad (R^2 = 0.950; P_A = 4 \times 10^{-5}; P_T = 0.006)$$

Mammalia:

$$\log S_{\text{mamm}} = -9.65 + 1.07 \log A + 1.74 \log AE \quad (R^2 = 0.951; P_A = 4 \times 10^{-5}; P_{AE} = 0.017)$$

$$\log S_{\text{mamm}} = -5.28 + 1.04 \log A + 0.04 T \quad (R^2 = 0.943; P_A = 6 \times 10^{-5}; P_T = 0.029)$$

As expected based on their definitions, T and AE are well correlated ($r = 0.87$). Hence, unsurprisingly, the multiple linear regression of all three ($\log S$, $\log AE$, and T) does not improve the bivariate result.

In Fig. 4, we plot the composite independent variable, $0.654 \log A + 1.32 \log AE$, generated from the bivariate regression using $\log A$ and $\log AE$. This figure does not alter the statistical result but it does allow us to visualize the degree to which the regression accounts for the variance in S between zoological regions. A figure that uses the composite independent variable generated from the bivariate regression using $\log A$ and T is quite similar, and so we do not reproduce it here. But we do show one that visualizes the $\log A$, $\log AE$ results for the separate classes (Fig. 5a–d).

DISCUSSION

Theory has long implicated the area of a zoological region, A , as a causal variable in determining the steady-state number of species, S . The link is straightforward but has two levels. First, at any particular diversity, more area means a higher speciation rate and lower extinction rate. Second, at any particular area, greater S means a smaller geographical range for the average species. Smaller ranges tend to increase extinction and decrease speciation rates (but see López-Villalta, 2011, for a partial exception). The loops are clear and lead to the prediction of a negative feedback and a steady state in S .

Empirical evidence has supported the connection between S and A . This includes paleontological evidence (e.g. Jablonski, 1986) as well as patterns of S today (Rosenzweig, 1995, 2001,

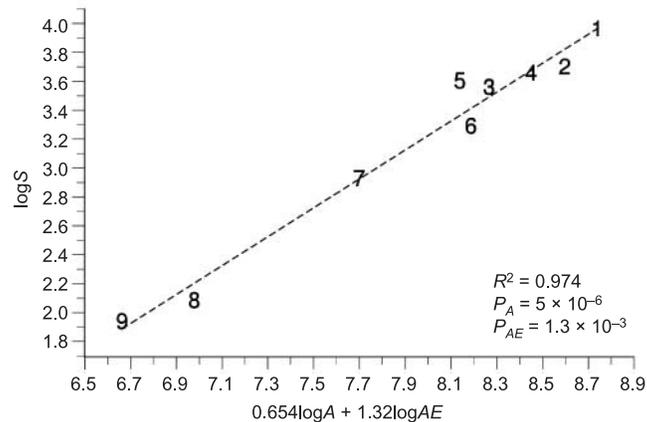


Fig. 4. The number of vertebrate species of the world's zoological regions fits a composite variable generated from bivariate regression. (Shown: the results for area and actual evapotranspiration. Not shown but almost the same: the results for area and temperature.) The datum for each zoological region is numbered as follows: 1 = Neotropics; 2 = Sub-Saharan Africa; 3 = Palearctic; 4 = Indo-Malaysia; 5 = Australasia; 6 = Nearctic; 7 = Madagascar; 8 = New Zealand; 9 = Hawaii. See text for statistics.

2003a). The most recent comes from López-Villalta (2011), who showed how the probability of speciation in Mediterranean birds is influenced by range size.

Given that science prefers to proceed from predictions made by theory and strongly prefers those predictions with empirical support, we might have been excused for simply assuming a role for A and testing any other variable as a subordinate or secondary variable. But we did not do that. We made area earn its keep anew.

Area met this challenge easily. It explained 84% of the variance of S in the world's terrestrial vertebrate species. Even after we divided the species into their classes, A retained its power to fit the data (amphibians, 62%; reptiles, 63%; birds, 80%; and mammals, 86%).

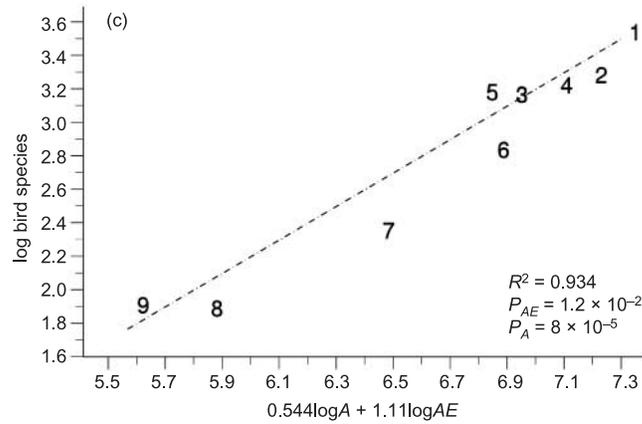
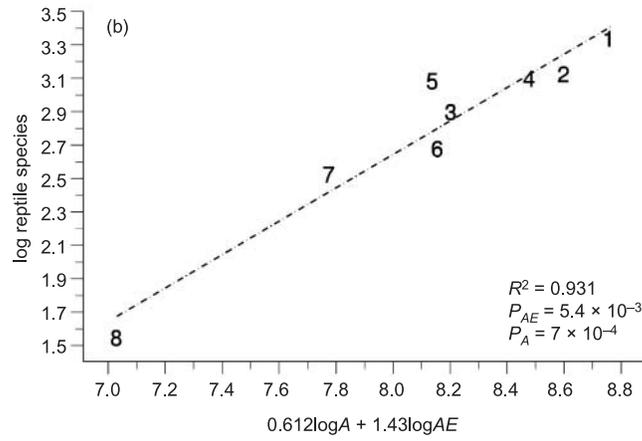
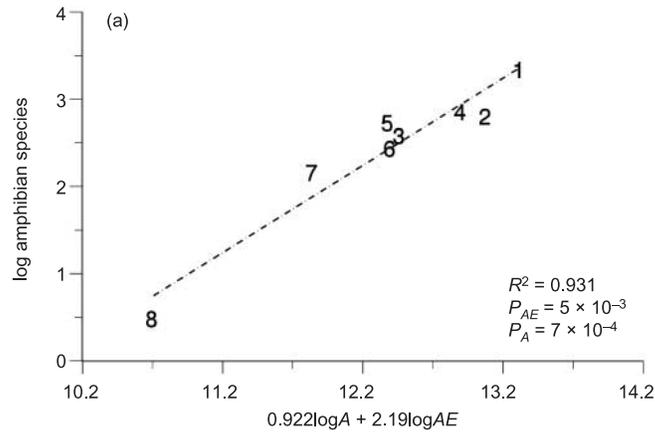
Part of the success of A may be due to our decision to apportion the data set into its zoological regions. We focused on them because we were proceeding from a theory and the theory presupposed independent zoological regions. Although no such totally independent regions actually exist, getting as close as we could to delimiting them had to have helped the prospects for a fair test. Also, we were able to deploy A over a range of 3.5 orders of magnitude. Such a range is bound to help tease signal from noise.

Although we fully expected the success of area, nonetheless we were astonished that neither of the climatic variables could stand on its own. The ecological literature overflows with claims that large-scale S -values stem from climatic conditions. Such claims have proved immune to the clear and reasonable warning of Terborgh (1973), who may have been the first to point out their tautology. Imagine if Costa Rica, say, had only 14 species of vertebrates and people tended to die there of heat exposure, whereas Newfoundland, say, had 514 species and people went there for climate-based holidays spent rolling in snow . . . perhaps you now appreciate Terborgh's point. Humans, including ecologists, assess the favourableness of an environment through human eyes (and cold toes). And to the extent that the judgement is based on comparisons of diversity, it can never be anything except a tautology when we use it to explain variation in diversity. That our science has largely minimized Terborgh's insight suggests the possibility that the role of climate in setting diversity has been reified (Slobodkin, 2001), that it has become a conclusion rather than a scientific proposition. Few bother to test it, and all too often, evidence that calls it into question gets ignored.

Of course, we do not suggest that climate is unimportant. Some very large zoological regions do not have as many species as some very much smaller ones, and the former tend to be rather cold and unproductive. In fact, when we envisioned this study, the idea was to find a formula to combine area with climate, giving both their due. Using climate as a secondary variable has led us to success.

Adding either annual actual evapotranspiration (AE) or mean annual temperature (T) to the regression analyses improved R^2 significantly in every case we examined. For all four classes analysed together, the proportion of variance explained went from 84% to 97.4% and 97.3% respectively. Probabilities associated with the climate variables were less than 2×10^{-3} in both cases. No one should doubt that climate matters.

How is it possible that this project could have succeeded? For one thing, the data set is hardly ideal for the purpose. Its zoological regions are replete with non-endemics; a laboratory scientist would have returned to the bench to purify the samples. And there surely has been inadequate time for life to bounce back to its steady states after the last 40,000 years of substantial human-driven extinctions of birds and mammals – especially in the three smallest zoological regions. Moreover, the climate variables are almost preposterous caricatures. Each of the pair of climate variables is a single value that we used



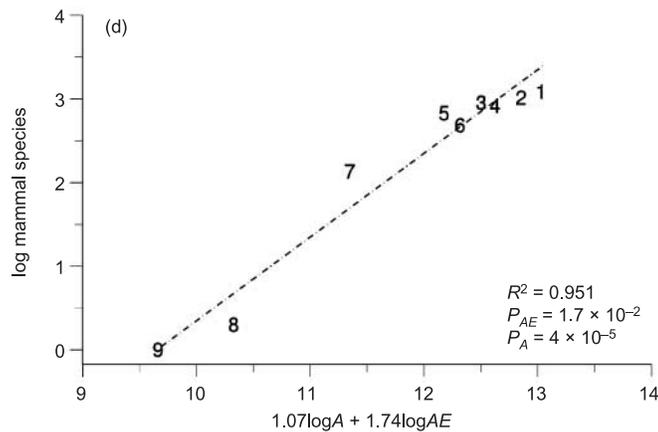


Fig. 5. Bivariate regressions of the species diversity of the four vertebrate classes with area and actual evapotranspiration: (a) Amphibia; (b) Reptilia; (c) Aves; (d) Mammalia. Each zoological region is numbered as in Fig. 4. See text for statistics.

to represent an entire, complex, variable zoological region. For example, we used merely one temperature and one actual evapotranspiration to represent the climate of the entire Palearctic, encompassing extensive deserts, forests, shrublands, wetlands, and grasslands, not to mention the Earth's highest and lowest terrestrial elevations.

And yet it works. Eight of the nine zoological regions have diversities that are astoundingly close to the regression line of Fig. 5. Only Australasia's diversity exhibits even a moderate departure; it is about 0.3 orders of magnitude above the line. That translates to about twice as many species as the regression predicts. Indeed, Pianka (1969) and Pianka and Huey (1971) discovered that both the reptiles and birds of Australia are much more speciose than are those same taxa in other zoological regions. Orians and Milewski (2007) gather together numerous aspects of the unusual ecology of Australia and present a powerfully reasoned explanation for them. Australia is different. So the fact that the results of our analysis agree with Australian exceptionalism may be taken as reassurance of their basic reliability.

Comparison with another success

Jetz and Fine (2012) also sought and found a combined statistical model to fit vertebrate diversity at the global scale. Their model resulted in an R^2 of 0.78, an impressive R^2 . But it is less than our $R^2 = 0.974$. What might account for the difference?

Jetz and Fine do not use zoological regions as units in their regressions. Instead, they begin with zoological regions but then divide each one into 'bioregions' by allocating its area into separate broad vegetation types (e.g. desert, tundra, Mediterranean). They do consider Madagascar as a separate zoological region, as we do, but not New Zealand or Hawaii. In the end, they designate 32 fundamental biogeographical regions.

Generally, one prefers to have more data points. In this case, however, dividing essentially the same information into smaller bins may actually have weakened the R^2 . We suspect that the bioregions do not represent units in which we might expect steady states in S . So, if that

is what we wish to understand, splitting up zoological regions in preparation for analysis will add noise to the data set because we do not understand the rules by which S of a region is apportioned among vegetation types. Moreover, splitting them up by vegetation type prejudices the result: it implies that vegetation type influences the dynamics of S . Yet our goal is to discover what does influence the dynamics of S .

On the other hand, lumping New Zealand with Australasia and not recognizing the biogeographical independence of Hawaii does cost data points and could easily have contributed somewhat to reducing R^2 .

Jetz and Fine (2012) define and analyse three measures of the number of species: total, resident, and endemic. The ‘total richness’ of Jetz and Fine is the same as ours. However, at the level of whole ‘bioregions’, Jetz and Fine use total richnesses only to analyse the separateness of the bioregional lists of species. At the level of whole ‘bioregions’, their analyses depend only on ‘resident richnesses’ or ‘endemic richnesses’. To arrive at ‘resident richness’, Jetz and Fine assign each species to one and only one ‘bioregion’. (Always careful to avoid tautology, they defined an algorithm to make the assignment objectively.) To arrive at ‘endemic richness’, Jetz and Fine count only those species restricted to a single ‘bioregion’. But both resident and endemic measures deprive bioregions of some of their diversity for the analyses. To the extent that all bioregions do not have the same proportions of their species excluded, the restrictions add noise. In addition, excluded species are similarly likely to interact with those that get counted and thus to contribute to the dynamics of S .

Jetz and Fine’s analysis uses four variables rather than just two: area, temperature, productivity (energy flow), and bioregional age (‘time’). Often Jetz and Fine combine them to make composite variables. One variable called ‘time-area-productivity’ is actually a composite of three: area \times energy-flow \times duration-in-geological-time. ‘Time’ is a nod towards history. It recognizes the fact that some of the regions they study are much younger than others and have had less time for their area to generate new species. For example, they estimate an age of 8 million years for grasslands and 55 million years for the Mediterranean bioregion at the southern tip of Africa. These variables raise several questions.

There is a mathematical problem with using history (i.e. time) as a variable to account for steady states. History can be relevant – and sometimes is – in understanding a dependent variable that has been perturbed from a steady state (or has none). How far has it been perturbed? How long ago? But history does not matter after a dynamic system has righted itself. That is why we did not think to use it. To the extent that regions are at steady state, ‘time’ is just a random number that adds noise and tends to decrease R^2 .

Second, we have seen that temperature and productivity are closely correlated ($r = 0.87$). Using both in a single regression analysis is therefore not so much like adding a variable as it is like adding a transformation as a separate variable (which, of course, one does commonly, such as in polynomial regression). Not at all wrong, but one must be especially careful about interpreting the results. In particular, one cannot conclude that because both temperature and productivity are used in the best fitting regression equation, both are significant influences on S .

Other, more minor differences exist between our data set and that of Jetz and Fine. For instance, we included data from mountains; Jetz and Fine did not. And we excluded much island data that they used.

Of course we are pleased that our theory-driven, simpler approach accounted for considerably more variance than their more complex one. Garrett Hardin (1993, p. 102) once

pointed out that scientific progress often involves being able to say more with less, thanks to theory. ‘There are times,’ he wrote, ‘when we fear that the snowballing “information overload” may be the downfall of civilization. Fortunately there is a counterforce to information overload: theory construction. A good theory compacts a vast body of facts into a few words or equations.’

But the bottom line is that both studies succeeded in showing that a measure of area together with one(s) of climate fits large-scale terrestrial vertebrate species diversity very, very well.

T or AE?

Our analyses showed that two variables gave a fine accounting of vertebrate species diversity at the scale of zoological regions. But which two? $\log A$ and $\log AE$ or $\log A$ and T ?

The results in every pair of our regressions were almost indistinguishable. In the analysis of all four classes together, $P_{AE} = 0.00127$ and $P_T = 0.00156$. In two of the four separate class analyses, P_{AE} was just under P_T . In the other two, P_{AE} was just over P_T . The statistics give us no help in our choice.

What might help? A theory to predict that higher temperatures lead to higher speciation rates would help. Or (recalling that AE is a surrogate for productivity) a theory that predicted that higher energy flows (i.e. productivities) lead to higher speciation rates would help. Or else we could deduce a theory that predicted reduced extinction rates with higher temperatures or energy flows. Note that we do not require either T or AE to produce a negative feedback; area has already provided that negative feedback and that is enough.

Ecologists have wrestled with a theory of S and productivity for decades. In the day when we assumed that in a certain time interval, the death of each individual was independent of the death of the others in its species, we thought we had a theory of S and productivity. We could imagine multiplying together all the probabilities of survival and concluding that a species obtaining more energy would have more individuals and less of a chance that all its individuals would die in the same time interval. More productivity would mean lower extinction rates. Just what we need! Alas, we now realize that individuals may not suffer death independently. Many attempts have been made to replace this theory. In fact, the senior author is one who has tried. But we do not believe a successful theory of S and productivity has yet emerged.

Linking S to temperature is an endeavour initiated by Rohde (1978). It depends on observations suggesting that higher temperatures lead to higher mutation rates and are associated with higher diversification rates (e.g. Gillman *et al.*, 2009). If the evolution rate of new species is constrained by a shortage of new mutations [i.e. genostasis (Bradshaw, 1984)], then raising mutation rates might indeed raise speciation rates. Such a mechanism could easily work in amphibians and reptiles. But, as James Brown cogently observed, ‘The most likely mechanism [to explain the results of Gillman *et al.*], which would have to do with the effect of temperature, can’t hold for birds and mammals’ (quoted in Akst, 2009) – because they are both warm-blooded. Ambient temperature does not determine their internal temperature. And yet there is a pattern to be explained: diversification appears to proceed faster in warmer climates, although we do not yet know why.

It is worth mentioning that both temperature and energy flow could be involved. One could raise speciation rates, the other lower extinction rates, for example. It does not matter

that they are so closely correlated as to prevent our using them both in a regression model. In each case, T or AE , we were incorporating a variable that could represent the joint effects of both.

Meanwhile we can point to one very suggestive empirical pattern that one day may help us decide the issue. Huston and Wolverton (2009) point out the severe discrepancy between the latitudinal gradients of NPP in the ocean versus the land. On land, NPP peaks near the equator. But in the oceans, NPP is highest in the colder waters of high latitudes. Evidently, photosynthesis proceeds faster in cooler water. Perhaps that is true simply because cooler water has a greater capacity to hold carbon dioxide (Wiebe and Gaddy, 1940). Whatever the reason, marine productivity is decoupled from temperature, allowing ecologists to compare marine diversity gradients separately with temperature and productivity.

But marine diversity gradients are still poorly known. Powell *et al.* (2012) search for the patterns of species diversity in the oceans and find that peaks occur 10–20 degrees away from the equator. That puts them some 20 degrees further towards the equator than peak productivities and a similar latitudinal distance (in the opposite direction) away from temperature peaks. Does this mean that both temperature and productivity are involved in controlling the steady state in S , and that peak S depends on a Goldilocks combination of the two? Or does it mean that temperature and productivity are mere correlates of the controlling variable? And what about the effect of area on marine diversity? Like its land systems, the Earth's marine systems have separate biogeographical regions (Spalding *et al.*, 2007). They may be leaky but they probably do exert some biogeographical effects. Is that why peak marine diversity does not correspond to either peak temperature or peak productivity?

The z -values

Intra-regional dynamics of species diversity depend on the relatively slow process of geographical speciation (Rosenzweig, 2003c). Owing to that slowness, theory confidently predicts that the slope of $\log S$ vs. $\log A$ in a multi-regional regression should exceed that slope obtained at the scale of island biogeography (which is characterized by the speedier origination process of immigration). Available data confirm the extra steepness. They also suggest that actual z -values among zoological regions may be unity or nearly so. How do the present results compare with those two hypotheses?

In our case, the z -values are the coefficients of $\log A$ in the bivariate regressions. Because these regressions tease out the effect(s) of climate, leaving z fully exposed, one might expect that they are more revealing than previous estimates of z (in which any effect of climate might have been conflated with the area effect).

Our four-class results confirm the prediction of theory. With $\log AE$ as the climatic variable, $z = 0.654$; with T , $z = 0.631$. Both these values exceed those of island systems. So do the results for the separate classes. For $\log AE$, Amphibia have $z = 0.92$, Reptilia $z = 0.61$, Aves $z = 0.54$, and Mammalia $z = 1.07$. For T , Amphibia have $z = 0.89$, Reptilia $z = 0.59$, Aves $z = 0.53$, and Mammalia $z = 1.04$. Note again that it does not matter whether AE or T represents climate; each class is characterized by a pair of z -values within a few hundredths of each other. But the class itself most certainly does matter. Mammals have the highest z -values; amphibians' values are almost as high; and birds have the smallest z -values. The bird z -values lie close to the upper range of bird z -values for islands (Rosenzweig, 1995); they come close to contradicting the prediction.

Two of the classes, amphibians and mammals, have z -values close to unity – as has often before been the case for inter-regional SPARs. But the other two classes, as well as the four-class analysis, have high z -values but well below unity. We do not yet have a theory to predict these z -values, so we cannot know whether these results contradict it. Moreover, keep in mind that the data sets themselves have enough rough edges to make it possible that the z -values we measured in them contain inaccuracies sufficiently substantive to mislead us about the exact z -values. For example, the endemic vertebrates of Hawaii, New Zealand, and Madagascar have suffered great losses to human beings in the past two millennia (Steadman, 1995). New Zealand lost at least 40 endemic birds, Hawaii at least 63. Because Hawaii, New Zealand, and Madagascar are the globe's three smallest zoological regions for vertebrates, adding their extinct species to their data sets would raise the regressions on the left-hand sides of the composite x -axes, thus reducing estimates of z . But adding them back would have constituted tampering with the data set – against our rules! We would at least have had to attempt to add back all the extinct species of all the zoological regions. Nonetheless, we did amuse ourselves informally and off the record by adding back the extinct birds of Hawaii and New Zealand. The additions had a very tiny effect on the results.

Another problem with the data sets is the degree to which they fail to achieve complete biogeographical independence. They are what they are and we cannot make them entirely independent, but we can say a few things about their endemisms (see Table 1 and remarks in the previous paragraph about extinctions) that will underscore the difficulty of relying solely on empirical analyses to estimate inherent inter-regional z -values.

Two classes, reptiles and birds, are responsible for the low z -value of the entire group. Let us look more closely at the bird data set.

The WWF excluded a bird from an ecoregion if it is observed there only as a passage migrant. But it included a bird whether it breeds in an ecoregion or merely overwinters there. That criterion accounts for the extremely low endemisms of both the Palearctic and the Nearctic. With so many species migrating back and forth, the ensemble should begin to move towards islandness and the lower z -values of islands. A similar thing may be happening in Hawaii and New Zealand. Each of these has a very high proportion of endemics that live in terrestrial habitats but also a large number of shorebirds that are usually not endemics. And then there are all those recent extinctions of birds that have fallen entirely on the endemics. Taking account of them raises New Zealand's vertebrate endemism to 74% and that of Hawaii to 66%.

On the other hand, except for some bats, neither mammals nor amphibians overwinter in other zoological regions. A very high proportion of them are endemics (see Table 1). Perhaps that explains why their z -values are near unity? But reptiles also do not move seasonally between regions. Their endemisms mostly exceed those of mammals a little bit, yet their z -values are almost as low as those of birds. So we must conclude that, although inter-regional z -values do exceed archipelagic z -values, we cannot yet predict by how much they should do so, or understand any variation in them.

Using the telescope

Using our telescope, let us peer into the future of terrestrial vertebrate species diversity. We can now create a map of the sustainable proportion of species as a function of the proportions of area, p , and actual evapotranspiration, q , that remain available to wild species. (As before, we use AE , actual evapotranspiration, as a surrogate for energy flow. But

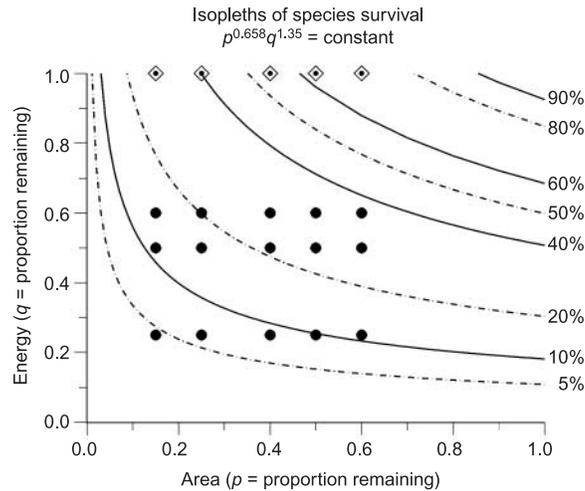


Fig. 6. Isopleths of the proportion of species that remain in steady state following the losses of some area and some productivity. Dots show a few sample scenarios. Species that remain after area loss alone are marked by diamonds at the top of the graph; these are relevant if temperature rather than productivity proves to be the causal climatic variable.

AE and *NPP* are linearly related, so the two proportions are the same.) We next set the diversity to a proportion and calculate the set of points in the graph that satisfy that proportion. We change the proportion repeatedly and redo the calculation each time. Thus we obtain a set of isopleths of residual diversity (Fig. 6).

Read Fig. 6 just like a topographical map. Fix a test point representing the area and *AE* that remain. Then read the proportion of species that will remain after the system reaches the new steady state produced by the test point. Recognizing that humans have had a profound impact on the land available to other species, particularly in the past century (Steffen *et al.*, 2007), we plot some points as examples. (Refer to Fig. 6 and the following paragraphs.)

Using both ‘the most conservative land-use model’ and the ‘least conservative land-use model’, Ellis (2011) estimates that we have converted 60–75% of the ice-free land already. Mittermeier *et al.* (2003) find that just over 50% is no longer wild. A progress report on how much of the land in 2010 was protected for nature (at least minimally) estimates only 12.7% (IUCN and UNEP-WCMC, 2011). This figure has increased from 8.8% in 1990. Vitousek *et al.* (1997) reported smaller numbers: ‘Estimates of the fraction of land transformed or degraded by humanity (or its corollary, the fraction of the land’s biological production that is used or dominated) fall in the range of 39 to 50%.’ But they quickly added: ‘These numbers have large uncertainties, but the fact that they are large is not at all uncertain.’ Based on the numbers we recovered from the literature, we plot sample residual areas of 60%, 50%, 40%, 25%, and 15%.

What proportion of the Earth’s energy flow do we permit nature to retain? Mittermeier *et al.* (2003) suggest that less than 60% remains. Vitousek *et al.* (1997) use the same values as for area, 50–60%. Ellis (2011) estimates that 11% of the Earth’s terrestrial energy flow comes in wildlands and 13.9% in semi-natural lands. Assuming for the sake of a crude estimate that all *NPP* in wildlands and semi-natural lands remains for wild species and none remains in

rangelands, croplands, and densely settled lands, then 24.9% of terrestrial productivity remains for nature. We plot sample residual productivities of 60%, 50%, and 25%.

Let us suppose the least intrusive human presence, i.e. we take 40% of the land area and 40% of Earth's terrestrial productivity. Then we will lose roughly 64% of terrestrial vertebrate species (Fig. 6). Suppose we take 85% of the land area and 25% of Earth's terrestrial productivity. Then we will lose roughly 96% of terrestrial vertebrate species. Because of the curvilinearity of the isopleths, once we enter into the range of extreme depletion either of area or productivity, improvement in the other does little to relieve the problem: If we take 85% of the land area, residual diversity ranges only between 4% and 14%. If we leave only 25% of productivity, residual diversity ranges only between 4% and 11%. All of these outcomes mean mass extinction for the globe's terrestrial vertebrates.

Now suppose that climate influences diversity through temperature instead of productivity. Human activity does not remove heat from the Earth. If anything, we seem to be increasing it. So we ignore the *AE* axis and read only the top horizontal of the map because now, loss of area by itself will predict the proportion of species in the new steady state (Fig. 6; diamonds). If 60% remains, so will about 70% of species. If 15% remains, only about 26% of species will survive. These are higher numbers but still ominous. Even with such numbers, the telescope predicts a mass extinction much more severe than those predicted by island biogeography models.

Why are estimates of loss of species diversity based on island biogeography so relatively mild compared with those of the telescope? Because island biogeography is applied only by analogy to the question of sustaining global diversity. Here is what we do. We look at a map of our remaining natural areas; we see what looks like an archipelago of isolates; and we invoke the theory of island biogeography. But actually the analogy is deceptive and island theory does not apply. In island theory, the source of new species is immigration from an invariant species pool. In island theory, no species ever becomes globally extinct. The mainland keeps a permanent stock of species to serve as ready replacements for any species that vanish from an island. Islands, by assumption, do not truly sustain their own diversities. In contrast, species can and do become globally extinct in zoological regions. And the source of new species in zoological regions is the comparatively slow process of speciation rather than immigration. So, in zoological regions, origination is slow and extinction is permanent. The result is a considerably poorer steady state.

But hope is alive. Some human uses result in wild species and humans sharing a landscape. Daily *et al.* (2001) call such uses 'countryside biogeography'. Pereira and Daily (2006) develop quantitative methods to take account of the diversity that such uses protect. Rosenzweig (2003a) suggests that an attitude of reconciliation ecology supported by good science can deliberately replace many of the pernicious methods of exploiting the land with other methods that preserve both human and wild-species uses. Franklin and Lindenmayer (2009) also emphasize the crucial value of conserving diversity outside of reserves. With luck and determination, one day we will have to recalibrate our telescope to take cognisance of such changes.

Our telescope may see into the future but we do not know how far. In that weakness, it may resemble early telescopes whose users did not know about red shifts. In any case, changing a steady state is changing an integral, not a derivative. It is the result of change in a panoply of dynamic interactions and processes whose differential equations we know not how to express, let alone how to solve. So far, Brooks and colleagues' (1999) is the only attempt we know to face successfully the challenge of developing rates of change associated

with species–area relationships. But their effort focused on the smaller scale, intra-regional problem. And without a successful theory linking diversity to productivity, there cannot be a method to estimate extinction rates associated with loss of productivity. Meanwhile, confronting with theory the combination of area loss and productivity loss is just a dream for now. Thus the telescope, focused as it is on the inter-regional scale, does not tell us how long life will take to become impoverished globally.

If that makes you relax, it should not (Pimm *et al.*, 1995). We have already lost some 20% of the Earth’s bird species and over 10% of Australia’s mammal species (Flannery, 2001). Flannery counts 103 global extinctions of mammals, birds, and reptiles between 1500 and 1999. ‘Based on recorded extinctions of known species over the past 100 years,’ the Millenium Ecosystem Assessment (2005) concludes that ‘extinction rates are around 100 times greater than rates characteristic of species in the fossil record.’ And global threats to climate threaten entire polar and montane habitats in the fairly near future; such losses have the potential to bring the axe down instantly on many, many species. No, if we were to relax, time would not be in our favour.

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