Species diversity can drive speciation

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A fundamental question in evolutionary ecology and conservation biology is: why do some areas contain greater species diversity than others? Island biogeographic theory has identified the roles of immigration and extinction in relation to area size and proximity to source areas[1,2], and the role of speciation is also recognized as an important factor[3–6]. However, one as yet unexplored possibility is that species diversity itself might help to promote speciation, and indeed the central tenets of island biogeographic theory support such a prediction. Here we use data for plants and arthropods of the volcanic archipelagos of the Canary and Hawaiian Islands to address whether there is a positive relationship between species diversity and rate of diversification. Our index of diversification for each island is the proportion of species that are endemic, and we test our prediction that this increases with increasing species number. We show that even after controlling for several important physical features of islands, diversification is strongly related to species number.

Investigating why some areas contain greater species diversity than others offers a way to identify factors important for both generating and maintaining species diversity. The analysis of species–area curves has produced a wealth of data, with the evidence clearly supporting the simple rule that if you sample a larger area, you will find more species[7]. In their theory of island biogeography MacArthur and Wilson[1,2] developed this basic principle to demonstrate that islands with non-zero immigration rates and different degrees of isolation should exhibit different degrees of species diversity. The consequences of this are demonstrated in numerous studies showing that in island systems, not only do larger islands contain more species, but for equivalent-sized islands those closer to a mainland source harbour a greater diversity of species. An implicit feature of MacArthur and Wilson's work is that both immigration rate and extinction rate are nonlinear. As the number of species on an island increases, extinction rate increases at a greater than linear rate. MacArthur and Wilson considered the increased interactions on an island with many species and reasoned that an increased number of species increases the likelihood of any given species dying out. So in the early stages of the colonization of an island and the development of a community of species, the extinction rate would be low because there would be little competition. However, as more species arrived, competition would assume a greater role, with population sizes tending to become lower on average and species facing an increased probability of competitive exclusion and predation[7].

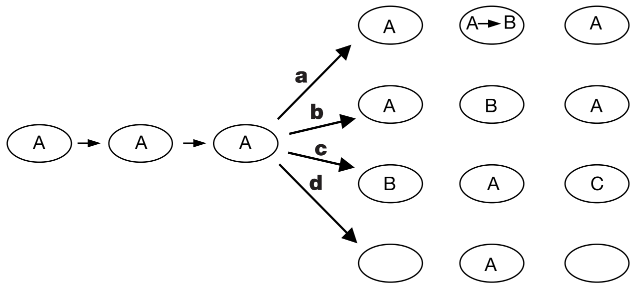

Figure 1 Origin of island endemism. Species A originates in the westernmost island and then colonizes the remaining two islands. After this there are four possible scenarios that may result in endemism on the middle island. **a**, Species B is the result of intra-island speciation from the founding species A. **b**, Species B is the result of inter-island speciation. **c**, Inter-island speciation on the first and third islands results in endemism for species A on the middle island. **d**, Extinction of species A on the first and third islands results in endemism on the middle island. In these last two scenarios, endemism of species A is not due to intrinsic factors within the island in which it occurs.

An important but untested outcome of the situation outlined above is that the same factors that lead to an increased probability of extinction might also lead to an increased probability of diversification. In other words, species diversity itself could be a driver of species diversification. Increased competition and predation can have two consequences for any individual species on a given island. A species may succumb to these pressures and become extinct, or it may respond to these pressures, adapt, and survive. Additionally, as species diversity increases and average population size decreases, population genetic theory predicts that there will be an increasing probability of divergence of island populations from the source population of a species through genetic drift. Finally, increasing species diversity may lead to greater community structural complexity, and this has been suggested as a possible evolutionary force driving speciation[8]. To test the possibility that species diversity can drive speciation requires a demonstration that areas with greater species diversity also have greater diversification rates. Volcanic island archipelagos such as the Canary and Hawaiian Islands provide the best opportunity to examine this question because of their discrete geographical nature and the general absence of historical connection between their component islands to each other or to a mainland, although there have been historical connections between a few of the Hawaiian islands[9,10]. Model systems such as the Canary and Hawaiian Islands permit the relative influences of variables to be readily considered compared with more complex continental areas[11]. The flora and fauna of each island is the result of the accumulation of species through time by chance dispersal from mainland sources or neighbouring islands, *in situ* speciation and extinction. This contrasts with mainland biogeographic areas that historically may have had differing degrees of floral and faunal connectivity due to climate-mediated contractions and expansions in species range.

Both the Canary and Hawaiian Islands have an exceptionally well characterized flora and fauna for each of their component islands, and maximum geological ages are available for each island. To test our prediction that higher species diversity should lead to a higher rate of diversification, we investigated whether there is a positive relationship between the number of native species on an island and the diversification rate for arthropods and plants within each archipelago. By focusing on plants and arthropods, we were able to cover two highly diverse and disparate groups of organisms to test the generality of our hypothesis. Our index of diversification for individual islands is the proportion of native species that are endemic to that island. This includes species arising through intrinsic factors within the island (Fig. 1a, b) and those arising as a consequence of extrinsic factors resulting in extinction or speciation events on other islands (Fig. 1c, d). Thus our index is an estimate of diversification (speciation within individual clades averaged over all clades) within an island (Fig. 1a, b), with an inflation factor resulting from extinction and speciation on other islands (Fig. 1c, d). The impact of this inflation factor is greater for

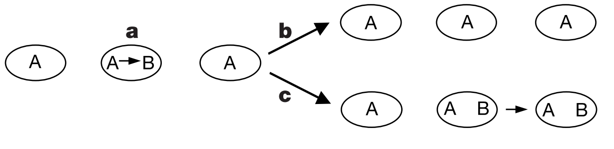

Figure 2 Elimination of island endemism. Intra-island speciation results in endemism of species B on the middle island (**a**). Either extinction (**b**) or the colonization of a new island (**c**) will eliminate this endemism.

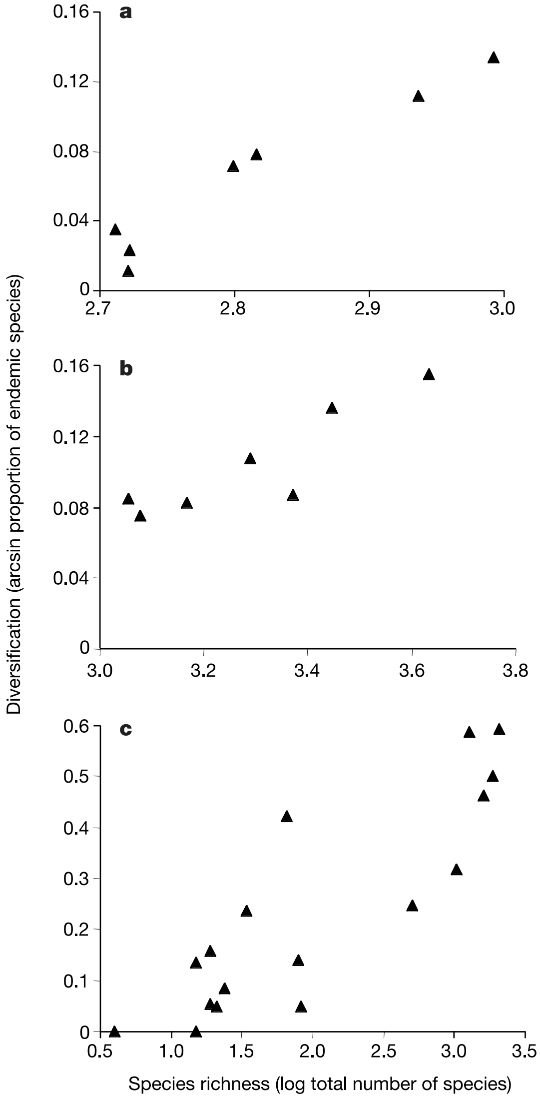

Figure 3 Bivariate plots for the relationship between diversification and species richness. **a**, Plants in the Canary Islands: $n = 7$, $r = 0.97$, $P = 0.0001$. **b**, Arthropods in the Canary Islands: $n = 7$, $r = 0.89$, $P = 0.007$. **c**, Arthropods in the Hawaiian Islands: $n = 17$, $r = 0.86$, $P = 0.0001$.

islands where we predict percentage endemism to be lower (see below), weakening rather than strengthening our predicted positive relationship between species diversity and diversification rate. Our index of diversification will also be diminished by intrinsic factors resulting in extinction (Fig. 2a) and extrinsic factors resulting in the successful establishment of endemics onto new islands (Fig. 2b) leading to a reduction of endemic species on a given island. Here again, both these factors will act to weaken rather then strengthen our predicted relationship. Extinction will have more effect on islands where we predict percentage endemism to be highest (see below) and, considering the probability of successfully colonizing a new island to be equivalent among endemics, this will feature more for islands with a greater percentage of endemics.

To allow for the obvious biogeographic and compositional differences between the two archipelagos we performed separate analyses for each. Data for vascular plants and arthropods for the Canary Islands ($n = 7$: El Hierro, La Palma, La Gomera, Tenerife, Gran Canaria, Lanzarote, Fuerteventura) were extracted from refs 12 and 13, respectively. Data for flowering plants ($n = 18$: Kure, Midway, Pearl and Hermes, Lisianski, Laysan, Gardner, French Frigate Shoals, Necker, Nihoa, Kaula, Ni'ihau, Kaua'i, O'ahu, Moloka'i, Lana'i, Maui, Kaho'olawe, Hawai'i) and arthropods ($n = 17$: as for plants except for Kaula) of the Hawaiian Islands were extracted from refs 11 and 14, respectively. Each of the four lists of species is a complete inventory of all described presumed native species, including presumed extinct species and excluding anthropogenic introductions.

We used multiple regression analyses (see Methods) to control for other physical factors that might also be important for diversification rates within island ecosystems: island age, island area, island altitude, and proximity to the nearest neighbouring island. Older islands may be expected to contain proportionately more endemic species as a consequence of the greater time during which speciation could have occurred within them[5]. Larger and topographically more complex islands might also contain proportionately more endemic species because of an increased probability for intra-island allopatric speciation[5,15]. Higher islands support more habitat diversity than lower ones[16] and this could lead to proportionately more endemics. Islands closer to a neighbouring island might be expected to contain proportionately fewer endemic species because of a greater probability of receiving immigrants[1], increasing the proportion of non-endemics. Although these other physical factors may be considered particular to island ecosystems, our principal factor of interest, species diversity, is of much broader biological interest.

Our analyses show that species richness is indeed a strong predictor of the level of diversification both across taxa and island groups (Table 1). For arthropods on the Canary Islands, species richness was in fact the only independent variable that entered the final model and explained a vast amount of the variation in diversification (Table 1). Among the physical factors of the islands that we considered, island altitude covaried positively with diversification for plants on both the Hawaiian and Canary Islands and for arthropods on the Hawaiian Islands. Island area was a significant negative covariate with diversification for plants on the Canary

Table 1 **Regression results (diversification as the dependent variable)**

Island group	Taxon	Independent variables entering the final model	n	β	s.e. of β	t	P
Canary Islands	Arthropods	Number of species	7	0.89	0.20	4.45	**0.007**
	Plants	Number of species	7	1.02	0.07	14.3	**0.0007**
		Island altitude		0.10	0.06	1.7	0.18
		Island area		−0.22	0.05	4.4	0.02
Hawaiian Islands	Arthropods*	Number of species	17	0.74	0.10	7.3	**< 0.0001**
		Island altitude		0.54	0.12	4.6	0.0005
		Distance to nearest island		0.54	0.10	5.7	<0.0001
	Plants†	Number of species	18	0.61	0.17	3.6	**0.0028**
		Island altitude		0.67	0.17	4.0	0.0013
		Distance to nearest island		0.70	0.18	3.8	0.0020

Separate forward stepwise multiple regression analyses were performed for each island group and taxon. Canary Islands, arthropods (final model): multiple $r^2 = 0.80$, $F_{(1,5)} = 19.8$, $P = 0.007$. Canary Islands, plants (final model): multiple $r^2 = 1.0$, $F_{(3,3)} = 241.2$, $P = 0.0004$. Hawaiian Islands, arthropods (final model): multiple $r^2 = 0.93$, $F_{(3,13)} = 60.7$, $P < 0.0001$. Hawaiian Islands, plants (final model): multiple $r^2 = 0.79$, $F_{(3,13)} = 17.6$, $P = 0.0005$. β is the standardized regression coefficient, t represents the test statistic.

*Because of collinearity between island altitude and island age, island age was dropped from the analysis of plants on the Hawaiian Islands (see Methods). Thus we cannot separate the effects of these two variables on diversification for this taxon and island group.

†Because of collinearity between number of species and island area, island area was dropped from the analysis of plants on the Hawaiian Islands (see Methods). Thus we cannot separate the effects of these two variables on diversification for this taxon and island group.

Islands, and distance to nearest island covaried positively with diversification for both plants and arthropods on the Hawaiian Islands. For plants on the Hawaiian Islands we could not separate the effects of species richness and island area because they were strongly correlated (see Methods). The strong relationship between diversification and species richness is revealed more readily with bivariate plots (Fig. 3) for vascular plants of the Canary Islands and arthropods of the Canary and Hawaiian Islands.

The strength of our analyses comes from the inclusive sampling of species within large taxonomic groups. The probability of speciation (and extinction) increases for each species on an island as total species number increases. However, this increase is small and is therefore unlikely to be apparent within an individual genus of flowering plants or arthropods. Of all factors considered in our analyses, species number was positively related to diversification for three of the multiple regression analyses, and was implicated in the fourth. Although other physical island factors also featured in the analyses, there was less consistency in both the number of comparisons in which they featured and the extent to which they offered positive explanatory power. Our results support an implicit but overlooked prediction of island biogeographic theory: as species number in an area increases, so should the rate of speciation. This is of great importance for the general understanding of patterns of species richness and community composition, and calls into question the validity of model-based approaches that do not incorporate this. The answer to questions such as why there are so many species in the tropics[8] might in part be because there are so many species in the tropics. Further testing of the relationship between species number and rate of diversification can be achieved as complete faunal and floral lists for other island archipelagos come to hand. Recent developments in using microbial systems to test evolutionary ecological theory might also provide further experimental evidence[17–19]. □

Methods

We used forward stepwise multiple regression analyses to control for the physical properties of the islands while investigating the relationship between diversification and species richness. All variables were transformed before analysis by using log transformation (species richness, island age, island area, island altitude, and proximity to the nearest neighbouring island) or arcsin transformation (diversification; that is, the proportion of endemic species) to ensure normality. Because collinearity between independent variables might confound the analyses we checked for redundancy by investigating tolerance levels for the variables for each separate analysis. Tolerance values were adequately high[20] for all except two pairs of variables across the four analyses (that is, more than 0.13), and no standard errors in β were inflated. Collinearity featured within the analyses of plants and arthropods for the Hawaiian Islands only. For plants, we detected a strong positive correlation between total number of species and island area ($r = 0.94$, $P = 0.0001$) and therefore excluded island area from the analysis. This means that we cannot separate the effect of number of species from the effect of island area on the diversification of flowering plants on the Hawaiian Islands. For arthropods, we detected a strong negative correlation between island altitude and island age ($r = -0.94$, $P < 0.0001$); island age was therefore removed from the analysis. This has no bearing on our result of the importance of species richness for this taxon and island group, although it means we cannot separate the effect of island altitude from the effect of island age on the diversification of arthropods on the Hawaiian Islands. To further assess that our results were not simply artefacts of our forward stepwise regression procedure[21], we also performed standard multiple regressions for all four combinations of islands and taxa. This procedure produced similar results to those of the forward stepwise regressions (all models were significant, with total number of species as a significant explanatory variable for diversification) except for arthropods on the Canary Islands. For this analysis the full model was not significant because of the limited data set and the lack of power caused by the many independent variables. Our results from the stepwise multiple regression analyses were therefore not simply caused by random inflation of independent variables. We also investigated interaction effects between species richness and the four physical variables of the islands in the standard multiple regression analyses. We checked separately for each variable, but none of the interaction terms was significant within any of the analyses. Because our measure of diversification is a proportion of, and hence not completely independent of, the key variable in our analyses, species richness, we performed additional analyses using the same measure of diversification but with only non-endemic species as the measure of species richness (see Supplementary Information). Because the results did not change (Supplementary Table 2) using this procedure, it is highly unlikely that our results are confounded by non-independence between diversification and species richness.

Received 30 November 2004; accepted 10 February 2005; doi:10.1038/nature03450.

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Supplementary Information accompanies the paper on **www.nature.com/nature**.

Acknowledgements We thank W. Sutherland, G. Hewitt, M. Taylor and T. Givnish for constructive comments.

Competing interests statement The authors declare that they have no competing financial interests.

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Sexual reproduction between partners of the same mating type in *Cryptococcus neoformans*

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Cryptococcus neoformans is a globally distributed human fungal pathogen that causes life-threatening meningoencephalitis in immunocompromised patients[1]. It has a defined sexual cycle involving haploid cells of α and a mating types[2], yet the vast majority of environmental and clinical isolates are α (ref. 3). Sexual recombination is normally expected to occur between