THE BIOGEOGRAPHY OF LARGE ISLANDS, OR HOW DOES THE SIZE OF THE ECOLOGICAL THEATER AFFECT THE EVOLUTIONARY PLAY?

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Résumé. — *La biogéographie des grandes îles, ou comment la taille de la scène écologique influence-t-elle le jeu de l'évolution ?* — Nous présentons une approche comparative des particularités de l'évolution dans des milieux insulaires de différentes surfaces, allant de la taille de l'île de La Réunion à celle de l'Amérique du Sud au Pliocène. Cette revue des formes actuelles et fossiles est centrée sur Madagascar, ainsi que sur la Nouvelle-Zélande, la Nouvelle-Calédonie et les îles Hawaii, dont les caractéristiques géologiques et historiques sont précisées.

L'étendue des terres isolées apparaît comme un facteur essentiel qui détermine la biodiversité, la taille des plus grands herbivores et celle des prédateurs au sommet des chaînes trophiques, le rythme de vie (fonction de la longévité et du métabolisme de base des animaux à taille égale), l'intensité de la compétition ainsi que la résilience de l'écosystème par rapport aux espèces envahissantes. Toutes ces caractéristiques dépendent aussi de l'éloignement des îles par rapport aux continents. Sur les plus grandes îles isolées pendant de longues périodes, des radiations adaptatives – à partir d'espèces colonisatrices ayant pu occasionnellement parcourir une longue distance – peuvent jouer le rôle écologique de groupes localement absents, même si l'ancienneté d'une colonisation et la relative protection vis-à-vis des compétiteurs continentaux qu'offre le nouvel habitat insulaire ne garantissent pas nécessairement une grande diversification des espèces qui en dérivent.

Diversification et endémisme : Bien que Madagascar et la Nouvelle-Zélande aient été reliées à des blocs continentaux, il y a un peu moins de 90 millions d'années, leurs biocénoses sont largement dominées par les descendants de formes colonisatrices ayant plus récemment traversé la mer. La phylogénie des espèces et leur datation en fonction de l'ADN montrent notamment qu'à Madagascar les formes actuelles de mammifères et d'oiseaux, ainsi que presque tous les reptiles et les plantes à fleurs (Tableau I) proviennent des colonisateurs qui ont traversé de vastes étendues marines. Des espèces endémiques qui sembleraient anciennes comme les baobabs sont arrivées à Madagascar il y a seulement dix millions d'années ; et la phylogénie moléculaire montre que certains groupes de vertébrés terrestres actuellement diversifiés en de nombreux genres et espèces endémiques (lémuriens, tenrecs), appartiennent chacun, en fait, à une seule radiation, donc à une seule colonisation réussie par la forme ancestrale. Inversement, les vagues successives d'espèces colonisatrices sont illustrées notamment par le hêtre austral (*Nothofagus*) ayant colonisé la Nouvelle-Zélande depuis l'Australie ; alors qu'il avait disparu à la suite de changements climatiques, il a de nouveau colonisé ce milieu insulaire. D'une façon générale, les datations en fonction de la phylogénie moléculaire montrent qu'on a longtemps sous-estimé l'importance d'espèces colonisatrices sur les terres qui furent anciennement séparées du continent.

Ainsi que l'a montré Darwin, les espèces colonisant les terres isolées ont tendance à évoluer vers de nouvelles espèces endémiques. La proportion de ces endémiques est plus grande sur les terres les plus isolées, par exemple aux îles Hawaii, notre site le plus éloigné, où le taux d'endémisme est particulièrement élevé. Le taux d'endémisme est aussi plus grand dans les groupes dont la dissémination est peu efficace : à Madagascar, ce taux est plus élevé pour les plantes à fleurs que pour les fougères et également plus élevé chez les amphibiens, les reptiles ou les mammifères terrestres que chez les oiseaux ou les libellules (Tableau II). De plus, un faible nombre de groupes peuvent se différencier sur des îles isolées et occuper des niches écologiques qui ne sont pas accessibles aux espèces des groupes continentaux apparentés. Les exemples cités à partir des données bibliographiques récentes ont permis de préciser les mécanismes de diversification des espèces sur les îles et les archipels. La spéciation fut allopatrique, aussi bien pour *Drosophila* sur les îles

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Hawaii, que pour les arbres de la section *Tieghemopanax* (*Polyscias*, Araliaceae) en Nouvelle-Calédonie, ainsi que pour les lémuriens de Madagascar. Cette différenciation des espèces correspond généralement aux exigences contrastées des différents habitats et des divers modes de vie possibles. La sélection dans les populations en train de se diversifier va dans le sens d'une diminution de la compétition pour les ressources limitées. Ainsi à Madagascar, les plantules des différentes formes de l'arbre du voyageur (*Ravenala*) sont respectivement adaptées aux sous-bois, aux espaces dégagés ou aux milieux marécageux et le décalage des floraisons des formes arborescentes adultes permet la sympatrie dans certains cas. Sur les îles les plus isolées et sur celles d'étendue suffisante pour héberger une grande diversité, on trouve les radiations évolutives les plus spectaculaires telles les drosophiles et les Drepanididae d'Hawaii ou, à Madagascar, les palmiers *Dypsis*, les batraciens Mantellidae et les lémuriens.

Selon le modèle darwinien, les innovations sont bien plus fréquentes sur les terres de grande étendue. Tous les continents sauf l'Antarctique (l'Australie et l'Amérique du Sud indépendamment des autres) ont permis l'émergence des écosystèmes prairiaux (ou graminéens) incluant de grands herbivores. Toutefois à Madagascar, l'hippopotame, un brouteur qui occupa les milieux ouverts et s'y différencia, dérive d'une forme venue du continent ; et aucune des îles de plus petite surface que Madagascar n'a vu évoluer ce type d'écosystème prairial.

Diversité, taille, convergence et rythme de vie : La probabilité d'extinction est plus faible et les possibilités de diversification sont plus grandes sur les îles de grande surface ; c'est donc dans ces milieux que la diversité des espèces, locale et/ou totale, est la plus grande (Tableaux VI et VIII). L'analyse des relevés botaniques, par le calcul de l'indice α de Fisher selon la formule S = α ln(1 + N/α) où S est le nombre d'espèces et N le nombre des arbres, a permis de mettre en évidence ces différences. Alors qu'en Nouvelle-Calédonie (riche de 3 061 espèces indigènes), un échantillon de 500 arbres de forêt dense correspond à 76 espèces, à Madagascar (11 000 espèces indigènes) il correspond à 123 espèces et en Nouvelle-Guinée (15 000 espèces indigènes) à 196 espèces. De la même façon, les oiseaux insulaires utilisent davantage d'habitats, avec un régime alimentaire plus éclectique que celui de leurs équivalents continentaux. Il en résulte une plus grande compétition sur les îles de grande surface, alors que la pression des herbivores et des prédateurs se fait d'autant moins sentir que les îles sont petites, avec également, dans ces cas, une tendance vers une plus faible production primaire et un rythme de vie plus lent.

Ainsi, avant l'apparition de l'homme, les plus gros herbivores étaient de moindre taille dans les milieux insulaires et d'autant plus petits que la surface des îles était réduite. Alors que les éléphants et les mammouths dépassaient 5 tonnes sur les blocs continentaux de grande surface, l'oiseau-éléphant de Madagascar (*Aepyornis*) pesait 275 kg et le plus gros herbivore d'Hawaii seulement 8,6 kg. La productivité primaire des écosystèmes est actuellement plus faible là où ces consommateurs primaires étaient de plus petite taille, notamment à Hawaii et probablement aussi à Madagascar (Tableau XIV). Parallèlement il apparaît qu'il y a moins d'espèces pionnières efficaces pour la régénération forestière sur les îles que dans les forêts continentales. Cela pourrait s'expliquer par le fait que, sur les îles, les plus gros folivores ne pouvaient pas créer de nombreux chablis en faisant chuter les éléphants peuvent le faire). Les carnivores sont également de moindre taille dans les milieux insulaires de surface réduite, comparés aux grands félins d'Afrique ou d'Asie, avec seulement 17 kg pour *Cryptoprocta spelea* à Madagascar et à Hawaii 5 kg pour l'aigle qui était localement le plus gros des prédateurs (Tableau XIII).

Dans la mesure où, sur les îles, les espèces sont exposées, au stade adulte, à de moindres dangers de prédation, elles peuvent consacrer une plus grande partie des ressources à un allongement de la durée de vie et moins investir pour se reproduire rapidement et en grand nombre. Ces particularités des milieux insulaires furent observées et décrites chez les rongeurs par Adler et Levins, sous le nom de " syndrome îlien ". Elles s'observent notamment chez le genre *Anolis* qui, sur les îles Caraïbes, vit plus longtemps et se reproduit plus tardivement et en moindre nombre que les espèces continentales équivalentes, ainsi que chez de nombreuses espèces de Nouvelle-Zélande réputées pour leur longévité et leur reproduction extrêmement lente. La faible pression de prédation se traduit également, chez les herbivores, par des convergences de formes et de fonctions entre des espèces insulaires et continentales là où les prédateurs sont peu efficaces. Par exemple, des lémuriens fossiles présentent des convergences avec des paresseux terrestres ou arboricoles d'Amérique du Sud et avec les koalas d'Australie, qui vivaient dans un environnement où les prédateurs marsupiaux étaient relativement peu efficaces. De même, les moas (*Dinornis*) de Nouvelle-Zélande ont évolué de façon convergente avec les moa-nalos (*Branta* et *Chelychelynechen*) des îles Hawaii et les oiseaux-éléphants (*Aepyornis*) de Madagascar.

Lorsque la limitation des ressources alimentaires a des répercussions plus importantes que la prédation ou la compétition sur les populations animales, le métabolisme basal tend à diminuer. Si on le compare à celui d'espèces du continent de taille équivalente, le métabolisme est d'autant plus réduit que l'espèce habite une île de petite dimension. McNab a observé cette réduction du métabolisme chez certains pigeons insulaires. Elle est également connue chez les lémuriens de Madagascar, dont le métabolisme est inférieur à celui des primates continentaux de poids équivalent, ainsi que chez les tenrecs si on les compare aux Lipotyphla du continent. Ces variations globales qui portent à la fois sur le niveau d'activité et sur l'efficacité de l'utilisation de l'énergie permettent de maintenir des populations plus grandes sur des ressources limitées.

Formes reliques et compétition avec les espèces envahissantes : Les terres anciennement isolées, suffisamment grandes pour amoindrir le risque d'extinction aléatoire, hébergent des formes reliques. Alors que des compétiteurs les ont remplacées sur les grands blocs continentaux, on trouve encore en Australie les monotrèmes, en Nouvelle-Zélande les rhynchocéphales (*Sphenodon*) et les Acanthisittidae (une famille ancestrale à la base de l'ensemble des passereaux), en Nouvelle-Calédonie, le genre *Amborella*, qui phy-

logénétiquement se situe vers l'origine de toutes les plantes à fleurs, et à Madagascar le genre *Aepyornis* récemment disparu.

Les espèces végétales des îles de grande surface possèdent généralement des défenses biochimiques contre leurs consommateurs, comme sur les continents. Mais il apparaît que si, sur un vaste bloc insulaire comme Madagascar, on trouve une proportion d'espèces riches en produits secondaires comparable à celle observée dans des milieux analogues continentaux, les végétaux des îles de petite surface en renferment d'autant moins que la surface est réduite. Ainsi les plantes des îles Hawaii et celles des Channel Islands, au large des côtes californiennes, sont moins bien défendues contre les vertébrés herbivores que celles du continent. De plus la compétition pour la lumière est plus faible : les plantes de sous-bois des îles Hawaii sont moins tolérantes à l'ombre que celles des forêts denses continentales. Il en résulte une plus grande sensibilité aux espèces envahissantes introduites sur les îles les plus petites. Les plantes pionnières introduites peuvent surcimer les végétaux indigènes qui ne font pas assez d'ombre pour les supprimer. De la même façon, les prédateurs peuvent se montrer redoutables faces à des proies dont la reproduction est très lente. Une bien plus grande efficacité dans l'utilisation des ressources ou l'utilisation, par des prédateurs, de techniques de chasse auxquelles les espèces insulaires n'ont jamais eu à faire face, confèrent aux espèces introduites une dangereuse supériorité. Nous présentons une revue de ces espèces envahissantes, végétales et animales, en fonction des effets observés sur des îles de différentes surfaces, avant et après l'intervention de l'homme.

L'isolement géographique affecte profondément le potentiel évolutif d'un écosystème, et, à surface égale, les îles les plus isolées sont moins diversifiées que celles plus proches du continent. C'est le cas en particulier des petites îles où le risque d'extinction est élevé lorsqu'il n'y a pas d'opportunité pour une nouvelle spéciation et où les espèces colonisatrices sont peu fréquentes. L'isolement géographique a joué particulièrement contre les invasions spontanées de mammifères terrestres, qui ont pu atteindre plusieurs fois Madagascar mais qui n'ont jamais atteint ni la Nouvelle-Calédonie ni les îles Hawaii avant que l'homme n'intervienne. Dans les milieux insulaires où les mammifères terrestres furent absents, d'autres formes animales, dont les oiseaux, ont pu jouer un rôle équivalent au niveau du sol, tel ce perroquet terrestre et folivore du genre *Strigops* en Nouvelle-Zélande. L'intensité de la compétition et la moindre possibilité de colonisation dépendent également de l'isolement d'un milieu insulaire. Bien que l'isolement d'un bloc quasi-continental comme l'Australie n'ait pas empêché l'évolution de carnivores de taille respectable, Webb a fait remarquer que l'Amérique du Sud, longtemps isolée au début du Pliocène, semble avoir été trop petite pour permettre l'émergence de mammifères carnivores efficaces. En Australie les carnivores étaient de plus grande taille que ceux de Madagascar, arrivés du continent il y a environ 20 millions d'années. Mais alors que le plus grand carnivore australien connu de l'Holocène, le loup de Tasmanie (*Thylacinus*), n'a pas résisté à la compétition des dingos et des chiens introduits par l'homme, les carnivores de Madagascar ont survécu aux introductions de chiens, de chats et de rats. La présence de ces carnivores indigènes a considérablement limité l'impact des espèces introduites sur le reste de la faune de Madagascar.

Ces différences entre les écosystèmes insulaires pourraient se comparer à celles que l'on observe entre des systèmes économiques. Les ensembles économiques ayant la plus grande production globale et qui sont les moins isolés des autres, comprennent une plus grande diversité de professions avec une compétition plus intense, un rythme des échanges plus rapide et une plus forte productivité *per capita*. Dans les écosystèmes les plus vastes, comme dans les plus grands ensembles économiques, les espèces – ou les professions – sont davantage spécialisées, ce qui implique davantage d'interdépendance, avec un réseau d'échange et de coopération plus vaste et plus complexe pouvant aller jusqu'à la symbiose.

SUMMARY. — We compare selected aspects of the biotas of long-isolated islands ranging in size from Réunion to early Pliocene South America, focusing on Madagascar, New Zealand, New Caledonia and the Hawaiian Islands. Although Madagascar and New Zealand were joined to larger land masses less than 90 million years ago, their biotas are overwhelmingly dominated by descendants of colonists from overseas. The size of a long-isolated land mass decisively influences major features of its ecosystem. On smaller islands, extinction is more likely, colonization is rarer, and there are fewer opportunities for diversification. The largest herbivores and the largest carnivores are smaller on smaller islands. Reduced diversity, lower predation pressure and diminished evolutionary innovation reduce the severity of competition on smaller islands: their plants are less well defended against vertebrate herbivores, and their primary productivity is lower, while their animals are longer-lived, less fecund, and have lower basal metabolism than mainland ecological counterparts. Herbivores are most likely to evolve convergently with counterparts on other land masses with predators of similar size and/or efficiency. Thus sloth lemurs converged on tree sloths, *Megaladapis* on koalas, and moa-nalos on moas and elephant birds. The degree of an island's isolation also affects its ecosystem's characteristics. More isolated islands receive fewer immigrants, so diversity is lower on more isolated islands, especially small islands with high risks of extinction. Fewer mainland immigrants, whose efficiency was tested against a variety of competitors and well-defended prey, reach more isolated islands, so competition is less intense on these islands, and these islands' predators are less efficient. Smaller size and greater isolation therefore make a land mass more invasible. Islands with the fewest predators and the slowest pace of life are most likely to be catastrophically disrupted by mainland invaders. All these phenomena have analogues in human economies. As a rule, economies with higher total production support more intense competition, more innovation, a greater diversity of occupations, a faster pace of life, and greater productivity per capita.

Islands play a central role in our understanding of the mechanisms of evolution. Study of species diversity on small islands (MacArthur &Wilson, 1967) prompted the insight that species diversity in any region represents a balance between immigration or diversification and extinction (Terborgh, 1973; Rosenzweig, 1975). Study of archipelagoes shed light both on the mechanisms of speciation and on the role of ecological opportunity in promoting successful speciation (Lack, 1947; Carson & Kaneshiro, 1976; Grant, 1986).

Here, we use studies of larger, long-isolated land masses to learn how the area of such a land mass influences the characteristics of the biota that evolves there. Darwin knew that competition drove adaptive divergence. Indeed, he proposed a principle he called "Divergence of Character" (Darwin, 1859: 111), according to which divergence is driven by the advantage of reducing competition with related lineages (Darwin, 1859: 112-115). Such adaptive divergence confers an advantage on an ecosystem like that conferred on an animal by "the physiological division of labor in the organs of the same individual body" (Darwin, 1859: 115) and that conferred by division of labor on either an individual factory or a whole economy (Smith, 1776). How does the area of a land mass affect the outcome of adaptive divergence thereon?

Darwin inferred that on distant islands, isolation prevents "the immigration of better adapted organisms, after any physical change, such as of climate or elevation of the land, etc; and thus new places in the natural economy of the country are left open for the old inhabitants of the country to struggle for, and become adapted to" (Darwin, 1859: 104).

By Darwin's (1859: 111) principle of "divergence of character," at least some of this island's lineages will diversify because "the more diversified the descendants from any one species become in structure, constitution, and habits, by so much will they be better enabled to seize on many and widely diversified places in the polity of nature, and so be enabled to increase in numbers" (Darwin, 1859: 112).

In short, if an island is large enough to allow speciation and diversification, selection allows a lineage that reaches this island to radiate into ways of life that its continental counterparts will never occupy. On the other hand, if "an isolated area be very small, ... the total number of individuals supported on it will necessarily be very small; and fewness of individuals will greatly retard the production of new species through natural selection, by decreasing the chance of the appearance of favourable variations" (Darwin, 1859: 105).

In support of this argument, Darwin observed that on "any small isolated area, such as an oceanic island, ... the total number of the species inhabiting it, will be found to be small ... yet of these species a very large proportion are endemic" (Darwin, 1859: 105).

On the other hand, Darwin was inclined to believe that: "largeness of area is of more importance [than isolation] ... in the production of species, which will prove capable of enduring for a long time, and of spreading widely. Throughout a great and open area, not only will there be a better chance of favourable mutations arising from the large number of individuals of the same species there supported, but the conditions of life are infinitely complex from the large number of already existing species; and if some of these many species become modified and improved, others will have to be improved in a corresponding degree or they will be exterminated. Each new form, also, as soon as it has been much improved, will be able to spread over the open and continuous area, and will thus come into competition with many others. Hence more new places will be formed, and the competition to fill them will be more severe on a large than on a small and isolated area" (Darwin, 1859: 105-6).

Finally, Darwin concluded that because, on "a small island, the race for life [is] less severe, and there [is] less modification and less extermination" "continental productions have everywhere become so largely naturalized on islands" (Darwin, 1859: 106).

Moreover, thanks to the same cause, "the productions of the smaller continent of Australia have formerly yielded, and are apparently now yielding, before those of the larger Europaeo-Asiatic area" (Darwin, 1859: 106).

In sum, Darwin's arguments predict that

1. On isolated islands and archipelagoes large enough to allow speciation, a high proportion of the species will be endemics (Darwin, 1859: 105), especially in those groups whose members rarely colonize.

2. Some of the groups reaching particularly isolated islands will diversify in adaptive radiation (Darwin, 1859: 104-5), often far exceeding their diversification in mainland settings.

3. Nonetheless, larger land masses support greater diversity, both total and local (a group's local diversity is its α-diversity, its diversity in an area too small to allow habitat-related species turnover or "β-diversity").

4. Competition is more severe on larger land masses.

5. Larger land masses allow more effective evolutionary innovation.

6. Larger land masses are less invasible by species introduced by human beings from continents.

Since Darwin's time, most of these topics have received detailed study. Assessing the number of endemic species in a region's biota is a basic tool in conservation planning (Gentry, 1986; Myers *et al.*, 2000). Study of adaptive radiation, however, aroused major philosophical conflicts in evolutionary ecology. Lack's (1947, 1976) field observations suggested that, where related bird species overlap, they evolve divergently to reduce competition for the same limiting resources. Roughgarden (1976, 1979) derived mathematical theory showing how such "character displacement" could evolve. Roughgarden *et al.* (1983) derived theoretical predictions of what differences would allow two species of *Anolis* lizard to coexist on small West Indian islands: these predictions matched observation. Connell (1980), among others, objected that there was little empirical evidence that competition drives character displacement. Schluter (1994), however, experimentally demonstrated that where two populations of sticklebacks, *Gasterosteus*, are competing for similar resources, natural selection promotes resource partitioning and divergent adaptive radiation. Later, Grant & Grant (2006) tracked the course of adaptive divergence in detail for two species of Darwin's finches, *Geospiza*, competing for similar resources on a small Galapagos island. These experiments and observations showed how competition could drive adaptive divergence. Wagner & Funk (1995), Givnish & Sytsma (1997), Grant (1998), Schluter (2000) and many others summarized studies using molecular phylogenetic techniques in the context of geological history to infer the course of adaptive radiations of various plants and animals on both archipelagoes and continents.

Learning what factors govern the number of species a given region supports has been a central and contentious theme of ecological research (Leigh *et al.*, 2004). MacArthur and Wilson (1963, 1967) used mathematical techniques to show how the balance between immigration and extinction governs the number of species of a given group on an island, and predicted how this number should vary with the island's area and degree of isolation. Mayr had adumbrated similar ideas in 1940 (Vuilleumier, 2005), but MacArthur and Wilson made these ideas a central theme of ecological research (Vuilleumier, 1975: 421-422). Diamond (1975) showed how diversity and species composition of birds on islands near New Guinea varies with island size. He showed that some bird species, and some combinations of bird species, only occurred on larger islands, while a few generalist "supertramps" only lived on smaller ones. He also showed that certain species, or certain combinations of species, could resist invasion by certain other bird species with similar requirements. Connor & Simberloff (1979) tested a null hypothesis of bird distributions on these islands and concluded that bird species colonized islands independently of what other birds were present. Wright & Biehl (1982), however, showed that their null hypothesis was poorly formulated: a null hypothesis incorporating the size range of islands occupied by each species detected pattern more effectively. Diamond (1972, 1973, 1986) also showed that birds speciated allopatrically within New Guinea, and coexisted by partitioning habitats or resources. Similarly, Mayr & Diamond (2001) showed how bird diversity arose in

the archipelagoes of northern Melanesia. Elsewhere, Williams (1983), Roughgarden (1995), Jackman *et al.* (1997) and Losos *et al.* (1998) have shown how guilds of *Anolis* lizards have evolved and diversified on Caribbean islands of different sizes.

There is increasing focus on how an island's area affects the characteristics, evolutionary potential, and competitiveness of its ecosystem. Faaborg (1977) showed that in the West Indies, the proportion of non-passerines among an island's bird species is higher on smaller islands. Since the average metabolic rate for birds of given weight is lower in non-passerines, he concluded that average metabolic rate of bird species resident on smaller islands was lower than for mainland birds of similar weight. Andrews (1979), Levins & Adler (1993), Adler & Levins (1994) and Adler (1996) have shown that animals that are less preyed upon on smaller islands live longer, and are less fecund, than mainland counterparts: in other words, the pace of life of these animals is slower on small islands. Burness *et al.* (2001) and Wardle *et al.* (1997) have considered other ecosystem correlates of a land mass' size. Lack (1947), Montgomery (1983) and Freed *et al.* (1987), among others, have described innovations that evolved on small islands. Finally, thanks to the seminal work of Elton (1958), biological invasions are now a major field of study (see, for example, Mooney & Drake, 1986; Rejmánek, 1996). Nevertheless, even though Darwin (1859) outlined the relationships among these topics with remarkable insight, later studies have usually considered one of these topics in isolation from most of the others.

This paper will explore and test Darwin's ideas concerning these topics. This task has recently become much easier. Inventories of flowering plants, birds, mammals, etc. on different land masses are more complete, and the history, both natural and geological, of these land masses is better understood (e.g. Carlquist, 1980; Worthy & Holdaway, 2002; and especially Goodman & Benstead, 2003). The role of competition in adaptive divergence has been demonstrated more clearly. Clocked molecular phylogenies are increasingly available. Finally, Burness *et al.*'s (2001) study of how the sizes of a land mass' largest carnivore and its largest herbivore vary with its area has opened new perspectives. We will focus mainly on Madagascar, New Zealand, New Caledonia and the Hawaiian Islands (Fig. 1), comparing them with other land masses as appropriate. First, we will briefly outline the geological and biological history of these islands. Next, we assess the independence of the evolutionary experiments they harbored, comparing their degree of endemism, the role of colonists from overseas, and the extent of their adaptive radiations. We then discuss the relation between their distances from the nearest continents, and patterns of endemism and diversification in ferns, seed plants, and birds. Next we compare local and total diversity on isolated land masses of different area. To compare the severity of competition and the pace of life on different land masses, we first ask

Figure 1. — Map showing the location, relative size, and degree of isolation of our four focal land masses (arrows): Madagascar, New Zealand, New Caledonia, and the Hawaiian Islands.

whether evolutionary convergence is most likely for land masses of roughly similar size. Then we compare more direct measures of the severity of competition, the pace of life required by this competition, and the susceptibility to invasion of these land masses.

BACKGROUND: GEOGRAPHY AND HISTORY

MADAGASCAR

Madagascar is an island of 587,000 km^2, 400 km off the coast of east Africa that extends nearly 1,600 km from 12° to 25.5° south latitude. Annual rainfall ranges from over 3,500 mm along parts of the east coast to less than 350 mm in the dry southwest (Humbert & Cours Darne, 1965). For most of its length, Madagascar's east coast is straight, running roughly SSW-NNE. A few tens of km back from the coast, mountain ranges rise from the coastal plain to a height of 1,500-2,500 m; the highest peak is 2,870 m. Beyond the mountain summits, the land slopes more gently down towards the west coast, and the climate becomes drier and more seasonal. Before humans settled, rain forest extended from the east coast up to the mountains, ranging from taller lowland forests to montane forests, and elfin forests on the summits. Evergreen plateau forests and more open woodland with grassy understory covered much of the island west of the summits, grading into seasonal dry forest towards the west coast, and drier "spiny forest" in the far south and southwest (Humbert & Cours Darne, 1965; Schatz, 2000). A tongue of monsoon forest extended to the northwest coast opposite the resort island of Nosy Be. Some grasslands were interspersed among Madagascar's forests before humans colonized (Burney, 2003), but the vast and sterile fire-maintained grasslands that now cover so much of central Madagascar were created by human settlers (Koechlin, 1972; Lowry *et al.*, 1997).

Together with India and Australia, Madagascar split off from Africa about 160 million years ago (Hay *et al.*, 1999; Flynn & Wyss, 2003). For another forty million years, one could walk dryshod from Madagascar across India and Antarctica to South America, and thence eastward to Africa, but after Africa split apart from South America 120 million years ago, there was no land connection between Madagascar and Africa (Hay *et al.*, 1999). Large islands may have existed between Madagascar and Africa between 46 and 25 million years ago (McCall 1997) but they never became a continuous land bridge from Africa to Madagascar (Poux *et al.*, 2005).

Madagascar became an island unto itself when India split away from Madagascar 88 million years ago and began to drift north toward Asia (Storey *et al.*, 1995). During the late Cretaceous, theropod dinosaurs of the families Abelosauridae and Noasauridae, sauropod dinosaurs of the order Lithostrotia, and gondwanatherian mammals of the family Sudamericidae lived in Madagascar, Patagonia and India (Krause *et al.*, 1997, 1999; Sampson *et al.*, 1998; Krause, 2003; Krause *et al.*, 2006). At this time a marsupial lived in Madagascar, which probably came via Antarctica from South America (Krause, 2001). India was still connected to Antarctica, and by that route to South America, when it split off from Madagascar (Hay *et al.*, 1999). Indeed, for 32 million years after separating from Africa, Madagascar remained connected to South America and Australia by India and Antarctica (Hay *et al.*, 1999). During the Cretaceous, Antarctica, which supported mixed forest, was a suitable corridor for the exchange of plants and animals. When the Cretaceous began, this forest was dominated by conifers of the families Podocarpaceae and Araucariaceae. During the latter half of the Cretaceous, several species of angiospermous trees came to dominate the forest (Cantrill & Poole, 2005).

Madagascar was centered near 30° S from the late Cretaceous into the Eocene (Wells, 2003). In consequence, Madagascar's climate was quite dry during the Paleocene and Eocene. Madagascar's oldest vegetation type is therefore the spiny forest, now restricted to Madagascar's southwest (Wells, 2003). Judging by when offshore sediments first showed signs of rapid erosion on Madagascar's eastern slopes, Madagascar's east coast first became sufficiently exposed to rain-bearing trade winds to support the growth of rainforest only in the Oligocene (Wells, 2003). Rainfall on Madagascar's northwest coast, near Nosy Be, became sufficient to support monsoon forest only about five million years ago (Wells, 2003). The proportion of native plant

genera that are endemic to Madagascar is highest, 47%, in Madagascar's southwest, while it is 41% in the west, 37% on the eastern slopes, 23% in the monsoon forest of the northwest, and 21% in central Madagascar (Koechlin, 1972). Correspondingly, the most primitive (basal and relictual) lineages of frogs and snakes in Madagascar are centered in Madagascar's dry southwest (Vences *et al.*, 2000).

Human populations settled Madagascar less than 2,000 years ago (Wright & Rakotoarisoa, 2003), eventually creating extensive grasslands (Lowry *et al.*, 1997). Their advent led to the extinction of Madagascar's largest birds and mammals (Burney, 2003; Dewar, 2003). Since European colonization began in 1895, forest clearing, habitat destruction, and introduction of aggressive invaders have accelerated markedly (Burney, 2003).

New Zealand

New Zealand is a pair of adjacent islands totaling 268,000 km^2 in area, now 1,500 km from Australia, its nearest continent. Unlike Madagascar, New Caledonia, and the Hawaiian Islands, New Zealand lies entirely within the temperate zone. It now extends from 34° to 47° S. latitude. Along South Island's west coast, the Southern Alps rise from the shore to 3,000 m in 25 km. Much of North Island was created by volcanoes; its highest peaks are above 2,000 m. Rain comes in abundance from the west, but the rain shadow of the Southern Alps reduces annual rainfall to 400 mm in parts of South Island (Worthy & Holdaway, 2002).

A New Zealand "minicontinent", extending over the Norfolk Island Rise to New Caledonia (Cooper & Millener, 1993), began to separate from Australia 85 million years ago (Kroenke, 1996). New Zealand was separate from Australia by 74 million years ago, and isolated from New Caledonia by 60 million years ago (Kroenke, 1996). Afterwards, New Zealand gradually eroded away to a flattened land with little relief, and subsided, until in the late Oligocene, 27 million years ago, only 18% of its current land area was above water (Cooper & Millener, 1993), but it was never entirely submerged (Pole, 2001). In the Miocene, uplift and volcanic activity increased New Zealand's land area. During the last five million years, from the Pliocene onward, the Southern Alps and other mountain backbones have arisen (Worthy & Holdaway, 2002), and New Zealand has become much cooler (Lee *et al.*, 2001).

Some of New Zealand's biota was inherited directly from Gondwana, including its moas, a family of passerines (Acanthisittidae) that is sister to all other passerines, leiopelmatid frogs, diplodactyline geckos (the sister clade of New Caledonia's endemic clade of diplodactylines), onychophorans, giant earthworms, wetas (large wingless orthopterans of the family Anostostomatidae), the tree genus *Pseudowintera* (Winteraceae), and at least some of its conifers (Chambers *et al.*, 2001, Worthy & Holdaway, 2002). Monotreme mammals were in southeast Australia 100 million years ago (Long *et al.*, 2002), long before New Zealand began drifting away, but if New Zealand inherited these mammals, they did not survive (Pole, 1994). New Zealand did inherit another archaic group of mammals that still survived 19 million years ago (Worthy *et al.*, 2006).

When New Zealand split from Australia, conifers dominated its forests: the first angiosperm-dominated forests appeared in New Zealand in the Eocene (Winkworth *et al.*, 2002: 515). Most of New Zealand's flowering plants (McGlone *et al.*, 2001; Winkworth *et al.*, 2002), and its bats, nearly all its flying birds, most of its insects, etc. crossed the water, usually from Australia or New Caledonia, to get there (Chambers *et al.*, 2001; Worthy & Holdaway, 2002; Arensburger *et al.*, 2004). Although an area of New Zealand greater than New Caledonia's escaped flooding by the sea during the Oligocene, most of the animal groups present in New Zealand when the Maoris arrived, even groups inherited from Gondwana, such as moas, diplodactyline geckos, and the clade of tree and giant weta (Deinacridinae), all began to diversify from unique common ancestors only twenty million years ago, when New Zealand's area began to recover after its Oligocene submergence (Chambers *et al.*, 2001; Baker *et al.*, 2005; Trewick & Morgan-Richards, 2005). The cool weather of the last five million years sparked an unusual spate of extinctions. Fire-adapted *Eucalyptus* (which border alpine meadows in Australia's Great Snowy Mountains) and *Acacia* died out, as did dominant groups of nitrogen-

fixing shrubs and trees, which are still present in Australia and New Caledonia (Lee *et al.*, 2001). Other warmth-loving groups, such as crocodiles, and tree genera such as *Bombax, Ilex*, several palms, a variety of Proteaceae, and *Casuarina* also disappeared from New Zealand at this time. Thanks to mountain uplift, great expanses of montane shrubland and tussock grassland appeared above the tree line (Worthy & Holdaway, 2002). The uplift of mountains, and the extinctions caused by cooling, opened many opportunities, and invasion has been particularly frequent in the last few million years (Winkworth *et al.*, 2002).

Transient voyagers introduced Pacific rats to New Zealand 2,000 years ago. Polynesians colonized New Zealand 750 years ago, wiping out moas and other large birds, and transforming half of South Island's forest and shrubland into tussock grassland. The animals they brought caused other extinctions. Since 1800, European settlement has accelerated forest clearing and the spread of exotic invaders (Worthy & Holdaway, 2002).

NEW CALEDONIA

New Caledonia is an island about 400 km long and up to 50 km wide, stretching roughly from 20° to 22.3° south latitude. Its area is now 16,750 km^2 (Virot, 1956; Schmid, 1981). New Caledonia is now 1,150 km from Australia, its nearest continent (Schmid, 1981). A spine of low mountains traverses the island from end to end: its highest peak is 1,630 m (Virot, 1956). The northeast side of New Caledonia now has a rainforest climate; Yaté, at the southeast end of this coast, averages 3,400 mm of rain a year, and 165 mm during its driest month (Virot, 1956). The slopes and shores along its southwest side are drier: some sites along this coast average less than 800 mm rainfall per year (Schmid, 1981).

Following New Zealand, New Caledonia separated from Australia between 74 and 65 million years ago, and was an island by 60 million years ago (Kroenke, 1996). New Caledonia was largely, perhaps entirely, flooded by the sea during the Paleocene. Between 39 and 36 million years ago, New Caledonia slowly became nearly entirely overspread by a layer up to 2,000 m thick of igneous ultrabasic rock (Jaffré *et al.*, 1987; Kroenke, 1996; Lowry, 1998). Much of this layer has since eroded away: now, only about a third of the island is covered by ultrabasic rocks (Lowry, 1998). New Caledonia has been a large island at least since the late Eocene (McLoughlin, 2001; Bartish *et al.*, 2005). Mountain ranges arose there in the Pliocene (Murienne *et al.*, 2005), but, on the whole, its climate may have changed very little during the Cenozoic (Morley, 2000: 274).

Should New Caledonia be treated as a continental fragment or an oceanic island? The absence from New Caledonia of onychophorans and leiopelmatid frogs, inherited by New Zealand from Australia, suggest that New Caledonia was entirely flooded after it separated from Australia. Other, more doubtful, arguments have been advanced for the same conclusion. Pole (1994) argued that because plant groups supposedly inherited from Gondwana tend to be concentrated on ultrabasic substrates, which became available only 20 million years after New Caledonia became an island, these groups must descend from colonists that crossed the sea after these rocks formed. Yet, it is often the most marginal and/or unproductive habitats that provide refuge for a region's earliest substratum of inhabitants whereas infertile habitats are most resistant to colonists from overseas (Fine, 2002). Pole (1994) also argued that because many of these "Gondwana relicts" also lived on the oceanic island of Fiji, they provided less than compelling evidence that part of New Caledonia escaped submergence beneath the sea. Since Pole wrote, however, Kroenke (1996) reports that a fragment of New Caledonia split away 41 million voyars ago and drifted east. Part of this fragment became attached to Fiji 6 million years ago, and the remainder became 'Eua, a small island that now belongs to the Kingdom of Tonga. Did this fragment introduce Gondwana relicts to Fiji?

On the other hand, New Caledonia's distinctive clade of endemic figs, *Ficus* (Corner, 1967: 39-40), its array of conifers, many of whose genera are not found on truly oceanic islands (Schmid, 1989; De Laubenfels, 1996), its endemic Winteraceae (Lowry, 1998), its endemic clade of diplodactyline lizards (Bauer, 1999) and many other groups suggest a direct inheritance

from Gondwana. For *Araucaria*, *Agathis*, and diplodactyline geckoes, these conclusions accord with clocked molecular phylogenies (Chambers *et al*., 2001; Givnish & Renner, 2004).

Melanesians settled New Caledonia 3,000 years ago (Stevenson & Hope, 2005), transforming substantial areas into savanna (Virot, 1956), and wiping out crocodiles, many birds and other animals (Bauer, 1999). During the last century and more, European colonization has destroyed habitat, primarily by logging and mining, and introduced destructive animals, primarily cats, dogs and pigs (Schmid, 1981; Letocart & Salas, 1997).

The Hawaiian Islands

The Hawaiian Islands are a chain of oceanic islands stretching northwest from the largest and highest island, Hawaii, which is 3,800 km from North America, the nearest continent. The total area of these islands is 16,710 km^2. The largest island, Hawaii, has an area of 10,458 km^2: its highest point is 4,200 m. The westernmost large island, Kauai, 600 km northwest of Hawaii, has an area of about 1,600 km^2, and its highest point is 1,600 m. Like Madagascar and New Zealand, the Hawaiian Islands have a great variety of climates. The larger Hawaiian islands are mountainous, and most of the rain is brought by the trade winds from the north or northeast. Therefore, lands in the rain shadow of great mountains are quite dry, with an annual rainfall as low as 250 mm, whereas windward slopes are quite wet (Howarth & Mull, 1992); lowlands are warm, whereas it often freezes atop the highest mountains (Carlquist, 1980: 64-65).

The Hawaiian Islands were formed as a tectonic plate moved northwest over a volcanic hotspot. The youngest and largest island, Hawaii, is about a half million years old; the oldest large island, Kauai, is 5.1 million years old (Carson & Clague, 1995). This hotspot has been generating islands for 80 million years on a tectonic plate that was moving north until 43 million years ago, when its direction shifted to northwest at a speed of 8.5 cm/yr (Carson & Clague, 1995). Each island begins as one or more great volcanoes. Afterwards, the island subsides and shrinks as its mountains erode away. The newest island has a 4,200 m volcano; the 5.1-million-year-old Kauai's highest point is 1,600 m, and the 10.3 million-year-old Necker's highest point 84 m, above mean sea level. The island may persist much longer as an atoll, as have 29-million-year-old Midway and 30-million-year-old Kure, before becoming a submarine seamount (Carson & Clague, 1995). The Hawaiian archipelago is therefore far older than any of its extant large islands. Do some of Kauai's plants and animals descend from colonists from older islands long since sunk beneath the waves?

A high Hawaiian island receives much of its biota by colonization from the next older high island in the chain. The phylogenetic pattern characteristic of Hawaii's more diverse endemic clades is for the most basal members of a clade to occur on the oldest high island, Kauai, and for successively more recently derived members of the clade to occur on successively younger islands (Wagner & Funk, 1995; Fleischer *et al.*, 1998; Roderick & Gillespie, 1998). There was a lull in the formation of islands, however, between 33 and 23 million years ago (Price & Clague, 2002; Schneider *et al.*, 2005). At the end of this lull, all that remained of the Hawaiian Islands were a few, scattered, small, low islands and atolls. Today, those Hawaiian islands over seven million years old, which are all small and low, support 8 species of endemic land snail compared to 1,000 on the younger islands, 12 endemic species of flowering plant compared to 850 on the younger islands, and no species of endemic fern, compared to over 100 on the younger islands (Carson & Clague, 1995). The ten million year lull in island formation must therefore have nearly annihilated the diversity of terrestrial colonists on older islands that were available to colonize the next island. Almost all terrestrial radiations in the Hawaiian Islands are accordingly less than 23 million years old (Schneider *et al.*, 2005). Moreover, the islands formed between 10-million-year-old Necker and 5-million-year-old Kauai were few, small and rather low, so Kauai must have received a far smaller proportion of its colonists from older Hawaiian islands than have more recently formed islands (Price & Clague, 2002). Thus, most of the Hawaiian Islands' endemic clades are no more than 5 million years old.

Polynesians settled Hawaii 1,500 years ago (Gray & Jordan, 2000), clearing lowland forest, introducing rats, pigs and other animals, and wiping out many species of birds, begin-

ning with the largest (Olson & James, 1982; Burney *et al.*, 2001). After 1800, settlers from North America and Asia cleared more forest, introduced many more exotic species, and caused extinction of more native animals, and some plant species as well (Carlquist, 1980).

DIVERSIFICATION AND ENDEMISM

MECHANISMS AND PATTERNS OF SPECIATION

Speciation is normally a response to divergent selection for different, incompatible adaptations (Fisher, 1930: 126), a process of diversification in response to trade-offs. A trade-off occurs when enhancing one capability diminishes another, as where plants that grow faster in bright light survive worse in shade (Kitajima, 1994; King, 1994), and *Drosophila* whose larvae develop more quickly are shorter-lived as adults (Sevenster & van Alphen, 1993). As a rule, speciation occurs only if different populations of the parent species are isolated enough for their genetic composition to diverge. The two requisites of speciation are therefore niche opportunity, and sufficient reproductive isolation between differently selected parts of the population for divergent selection to generate genetic differences between them.

Accordingly, speciation is normally allopatric: the populations that diverge are separated geographically (Mayr, 1942; Coyne & Orr, 2004). If isolation is incomplete, and the adaptations of these populations are incompatible, selection favors avoidance of matings between these populations. Polyploidy, the main cause of sympatric speciation among plants, occurs very rarely among woody plants (Otto & Whitton, 2000). In animals, the most convincing cases of sympatric speciation involve host-specific fruit-eating insects that mate on the fruits of the species on which they grew as larvae (Feder, 1998). If the flies lay eggs on these same fruit, colonizing a new host with a different phenology or chemistry is very like colonizing a new habitat, or a new island. Sticklebacks, *Gasterosteus*, in ponds near the coast in British Columbia, were once considered prone to sympatric speciation: a cohort of marine sticklebacks invading a pond previously lacking sticklebacks was thought to give rise to a species of slender plankton-feeders and a species of larger, wider-bodied bottom feeders. Instead, such speciation resulted from two successive invasions of marine sticklebacks, which are all plankton-feeders (McKinnon & Rundle, 2002). The first invaders grew larger to eat benthic insect larvae as well as plankton, and the second invasion prompted the evolution of "character displacement," the first invaders' descendants becoming bottom-feeding specialists to reduce competition with their plankton-feeding successors.

In the absence of selection, it takes roughly three million years for the two halves of a divided population to evolve mutual sterility by the spread of alleles in one half that are incompatible with alleles newly spread in the other, for animals as varied as fish (*Bathygobius, Abudefduf*), *Drosophila*, fiddler crabs (*Uca*) and sea urchins (*Diadema, Echinometra, Eucidaris*) (Rubinoff & Rubinoff, 1971; Bermingham & Lessios, 1993; Knowlton *et al.*, 1993; Coyne & Orr, 1989, 1997; Knowlton & Weight, 1998). In woody plants, the process can take even longer (Ehrendorfer, 1982). Diversification is often too rapid for speciation to happen by this kind of accident: it is usually driven by divergent selection in response to incompatible niche opportunities. In plants, speciation must often be driven by a local invasion of a new habitat (presumably thanks to the evolution of cheaper or better anti-herbivore defense), followed by strong selection for reproductive isolation between plants in these two habitats (Stebbins, 1982; Leigh *et al.*, 2004a). The evolution of a new species of California *Mimulus* (Bradshaw *et al.*, 1995), and speciation among Central American *Costus* (Kay & Schemske, 2003), illustrate this process. Good species of *Costus* (Kay & Schemske, 2003) and of Neotropical Bignoniaceae (Gentry, 1989), live in sympatry although they can easily be artificially cross-bred to produce viable hybrids: they achieve reproductive isolation by attracting different pollinators or flowering at different times. This must also be true of many other plant groups.

Animals and plants can speciate within islands that are large or heterogeneous enough to isolate different populations of a species from each other. Birds diversify allopatrically within New Guinea (Diamond, 1972, 1973, 1986), Madagascar or New Zealand, but not within New

Caledonia or even the 36,000 km^2 oceanic island of New Britain (Diamond, 1977; Mayr & Diamond, 2001: 308). Trees speciate within New Caledonia: *Polyscias* spp. (section *Tieghemopanax*) do so allopatrically. In four of six pairs of sister species in this section, the sister species have disjunct ranges; in the fifth, the sister species occur at different, non-overlapping elevational ranges with different rainfall regimes, and in the sixth, one species is restricted to ultrabasic, the other to non-ultrabasic soils (Eibl *et al.*, 2001). *Anolis* lizards diversify within 9,000 km^2 Puerto Rico, but not within 1,700 km^2 Guadeloupe (Losos, 1998). For minute or slow-moving animals, allopatric speciation can occur within islands far too small to allow speciation within a resident population of birds or lizards. Paulay (1985) found 67 species of flightless weevils, *Miocalles* (Curculionidae), ranging from 1 to 4 mm long, on the 40 km^2 Rapa Island in southeast Polynesia. This island is five million years old. It has several distinct mountaintops separated by lowlands; it was originally entirely forested. Most weevil species have only a single species of host plant. Different weevil species living on the same plant species either specialize to different parts of the plant, are restricted to different altitudes, or (least often) live on different mountaintops. Interchange with archipelagoes hundreds of kilometers away may have played some role in the diversification of these weevils. Nevertheless, most *Miocalles* speciation appears to involve either divergence on, and reinvasion from, small offshore islets, or differentiation of populations on different mountaintops (Paulay, 1985). On the 7-million-year-old Lord Howe Island, now 12 km^2 in area, formerly over 300 km^2, a wind-pollinated species of palm split into two, roughly one million years ago, when a subpopulation colonized a newly formed area of calcarenite soil (Savolainen *et al.*, 2006a,b). This event has been proposed as an instance of sympatric speciation (Savolainen *et al.*, 2006a,b) although speciation was more probably parapatric, in response to contrasting soils (cf. Stuessny, 2006). Now, hybridization is much reduced by differences in flowering time: genetic differences at a few key loci are preserved by selection in the face of occasional hybridization (Savolainen *et al.*, 2006a).

On islands too small to allow populations of a given group to speciate within them, diversity arises from successive invasions by different species. Speciation happens readily on archipelagoes far from continents, however, because animals and plants that are dispersed from one island to another are isolated from their parents, and often land in different environments (Lack, 1947; Carson & Templeton, 1984; Carson, 1987). The most careful analysis of diversification within a set of islands close to a continent is Mayr and Diamond's (2001) study of bird speciation in northern Melanesia (the Bismarcks and the Solomons). Here, New Britain, 340 km long, may be barely long enough to allow incipient speciation in a resident bird population (Mayr & Diamond, 2001: 168). Successive bird species, usually invading from New Guinea or Australia, spread over the islands. In a species where the exchange of migrants between islands is rare enough, populations on different sets of islands diverge, sometimes sufficiently that a bird will not mate with one from a different population if it can find a mate from its own population. In a few cases, descendants on the Solomons of an invading population have diverged enough in their ecological requirements from their Bismarck counterparts that one of these populations can invade the range of the other, and coexist stably with it.

In Madagascar, early stages of allopatric speciation are illustrated by the distribution of subspecies of *Eulemur fulvus*, with no overlap, around the forested rim of the island, just as are the species of *Lepilemur* and *Propithecus* (Paulian, 1961; Mittermeier *et al.*, 1994: 176, 232, 129). In Madagascar, the role of niche opportunity is illustrated by the varieties, probably distinct species, of the travellers' palm, *Ravenala madagascariensis*, whose ranges overlap widely. These varieties are distinguished primarily by the shapes of their juveniles. There are two sympatric rainforest varieties. One, adapted to the forest understory, has juveniles with leaves twisted into a secondarily spiral arrangement; the other, adapted to forest gaps, has juveniles with leaves arranged more nearly in an erect fan, like the adults. These two varieties flower at different times. Juveniles of a third variety, the most drought-adapted of the four, grow on open ground; seedlings of the fourth variant are adapted to root in swamps. The swamp variant is the only one that can sprout new stems from the base of the old (Blanc *et al.*, 1999, 2003).

Because colonists of new islands are isolated from their parents, speciation happens readily in the Hawaiian Islands (Carson, 1987). The endemic clade of swordtail cricket, *Laupala*, has 37 species on these islands, each endemic to a single island. Rainforests shelter 2-4 sympatric species of *Laupala*, which differ most obviously in their courtship calls: these differences reduce hybridization. Sister species, however, are usually allopatric, and each younger island has been colonized by several different *Laupala* species (Shaw, 2002), suggesting that each has an advantage when rare. Speciation also happens within an island: the larger Hawaiian islands are large enough to allow allopatric speciation in plants, insects, spiders and other animals with limited dispersal (Givnish *et al.*, 1995; Carson & Templeton, 1984; Gillespie, 2004). For example, a clade of *Laupala* crickets has diversified in Hawaii (the big island) during the last 430,000 years, yielding six species that differ in the pulse rates of their calls. A female prefers calls with the pulse rate characteristic of its own species, a circumstance that lowers interbreeding between species. Here, speciation appears to be driven by coevolution between the song males use to attract mates, and female preference for some songs over others (Mendelson & Shaw, 2005). Ecological opportunity has played a far more obvious role in other Hawaiian radiations, such as *Tetragnatha* spiders (Gillespie, 2004). An endemic genus of plant-hoppers with 40 species, *Sarona* (Miridae), each species of which feeds on one or a few plant species, often speciates when a lineage colonizes a new host (Asquith, 1995). Another clade of plant-hoppers, *Nesosydne* (Delphacidae), each species of which feeds on one, or a few closely related, species of the silversword alliance (Compositae, Madiinae), have speciated in parallel with their hosts (Roderick, 1997).

DO OLD ISLANDS REPRESENT INDEPENDENT EXPERIMENTS IN EVOLUTION?

No island represents an entirely independent experiment in evolution. Even before people arrived, the most distant oceanic islands were frequently invaded by successful colonists, as were ancient, now isolated continental fragments, such as Madagascar and New Zealand (see below) and even lowland tropical rainforests on continents. Although South America's history was far more stable than Madagascar's, at least 21% of the species, and 20% of the stems over 1 cm in diameter, on a 25-ha plot at Yasuní in Amazonian Ecuador are descended from overseas colonists (Pennington & Dick, 2004). Many groups distributed over fragments of Gondwana, once thought to have inhabited these fragments ever since Gondwana broke apart, are now shown by clocked molecular phylogeny to have evolved far more recently, and to have dispersed overseas to these fragments (de Queiroz, 2005). And indeed, large-seeded trees, such as *Symphonia globulifera*, have dispersed across the Atlantic from Africa to South America (Dick *et al.*, 2003), and animals as large as hippopotami (Goodman *et al.*, 2003) and as improbable as frogs (Vences *et al.*, 2003, 2004), chameleons (Raxworthy *et al.*, 2002), snakes (Nagy *et al.*, 2003) and freshwater fish (Vences *et al.*, 2001) have crossed the 400+ km of sea from Africa to Madagascar or vice versa.

Madagascar has been invaded by successful colonists throughout its long history of isolation (Table I). Although the ancestors of Madagascar's elephant birds probably walked there "dryshod" (Worthy & Holdaway, 2002), most of Madagascar's living plants (Zjhra *et al.*, 2004) and reptiles (Raxworthy *et al.*, 2002), and very probably, all of Madagascar's living mammals (Krause, 2003; Poux *et al.*, 2005) descend from ancestors that crossed to Madagascar from over the sea. Robert Martin, disagreeing with his coauthors, argued that primates evolved, and lemurs diverged from other primates, on "Indo-Madagascar" before India separated from Madagascar and drifted to Asia (Miller *et al.*, 2005: 87-88). Molecular evidence suggests, however, that strepsirrhines, including lemurs, split from ancestral anthropoids about 77 million years ago (Springer *et al.*, 2003), rather more recently than India separated from Madagascar (Storey *et al.*, 1995). Moreover, if primates did evolve on Indo-Madagascar, why did they not travel through Antarctica to South America, as marsupials and other South American mammals travelled through Antarctica to Indo-Madagascar (Krause, 2001, 2003: 46)? At the moment, the balance of evidence favors the view of Martin's coauthors that primates evolved in Africa and crossed the sea to Madagascar (Miller *et al.*, 2005).

TABLE I

Age, A, *in million years, and number of living and subfossil species,* S, *in selected endemic Malagasy clades*

Group	A, my	S	Authority
Mantellid frogs	41-80	141	Van der Meijden *et al.*, 2005; Glaw & Vences, 2003
Lemurs	58-80	62	Yoder & Zang, 2004; Goodman *et al.*, 2003; Springer *et al.*, 2003
Tenrecs	Ca. 50	27	Douady *et al.*, 2002; Goodman *et al.*, 2003
Carnivores	20-30	9	Yoder & Flynn, 2003; Goodman *et al.*, 2003
Nesomyine rodents	15-26	23	Poux *et al.*, 2005; Goodman *et al.*, 2003
Asities, Philepittinae	41	4	Barker *et al.*, 2004; Schulenberg, 2003a
Vanga shrikes, Vangidae	30	20	Barker *et al.*, 2004; Schulenberg, 2003a
Warblers, Sylviidae	9-17	9-12	Cibois *et al.*, 2001: Schulenberg, 2003a
Cichlid fish	35-56	33	Vences *et al.*, 2001; Sparks & Stiassny, 2003
Pseudoxyrophine snakes	Ca. 30	70	Nagy *et al.*, 2003
Mimophis, colubrid snake	Ca. 13	1	Nagy *et al.*, 2003
Hyperoliid frogs	19-30	11	Vences *et al.*, 2003; Glaw & Vences, 2003
Geochelone tortoises	14-22	4	Caccone *et al*, 1999
Adansonia (baobabs)	Ca. 11	6	Baum *et al.*, 1998
Gravesia, Melastom.	Ca. 10	107	Renner *et al.*, 2001
Medinilla, Melastom.	Ca. 2	70	Renner *et al.*, 2001

Some tree families have invaded Madagascar several times. At least five different groups of Sapotaceae have colonized Madagascar from overseas (Swenson & Anderberg, 2005). Figures 1 and 3 of Muellner *et al.* (2006) suggest that at least five different groups of Meliaceae colonized Madagascar from overseas during the Cenozoic. Schatz (2001) records four genera of Burseraceae in Madagascar. This family originated in or near Mesoamerica 60 million years ago and soon spread via Greenland and Europe and across to Africa (Weeks *et al.*, 2005). Judging by the phylogeny of Weeks *et al.* (2005), each of these genera invaded Madagascar separately. As studies of molecular phylogeny multiply, these counts will be refined and others added.

Indeed, invading plants have colonized Madagascar so often that although most of Madagascar's species and many of its genera evolved there, relatively few families did so. Although 96% of Madagascar's 4,220 species of trees and woody shrubs are endemic, only 161 of its 490 genera, and 7 of its 107 families, of such plants are endemic (Schatz, 2000). Moreover, endemic families and genera contribute disproportionately few of these 4,220 species: endemic families average < 14 species apiece, compared to > 41 species per non-endemic family, and endemic genera average only 5.8 species apiece, compared to 9.9 species per non-endemic genus. Moreover, the average non-endemic genus occurs in more habitats than the average endemic one (Schatz 2000). Endemism is even less prevalent among Madagascar's ferns, because fern spores travel further than tree seeds (Table II).

As Darwin (1859: 390-391) predicted, the proportion of endemic species and genera is particularly high among Madagascar's terrestrial, non-flying, vertebrates, much higher than among its strong fliers – its birds and bats, its dragonflies and damselflies (Odonata), and even its flies (Diptera), (Table II). Indeed, some groups, animal and plant, colonize rarely enough that successful colonizations sometimes lead to spectacular adaptive radiations. Molecular phylogenies suggest that in many genera, and some families and orders, of plants and animals, many, sometimes all, of Madagascar's species belong to a single adaptive radiation (Table III).

Table II

Number of species S *on Madagascar, proportion* P_S *of these species endemic to the Malagasy region (including Mauritius, Réunion and the Comoros), number of genera* G *among these species, and proportion* P_G *of these genera endemic to Madagascar in selected groups*

Group	S	PS	G	PG	Authority
Terrestrial (non-volant) mammals	101	99%	38	97%	Goodman, 2003a
Bats, Chiroptera	30	60%	17	6%	Eger & Mitchell, 2003
Birds, Aves (breeding)	209	59%	135	24%	Hawkins & Goodman, 2003
Reptiles	325	97%	58	78%	Glaw & Vences, 2000
Amphibians	230	99.6%	16	88%	Glaw & Vences, 2003
Tiger beetles, Cicindelidae	203	99.5%	17	53%	Cassola, 2003
Scorpions	40	100%	11	91%	Lourenço, 2003
Odonata	181	73%	52	23%	Donnelly & Parr, 2003
Butterflies, Rhopalocera	340	74%	83	11%	Lees *et al.*, 2003
Flies, Diptera	1,796	80%	538	14%	Irwin *et al.*, 2003
Pteridophyta	586	55%	106		Rakotondrainibe, 2003

Such phylogenies suggest, for example, that in each of Madagascar's four major extant orders of native mammals, the surviving species all belong to an adaptive radiation deriving from a single successful colonization (Yoder, 2003; Yoder & Flynn, 2003; Olson & Goodman, 2003; Poux *et al.*, 2005). Lemurs, which all descend from a common ancestor that colonized Madagascar about 65 million years ago (Yoder & Zang, 2004), comprise one of Madagascar's most striking radiations. Before people settled Madagascar, the island harbored 7 families and 62 species of lemurs, occupying a great variety of ways of life (Goodman *et al.*, 2003; Godfrey & Jungers, 2003). Madagascar has hosted other spectacular adaptive radiations (Table IV). Madagascar's 36 inland species of *Terminalia* (all endemic), its 100+ species of *Diospyros* (all endemic), and its endemic genus *Phyllarthron*, have all radiated into rain forest, plateau forest, western dry forest, and southwestern spiny bush (Guillaumet, 1981: 40; Schatz, 2001). An indigenous radiation of *Kalanchoe* (Crassulaceae) evolved crassulacean acid metabolism (as

Table III

Number of species native to Madagascar, S, *in a taxon and the number* S_R *of these species belonging to the taxon's largest radiation endemic to Madagascar*

Taxon	S	S_B	Authority
Begonia	50	50	Plana, 2003
Dioscorea	37	36	Wilkin, 2004: Wilkin *et al.*, 2005
Bignoniaceae	75	70	Zjhra, 2003; Zjhra *et al.*, 2004
Daleschampia	11	11	Armbruster & Baldwin, 2003
Euphorbia	170	80	Haevermans, 2003; Haevermans *et al.*, 2004
Malpighiaceae	71	24	Davis, 2002
Palmae	170	137	Dransfield & Beentje, 2003
Amphibians*	199	141	Glaw & Vences, 2003
Snakes: Colubridae	75	74	Raxworthy, 2003; Nagy *et al.*, 2003

* Described species only

did many lineages in other regions), and plants of this radiation occupy most of the habitats in Madagascar's varied terrain (Gehrig *et al.*, 2000). Nonetheless, no single endemic radiation in Madagascar is known to have produced over 200 species, although endemic radiations in quite different groups of plants and animals now have over 50 species apiece.

New Zealand's whole history has been one of spectacular extinctions driven by environmental change. Some extinctions were associated with the flattening of New Zealand and the reduction of its land area in the Oligocene to 20% of its current value. Other extinctions were associated with cooling and the rise of high mountain ranges during the last five million years (Lee *et al.*, 2001). This circumstance has facilitated colonization by invaders from overseas. For example, kiwis diverged from Australian emus and cassowaries 68 million years ago, and colonized New Zealand from overseas somewhat later (Worthy & Holdaway, 2002: 139). After *Nothofagus* died out on New Zealand, it recolonized about 23 million years ago (Knapp *et al.*, 2005). New Zealand's alpine flora derives from colonists that crossed the sea after New Zealand's mountains arose (McGlone *et al.*, 2001).

New Zealand's endemic adaptive radiations seem rather less extensive than those on some of our other sites. New Zealand's largest surviving vertebrate radiation is its 37 species of diplodactyline geckoes, whose most recent common ancestor lived about 23 million years ago (Chambers *et al.*, 2001). The most recent common ancestor of New Zealand's 14 Holocene species of moa, ranging from < 30 to 120 kg (Worthy & Holdaway, 2002: 144-145) lived 19 million years ago (Baker *et al.*, 2005). One of New Zealand's two clades of native cicadas, founded 10 million years ago by a colonist from New Caledonia, now has two species; the other, founded 9 million years ago by an Australian colonist, now has 38 species, in habitats ranging from lowlands to high mountains (Chambers *et al.*, 2001; Arensburger *et al.*, 2004). New Zealand's most diverse plant radiation is its roughly 100 species of *Hebe* (Scrophulariaceae), shrubs descended from a colonist that invaded New Zealand about 5 million years ago (Wagstaff & Garnock-Jones, 1998). Its two or three most diverse tree radiations were founded within the last 10 million years by colonists from Australia (Lee *et al.*, 2001). One of these radiations, *Carmichaelia* (+ *Clianthus*), papilionoid legumes, has 24 species of trees, shrubs

TABLE IV

Extensive Radiations Based on Madagascar: number of families, F, *subfamilies,* SF, *genera,* G, *and species,* S, *in different Malagasy radiations*

Group	F	SF	G	S	Authority
Mammals: lemurs	7		22	62	Godfrey & Jungers, 2003
Mammals: Tenrecidae		3	8	27	Goodman, 2003
Snakes: Pseudoxyrophiinae			14	70	Nagy *et al.*, 2003; Raxworthy, 2003
Frogs: Mantellidae		3	5	141	Glaw & Vences, 2003
Birds: Vangidae			15	20	Schulenberg , 2003a, 2003b
Fish: Cichlidae			5	33	Sparks & Stiassny, 2003
Butterflies: mycalesine satyrs				66	Lees, 2000
Beetles: Scarabaeidae, tribe Enariini			30	164	Andrianampianina, 2003
Beetles: Cicindelidae, *Pogonostema*				94	Cassola, 2003
Angiosperms: Bignoniaceae, Coleeae			5	70	Zjhra, 2003
Angiosperms: Sarcolaenaceae			8	88	Schatz, 2001
Angiosperms: Myrsinaceae, *Oncostemon*				100	Schatz, 2001
Angiosperms: Melastomaceae, *Gravesia*				107	Renner *et al.*, 2001
Angiosperms: Palmae, *Dypsis*				137	Dransfield & Beentje, 2003

and lianas (Wagstaff *et al.*, 1999); the other, *Pittosporum*, with 25 species, descends from two colonists (McGlone *et al.*, 2001: 210-211).

Phylogenetic analysis of New Caledonia's biota has barely begun but recent molecular studies in New Zealand, Madagascar and elsewhere, suggest that the role of overseas dispersal in forming the biotas of ancient continental fragments has been greatly underestimated. Many families and genera of New Caledonian plants are also present on oceanic islands to the north and east (Carlquist, 1974: 216; Morat, 1993: Fig. 4). Many of New Caledonia's more diverse genera and families, such as Araliaceae, Myrtaceae and *Psychotria* are well suited for long-distance dispersal (Carlquist, 1974). All of New Caledonia's land and freshwater birds descend from overseas colonists (Carlquist, 1974; Diamond, 1977), most of which have colonized so recently that they have not yet become distinct species (Table VI). Many, if not most, of New Caledonia's plants and animals descend from invaders, which crossed from over the sea (Bauer, 1999; Bartish *et al.*, 2005; Murienne *et al.*, 2005).

Carlquist (1974: 217) considered New Caledonia rather poor in adaptive radiations of plants. Nonetheless, this island has about 115 endemic species of *Phyllanthus* (Phyllanthaceae: Euphorbiaceae *sensu lato*). Seven of eight species sampled from New Caledonia for phylogenetic analysis belong to a single endemic clade (Kathriarachchi *et al.*, 2006), suggesting that this clade radiated spectacularly in New Caledonia. New Caledonia's endemic tree genus *Pancheria* (Cunoniaceae) has 30 species, largely concentrated on ultrabasic substrates (Jaffré *et al.*, 1987). A single adaptive radiation of the section *Tieghemopanax* of the genus *Polyscias* (Araliaceae) has produced 23 species in New Caledonia and exported colonists overseas that led to four species elsewhere (Eibl *et al.*, 2001). New Caledonia's 50 species of *Pittosporum* probably descend from two colonizations (Gemmill *et al.*, 2002).

Lizards, insects and snails have diversified in New Caledonia (Carlquist, 1974: 232-233; Bauer, 1999; Mayr & Diamond, 2001: 308). The list of land and freshwater bird species of New Caledonia, however, suggests that there were no adaptive radiations of birds on that island, because it was within dispersal distance of too many other species of land birds (Carlquist, 1974: 232). True, the flightless bird *Rhynochetos jubatus*, sole surviving member of a family endemic to New Caledonia, has a recently extinct congener there (Balouet & Olson, 1989): these species must have diverged within New Caledonia. Given New Caledonia's accessibility to invading land and freshwater birds, however, the overwhelming majority of New Caledonia's bird diversity must have been assembled from successive invasions (Diamond, 1977). Thirty-five of the 66 land and freshwater bird species living on New Caledonia (73 for the administrative district, less 7 restricted to the Loyalties: Ekstrom *et al*., 2002; Barré *et al.*, 2006) belong to species or superspecies also present in northern Melanesia – the Bismarck and Solomon Islands (calculated from appendix 1 of Mayr & Diamond, 2001). Five, including four of New Caledonia's endemic species, differ at the allospecies level, and another 24 at the subspecies level, from their closest northern Melanesian relatives. New Caledonia shares 12 other species with Australia and/or New Guinea.

In the Hawaiian Islands, all organisms descend from overseas colonists. According to the latest count, these islands' 1,000 native species of flowering plants descend from 263 successful colonists (Price & Wagner, 2004). The 59 species of native birds, including seabirds, that now breed on the Hawaiian Islands (Pyle, 2002) probably descend from 35 different colonizing species, as if birds colonized the Hawaiian Islands far more rarely than plants. Nonetheless, it appears that seeds of 3/4 of these islands' successfully colonizing plant species were carried there by birds – probably, half these species' seeds travelled in bird guts, to be defecated after arrival, while seeds of the remainder were stuck somehow to the outside of their carriers (Carlquist, 1980). Although relatively few bird species colonized these islands, shorebirds and waterbirds that migrate long distances, such as plovers, ducks and geese, are sometimes blown there. Such birds occasionally eat seeds and fruit, and retain seeds in their guts for long periods: they may have introduced many plant species to these islands (Carlquist, 1980).

Different groups differ in their ability to colonize and diversify on the Hawaiian Islands. These islands' 134 native species of fern (Eldredge & Everhuis, 2003) derive from over 100 successfully colonizing species, whereas the 1,000 species of land snails that lived on these

islands in 1800 descended from about 30 colonizing species (Sohmer & Gustafson, 1987). Most insects fly, and Hawaii has been colonized by about 375 different species of insects (Howarth & Mull, 1992: 17): their descendants now number 5,400 species (Eldredge & Everhuis, 2003).

Within a group, colonists differ in their ability to diversify on these islands: some colonizing clades never speciate, while others give rise to spectacular adaptive radiations, some as varied and diverse as any to be found on Madagascar (Table V). The Hawaiian Islands' two species of endemic dragonfly, *Anax strenuus* and *Nesogonia blackburni*, and their two species of endemic butterfly, *Vanessa tameamea* and *Udara blackburni*, have not diversified there, perhaps because they are such good fliers that their subpopulations cannot achieve reproductive isolation (Roderick & Gillespie, 1998). On the other hand, the 174 species of Hawaiian *Proterhinus*, Carabidae, descend from a single colonist (Gillespie & Roderick, 2002: 615), and these islands' 750+ species of fruit fly, Drosophilidae, descend from no more than two original colonizing species (DeSalle, 1995). Thrushes, *Myadestes*, and cardueline finches, both reached the Hawaiian Islands about five million years ago, but the colonizing thrush now has five descendant species, whereas before Polynesians arrived, the Hawaiian Islands had 50 species of drepanidines, descendants of the colonizing cardueline finch. The finches, also more diverse in mainland settings, radiated far more extensively on these islands, perhaps because these finches' greater capacity for variation in bill width and bill depth enabled them to evolve novel morphologies far more readily (Lovette *et al.*, 2002).

Colonizing plants also differ greatly in the degree to which they diversify on the Hawaiian Islands. Of the roughly 100 native, non-endemic species of flowering plants now living on these islands (Eldredge & Everhuis, 2003), one, a *Peperomia* (Piperaceae) is ancestor to 19 surviving endemic species, two are ancestors of two surviving endemic congeners apiece, and seven are ancestors of one surviving congener apiece, while the other 88 never diversified (Price & Wagner, 2004). Of these islands' wholly endemic clades, about 70 have only one species apiece. On the other hand, one endemic clade, the lobelioids, now has 98 species distributed among 5 endemic genera (Givnish *et al.*, 1995: 288). A second endemic monophyletic clade includes the 58 Hawaiian species of *Cyrtandra* (Gesneriaceae) (Cronk *et al.*, 2005). A third clade, descended from a colonizing species of *Phyllostegia* (Labiatae), whose one surviving congener outside Hawaii lives in Tahiti (Mabberley, 1997), now has 27 descendant species of

TABLE V

Age, A*, millions of years, and number of species,* S*, in selected endemic Hawaiian clades*

Clade	A	S	Authority
Drosophilidae (*Drosophila* + *Scaptomyza*)	30	750+	DeSalle, 1995
Trigonidiine crickets		133	Shaw, 1995
Platynini (Carabidae)		129	Cryan *et al*., 2001
Megalagrion (damselflies)	9.6	23	Jordan *et al*., 2003
Achatinellidae (snails)	< 3.7	99	Holland & Hadfield, 2004
Descendants of colonizing *Branta canadensis*	0.43	3	Paxinos *et al.*, 2002
Drepanidine honeycreepers	ca. 5	50	Lovette *et al.*, 2002
Lobelioids	10-20	98	Givnish *et al.*, 1995
Cyrtandra (Gesneriaceae)		58	Cronk *et al.*, 2005
Endemic clade of *Stachys* (Labiatae) & allies	2.6-7.4	60	Lindqvist & Albert, 2002
Alsinoideae (Caryophyllaceae)	8	30	Sakai *et al.*, 1997
Silversword alliance	4.4-6.0	28	Baldwin & Sanderson, 1998
Viola (violets)	ca. 3.7	7	Ballard & Sytsma, 2000
Diellia (fern)	23	5	Schneider *et al.*, 2005

Phyllostegia and 26 other descendant species distributed over two endemic genera (Sakai *et al.*, 1995). A colonizing species of *Melicope* (Rutaceae), a genus ranging from India and Malaysia to Australia and New Zealand (Mabberley, 1997) has 47 surviving descendant congeners (Sakai *et al.*, 1995). Five other colonizing plant species are now represented on the Hawaiian Islands by ≥ 20 descendent species apiece. On the average, clades whose colonizing ancestor survives without changing sufficiently to become a different species have diversified less than purely endemic clades, even though over half of the 200 purely endemic clades are now represented by only one species apiece. Thus clades whose ancestors colonized longer ago are more likely to have diversified, but colonizing long ago does not guarantee diversification (Table V).

In the Hawaiian Islands, endemic clades such as the drepanidine honeycreepers, the silversword alliance and the lobelioids have radiated into a far greater variety of habitats and habits than their ancestors ever occupied (Carlquist, 1980; Freed *et al.*, 1987). Only in Hawaii have lobelioids become trees; only in Hawaii do cardueline finches pollinate flowers. The absence of nocturnal predators of spiders has allowed the spider genus *Tetragnatha* to diversify far beyond the ancestral habit of building flimsy webs over water to catch midges and mosquitoes. One endemic radiation of *Tetragnatha* includes 35 species of nocturnal web-building spiders, (Blackledge & Gillespie, 2004); another includes 16 species of spiny-legged *Tetragnatha* that have abandoned web-building to pursue walking prey. As Darwin (1859) predicted, protection from immigrants allows descendants of (some!) colonists to occupy unusual ways of life or engage in surprisingly extensive adaptive radiations.

THE IMPACT OF ISOLATION

Madagascar is 400 km from Africa, its nearest continent; New Zealand is 1,500 km, and New Caledonia 1,150 km, from Australia, their nearest continent; and the Hawaiian Islands – by far our most isolated site – are over 3,800 km from North America. How does this degree of isolation affect their biotas?

Even the Hawaiian Islands are only relatively isolated. Forty-four of these islands' 229 plant genera have supplied at least two different species that successfully colonized the Hawaiian Islands. The sedge genus *Carex* has supplied seven different successful Hawaiian colonists, *Hibiscus* has supplied six, *Ipomoea* five or six, and *Mariscus* (Cyperaceae), and *Peperomia* (Piperaceae) four apiece (Sakai *et al.*, 1995). In historic times, moreover, these islands have been visited at least occasionally by 35 species of ducks and geese, 6 species of herons, and 7 species of plovers – not to speak of ten species of passerines representing six families that do not now breed on these islands (Pyle, 2002). None of these 56 species breed on the Hawaiian Islands. Indeed, it seems that before people settled, the biota of the Hawaiian Islands was able to prevent this plethora of potential invaders from establishing reproductive populations.

Among islands of equal size, the more isolated support lower diversity (MacArthur & Wilson, 1963; Diamond *et al.*, 1976; Mayr & Diamond, 2001). The larger the islands however, the lower the extinction rates of their species, and the more slowly diversity declines with distance from the source of colonists. In the region of Northern Melanesia, the number of land and freshwater species on a 2 km^2 island halves with each extra 70 km distance from the source of colonists, whereas the number of such bird species on a 4,000 km^2 island halves with each extra 830 km distance from the source of colonists (Mayr & Diamond, 2001: 57). Nonetheless, isolation affects even islands as large as Madagascar. Madagascar, with 587,000 km^2, is 400 km from Africa. It now supports 209 native species of breeding bird, 101 species of native terrestrial mammal, and 30 native bat species, of which 122, 101 and 18, respectively, are endemic to Madagascar plus the nearby Comoros (Hawkins & Goodman, 2003; Goodman *et al.*, 2003; Eger & Mitchell, 2003). Celebes is a smaller island of 190,000 km^2, separated from Asia for at least 25 million years and from New Guinea for at least 10 million years (Whitten *et al.*, 1987: 2-6). It was only 25 km from Asia during Pleistocene lows in sea level. Celebes now supports 247 native breeding bird species, at least 62 native terrestrial mammal species, and 61 native bat species, of which 88, 61 and 14, respectively, are endemic to the island (Whitten *et*

al., 1987: 38-45). On large islands, degree of isolation affects the diversity of different groups in different ways.

Groups that colonize infrequently are more likely to produce extensive adaptive radiations than those that colonize often, such as ferns or seabirds. Isolation reduces the frequency of attempted colonization. As Darwin predicted, greater isolation allows more extensive adaptive radiation. Before people arrived, Hawaii had 66 species of breeding passerine birds, all endemic, representing 6 families and not more than 7 different colonizations. Of these, 50 belonged to the largest radiation, the drepanidine finches (James & Olson, 1991). Before people arrived, New Zealand had 28 species of passerines, including 27 endemics, representing 11 families. The most diverse of the ten families colonizing from overseas, the currently endemic family Callaeatidae, apparently most closely related to the berrypickers, *Melanocharis*, and birds of paradise (Paradisaeidae) on New Guinea (Barker *et al.*, 2004) had only 5 species in the early Holocene (Worthy & Holdaway, 2002: 573-575). New Caledonia has 24 species of passerines, including ten endemics, representing 14 families (Mayr, 1945; Delacour, 1966; Keast, 1996). All these families colonized from overseas, and no passerine colonist has given rise to an adaptive radiation in New Caledonia (Carlquist, 1974: 232; Mayr & Diamond, 2001: 308). Landmass size, however, can override the effects of more frequent colonization. Madagascar had 69 species of passerines, including only 55 endemics, representing 17 families, all of which colonized from overseas during the last 41 million years (Hawkins & Goodman, 2003; Barker *et al.*, 2004). Yet Madagascar's largest endemic passerine radiation, the Vangidae, included 20 species (Schulenberg, 2003a), and its second largest included 9-12 species of Old World warblers, Sylviidae (Cibois *et al.*, 2001; Schulenberg, 2003a).

Indeed, factors other than isolation affect the frequency of successful colonization (Roughgarden *et al*., 1983). A species invading a land mass where its niche is unoccupied can spread rapidly while another, whose niche is already occupied, fails to establish (Darwin, 1859: 402). When, for example, a land bridge connected the Americas three million years ago, several genera or subgenera of South American freshwater fish invaded Mesoamerica, one after another. Occupation by one invading clade did not hinder the spread of the next. Each invading clade differentiated into a series of allopatric species or subspecies, but only once did a lineage invade a drainage occupied by another lineage of the same invading clade, and it did not spread far (Reeves & Bermingham, 2006). Similarly, on islands of the Lesser Antilles, the *Anolis* lizards already present exploit the available insect supply effectively enough to make successful colonization by other species of *Anolis* a very rare event (Roughgarden *et al*., 1983).

Similarly, the proportion of endemics among a land mass's native species in a selected group is not always clearly related to the land mass's degree of isolation. To be sure, the proportion of endemics among bird species – and among fern species – is highest in the Hawaiian Islands, the most isolated of our sites. Yet the proportion of endemics among native fern species is higher in Madagascar, our least isolated site, than in New Caledonia. The proportion of endemics among bird species, moreover, is far lower in New Caledonia than in any of our other sites (Table VI). As we have seen, over half of New Caledonia's land and freshwater bird species are shared at least at the superspecies level with northern Melanesia, because the New Hebrides (Vanuatu), 400 km from New Caledonia, provide convenient stepping stones from the Solomon Islands to New Caledonia. Nonetheless, the proportion of endemics is far higher among Madagascar's birds than among New Caledonia's, even though the Comoros seemingly provide equally convenient access to Madagascar from its nearest larger land mass. Even Celebes, an island of 190,000 km^2 separated from continental Asia by only 25 km during parts of the Pleistocene, has a proportion of endemics among its breeding bird species, 36% (Whitten *et al*., 1987), substantially higher than New Caledonia's. Are Madagascar, and even Celebes, more resistant than New Caledonia to colonizing birds because they are large enough to allow speciation *in situ*?

The degree of isolation is not a precise predictor of endemism among seed plants, either. The least isolated of our islands, Madagascar, has no lower a proportion of endemics among its species of seed plants than do the Hawaiian Islands (Table VI). Overall, the proportion of endemics among species of seed plants is lowest in New Caledonia, and only slightly higher in

TABLE VI

The number S *of native species, and the proportion* %E *of endemics among them for ferns and their allies, seed plants, and breeding birds (including seabirds and recently extinct species), on selected long-isolated land masses*

Land mass	Group	S	%E	Authority
Hawaii	Pteridophytes	134	79%	Eldredge & Everhuis, 2003
Hawaii	Seed plants	1,003	89%	Eldredge & Everhuis, 2003
Hawaii	Birds	118	83%	James & Olson, 1991; Olson & James, 1991; Pyle, 2002
New Caledonia	Pteridophytes	260	40%	Morat, 1993
New Caledonia	Seed plants	3,061	80%	Morat, 1993
New Caledonia	Birds	111	28%	Biodiversity Hotspots, 2006; Barré *et al.*, 2006, Balouet & Olson, 1989
New Zealand	Pteridophytes	208	44%	McGlone *et al.*, 2001
New Zealand	Seed plants	2,013	86%	McGlone *et al.*, 2001
New Zealand	Birds	132	67%	Calculated from Worthy & Holdaway, 2002
Madagascar	Pteridophytes	586	45%	Goodman & Benstead, 2005
Madagascar	Seed plants	ca. 11,000	92%	Goodman & Benstead, 2005
Madagascar	Birds	229	62%	Hawkins & Goodman 2003

Hawaii than in New Zealand (Table VI). On the other hand, the proportion of endemics is 91% among the 1,844 of New Caledonia's 3,061 native species of seed plant that occur on ultrabasic substrates, while it is 68% among the 1,840 species that occur on other substrates (623 species occur on both); this proportion is 98% among the 1,176 species restricted to ultrabasic substrates (Jaffré *et al.*, 1987; Morat, 1993). Poor soils are inhospitable to invaders introduced by human beings (Fine, 2002), and New Caledonia's ultrabasic substrates are no exception (Schmid, 1981). Other factors besides degree of isolation affect the susceptibility to colonization of an island of given area.

Various factors besides degree of isolation also influence the number of endemic families on a land mass. A land mass's age influences its numbers of endemic families: the Hawaiian Islands, our youngest focal site, have no endemic families of birds, bats or plants. The area of a land mass may also influence its number of endemic families of birds and bats. Madagascar now has five endemic families of birds, totalling 33 species (Schulenberg, 2003a; Hawkins & Goodman, 2003). New Zealand now has three endemic bird families, totalling nine species (Worthy & Holdaway, 2002: Appendix 1); a fourth died out after 1950 (Falla *et al.*, 1966: 240). New Caledonia has one endemic bird family (Letocart & Salas, 1997). Similarly, Madagascar and New Zealand have one endemic bat family apiece, each with one living species, whereas New Caledonia has none (Eger & Mitchell, 2003; Worthy & Holdaway, 2002; Flannery, 1995). Stability of climate during the last thirty million years may also influence the number of endemic plant families on a land mass. Madagascar has seven endemic families of flowering plants, totalling 95 species (Schatz, 2001), and New Caledonia has five such families (Schmid, 1981), totalling 19 species (calculated from Jaffré *et al.*, 1987; Mabberley, 1997); New Zealand has none.

Nonetheless, sufficient isolation prevents some groups from colonizing (Darwin, 1859: 393-394). No walking mammals reached New Zealand, New Caledonia, or the Hawaiian Islands without human help, although mammals have invaded Madagascar repeatedly (Table I). Nor did any frog colonize any of these sites from overseas on its own, although frogs have occasionally invaded Madagascar (Table I). More surprisingly, frogs have colonized the oceanic islands of northern Melanesia, and the frog genus *Platymantis* (Ranidae), which presumably originated

in New Guinea, has diversified extensively in northern Melanesia, and colonized Fiji and Palau (Mayr & Diamond, 2001). No reptile has reached the Hawaiian Islands without human help, but skinks colonized New Caledonia (Bauer, 1999) and perhaps also New Zealand (Daugherty *et al.*, 1993) from overseas, and various lizards and snakes have colonized Madagascar from Africa (Table I). Curiously, the Loyalty Islands have an endemic species of snake (Bauer, 1999), whose family, Typhlopidae, is one of the four snake families that have colonized and diversified in the archipelagoes of northern Melanesia (Mayr & Diamond, 2001). This snake never crossed the extra 105 km to New Caledonia. Was it excluded from New Caledonia by a more competitive biota? The Loyalty Islands have five non-endemic bird species, shared by, and presumably acquired from, northern Melanesia (calculated from Table V of Barré *et al.*, 2006, and Appendix 1 of Mayr & Diamond, 2001). These are the only non-endemic species of the Loyalties that have not colonized New Caledonia. Similarly, many marine species have crossed the 6,500 km of open water from the Line Islands and colonized islands just off the west coast of tropical America, but they have not established themselves along that continent's shores (Vermeij, 1978: 253-254). Greater isolation reduces the number of successful colonizations, but so does the greater resistance of a larger island's biota to colonization. In sum, the effect of isolation on an island's biota is modulated in complex ways by its area, age, and even its soil's fertility.

Finally, how does exclusion of walking mammals or other groups affect island ecosystems? On those islands that lack walking mammals, large birds have assumed the role of large herbivores (Darwin, 1859: 391; Burness *et al.*, 2001). On New Zealand, moas diversified into browsers of large twigs, consumers of mature leaves, and consumers of fruit and young leaves (Baker *et al.*, 2005). In New Zealand, moreover, a big flightless parrot, *Strigops*, eats leaves; the bat *Mystacina tuberculata* forages for invertebrates on and in the leaf litter like a rat or shrew, and even wetas help fill the role played by small omnivorous terrestrial rodents in continental ecosystems (Daugherty *et al.*, 1993; Worthy & Holdaway, 2002). More generally, what is the relative importance of limited area vs. exclusion by distant isolation of selected taxonomic groups in determining ecosystem characteristics? Indeed, to what extent do factors other than degree of isolation affect the characteristics of the ecosystem of an isolated land mass (Lack, 1976)? This will be the central question of the rest of the paper.

DIVERSITY

As Darwin's (1859: 106, 389) arguments predict, smaller, more isolated land masses have lower total diversity than larger ones (MacArthur & Wilson, 1963, 1967; Mayr & Diamond, 2001). Local diversity (α-diversity, diversity in an area so small that the species present are considered sympatric) is generally higher on islands (or in other regions) with higher total diversity (Ricklefs, 2004). However, besides area and degree of isolation, other factors also influence a land mass's diversity. In most groups of animals and plants, for example, species diversity is higher at lower latitudes (Dobzhansky, 1950; Fischer, 1960). Thus, as we shall see, temperate-zone New Zealand has lower diversity than one might expect from its area. Diversity is also higher where the habitat and pattern of climate have remained unchanged for longer (Fischer, 1960; Morley, 2000). This circumstance might imply low diversity for New Zealand and Hawaii. We consider animal diversity first, then tree diversity.

ANIMALS

Madagascar has lower total and regional diversity within groups of vigorously flying animals than comparable mainland settings, but a far higher diversity of such animals than smaller, more isolated land masses. Panamá, a country of 78,000 km^2, has 732 species of breeding birds (Ridgely & Gwynne, 1989), and 15 km^2 Barro Colorado Island in central Panamá had 121 species of forest birds in the 1920's, 15 years after it was isolated from the mainland (Robinson, 1999). Madagascar, with 587,000 km^2, now has 209 native species of breeding birds (Hawkins & Goodman, 2003), 114 of which are forest birds (Wilmé, 1996).

New Zealand now has 89 species of breeding birds (calculated from Appendix 1 of Worthy & Holdaway, 2002), New Caledonia has 98 (105 for the administrative region, less 7 restricted to the oceanic Loyalty Islands: Biodiversity Hotspots, 2006; Barré *et al.*, 2006), and the Hawaiian Islands have 60 (calculated from Pyle, 2002). Madagascar now has about 196 native species of breeding land and freshwater birds: at least 20 others have died out since people first arrived (Hawkins & Goodman, 2003). New Zealand now has 61 species of land and freshwater birds: at least 40 others have died out since people first arrived (calculated from Appendix 1 of Worthy & Holdaway, 2002). New Caledonia now has 66 species of land and freshwater birds (73 for the administrative district, less 7 restricted to the Loyalties: Ekstrom *et al.*, 2002; Barré *et al.*, 2006): at least 13 others have died out since people first arrived (Balouet & Olson, 1989). The Hawaiian Islands now have 37 native species of land and freshwater birds, and 61 others died out after people first arrived (calculated from James & Olson, 1991; Olson & James, 1991; Pyle, 2002).

About 120 bat species live in the 78,000 km^2 country of Panamá, of which 74 have been recorded from the 15 km^2 Barro Colorado Island (E. K. V. Kalko, personal communication). The 587,000 km^2 island of Madagascar now has 30 native species of bats (Eger & Mitchell, 2003). New Zealand has two living and one recently extinct species of bats, all endemic, stemming from two colonizations. Its endemic bat family Mystacinidae, with one living and the one extinct species, is most closely related to the Neotropical bat family Phyllostomidae. Mystacinid ancestors apparently colonized Australia (presumably by way of the still unfrozen Antarctica) from South America 35 million years ago, and crossed to New Zealand a few million years later (Worthy & Holdaway, 2002). The third species, *Chalinolobus tuberculatus* (Vespertilionidae) belongs to a genus centered in Australia (Flannery, 1995: 366). New Caledonia has 8 species of bats (Flannery, 1995). The Hawaiian Islands have two species of bats stemming from two colonizations (Sohmer & Gustafson, 1987, Table 2).

On a more local scale, the montane rainforest near Analamazaotra has 106 species of birds indigenous to, and breeding in, Madagascar, of which 63 are endemic (Langrand, 1990; Hawkins & Goodman, 2003). Local bird diversity at Analamazaotra is far higher than it ever was at any site in the Hawaiian Islands, but censuses of birds on a 97-ha plot in western Amazonia and a 100-ha mainland plot in central Panama, found 245 and 181 species of resident birds, respectively (Robinson *et al.*, 2000: 223).

Diversity of less mobile animals is usually higher on Madagascar than on New Zealand or New Caledonia. Madagascar has 232 native species of lizards, distributed among five families, including 68 species of Chameleonidae, 83 species of Gekkonidae (including no diplodactylines) and 60 species of Scincidae (Raxworthy, 2003). New Zealand has only 64 species of lizards, 29 species of diplodactyline Gekkonidae and 35 species of Scincidae (Worthy & Holdaway, 2002: 462). Even so, New Zealand now has more species of lizards than an equivalent area of mainland in the temperate zone (Daugherty *et al.*, 1993). New Caledonia has 63 indigenous species of lizards: 23 species of Gekkonidae, including 20 diplodactylines, and 40 species of Scincidae (Bauer, 1999). No lizard ever reached the Hawaiian Islands. Madagascar has 230 species of frogs, representing only 3 of the world's 28 frog families (Glaw & Vences, 2003). Before people arrived, New Zealand had only 6 species of frogs, all in the endemic genus *Leiopalma* (Worthy & Holdaway, 2002: 464-465). Although this clade of frogs has been in New Zealand ever since it broke away from Australia, it has not diversified extensively. No frog ever reached the Hawaiian Islands before people arrived. Madagascar has 1,000 of the world's 10,000 species of ants, in 6 of the world's 16 ant subfamilies and 46 of the world's 282 ant genera (Fisher, 2003). Madagascar has as many ant genera as an equivalent area of mainland tropics (Fisher, 1997). New Zealand has less than 12 species of ants (Worthy & Holdaway, 2002: xxviii). New Caledonia has 150 species of ants (P. S. Ward, personal communication), whereas the 15 km^2 Barro Colorado Island in central Panama has about 500 (M. Kaspari, personal communication). The Hawaiian Islands have no native ants. New Zealand has 18,500 native species of insects, 97% of which are endemic (Atkinson & Cameron, 1993), compared to Hawaii's 5,369 species, of which 97.4% are endemic (Eldredge & Evenhuis, 2003). Terrestrial mollusks buck the usual trend in diversity of species, but not of families: Madagascar has

671 species of native terrestrial mollusks, representing 24 of the world's 71 families (Pearce, 2003); New Zealand has over 1,000 species of terrestrial mollusks, representing ten families (Daugherty *et al.*, 1993). Before people arrived, the Hawaiian Islands had 1,000 species of terrestrial mollusks (Sohmer & Gustafson 1987) representing 9 families (Carlquist, 1980).

Local diversity of animals belonging to less mobile groups is sometimes as high in Madagascar as in comparable mainland settings. There are 51 species of frogs in montane rainforest Analamazaotra, in eastern Madagascar (Blommers-Schlösser & Blanc, 1993), while a similar extent of lowland rainforest at La Selva, Costa Rica has 48 species of amphibians – 41 species of frogs, and 7 species of other amphibian groups not represented in Madagascar, including three species of toads, *Bufo*, three species of salamanders, and one caecilian (Donnelly, 1994).

TREES

No one has calculated the total number of tree species for any of our sites. On the other hand, the best data for local plant diversity concern trees on plots of one hectare or less. We therefore focus on local diversity of trees. We measure diversity on a plot with N trees representing S species by Fisher's alpha, the solution to the equation $S = \alpha \ln(1 + N/\alpha)$, because α is relatively insensitive to sample size N or the lower diameter limit of trees measured (Leigh, 1999; Condit *et al.*, 2004). In continental tropical forest, tree diversity is governed primarily by the rainfall during the year's driest quarter (Table VII): tropical forests with wetter dry seasons have higher tree diversity (Givnish, 1999; Leigh *et al.*, 2004). The same is true in Madagascar (Table VIII). Tree diversity in Madagascar's wet forests is lower than in wet forests in Amazonia, South-East Asia or New Guinea, but far higher than in much smaller islands (Table VIII). Tree diversity is somewhat lower in seasonal forest of Madagascar than in seasonal forests of Central America (Table IX).

What might species diversity on an isolated land mass tell us about its ecosystem, or the factors shaping that ecosystem's properties? The factors that govern species diversity have been much disputed. Nonetheless, it is becoming clear that to understand why there are so many species of animals and plants, we must learn what differences in habitat, habits, diet and form allow different species to coexist (Hutchinson, 1959; MacArthur, 1972; Lack, 1976; Leigh *et al.*, 2004). On the one hand, a tree species, *Symphonia globulifera*, that invaded the Neotropics from Africa about twenty million years ago, is limited to a few trees per hectare exceeding 10 cm trunk diameter, even though it was able to spread throughout the forests of lowland Amazonia and Central America (Dick *et al.*, 2003; Leigh *et al.*, 2004). Despite its ability to

TABLE VII

Average annual rainfall, P*, mm, average rainfall during the year's driest quarter,* P_3*, mm, average number of trees ≥ 10 cm dbh,* N*, number* S *of species among them, and Fisher's* α**, for 6.25 ha subplots of CTFS Forest Dynamics Plots in lowland continental tropical forest. Climate data from Table 4.3 of Leigh (2004); tree data from Table 7.1 of Condit* et al. *(2004)*

Site	P	P_3	N	S	α
Yasuni, Ecuador	3,081	563	4,387	479	179
Lambir, Sarawak, Malaysia	2,664	498	3,979	591	194
Pasoh, peninsular Malaysia	1,788	318	3,319	440	136
Ituri (monodominant forest), Congo	1,674	180	3,576	159	34
Korup, Cameroun	5,272	172	3,074	181	42
Barro Colorado Island, Panamá	2,551	131	2,682	162	38
Huai Kha Khaeng, Thailand	1,476	46	2,734	130	28

* α is given by the equation $S = \alpha \ln(1 + N/\alpha)$

TABLE VIII

Altitude, number N of trees & lianas ≥ 10 cm dbh, (≥ 5 cm dbh for Manombo B and New Caledonia wet), number S of species among them, Fisher's α, basal area, BA; forest height (FH), m (height of emergents in parentheses); & forest type. All plots are 1 ha except Analamazaotra, 0.51 ha, Manombo B, 0.25 ha, and New Caledonia wet, the average of five 0.25 ha plots

Site	Altitude	N	S	α	BA, m²/ha	FH, m	Location
Papua New Guinea, wet	900 m	693	228	118.5	37.1		6° 43′ S, 145° 5′
*Andohahela, wet	440 m	739	121	41.1	34.1	15-20(30)	24° 38′ S, 46° 46′ E
	840 m	880	146	49.9	43.2	15-20(25)	24° 36′ S, 46° 44′ E
	1,150 m	1,216	126	35.3	43.8	12-20	24° 35′ S, 46° 44′ E
	1,550 m	675	65	17.7	63.8	25 (?)	24° 34′ S, 46° 44′ E
	1,875 m	1,365	50	10.2	65.9	11	24° 34′ S, 46° 43′ E
*Manombo, wet	80 m	787	119	39.0			23° 02′ S, 47° 44′ E
*Manombo B, wet	80 m	776	145	52.6		6-20	23° 02′ S. 47° 43′ E
*Ranomafana, wet	950 m	646	108	36.8	35.0		21° 17′ S, 47° 27′ E
*Analamazaotra, wet	1,000 m	540	126	51.7			18° 58′ S, 48° 27′ E
*Ambohitantely, seasonal	1,500 m	1,119	103	27.7	27.3		18° 11′ S, 47° 17′ E
*Manongarivo, seasonal	220 m	728	90	27.0	22.4	30	14° 04′ S, 48° 17′ E
*Kirindy, dry	30 m	778	45	10.4			20° 03′ S, 44° 39′ E
North Celebes, rather seasonal	lowland	408	109	48.7			
New Caledonia, wet	200 m	1,048	116	33.3	47.0	15-20	22° 06′ S, 166° 41′ E
New Caledonia, seasonal	450 m	1,256	97	24.5	55.5	20-25	20° 36′ S, 165° 47′ E
Puerto Rico, wet	380 m	876	42	9.2	34.0	20-25	18° 18′ N, 65° 44′ W
Mauritius, wet	550 m	1,710	52	10.1			20° 23′ S, 57° 27′ E
La Réunion, wet	250 m	1,079	40	8.2	81.5	8-15(20)	21° 20′ S, 55° 15′ E

* denotes sites from Madagascar.
New Guinea data are for Crater Mountain Biological Research Station (Wright *et al.*, 1997). Andohahela and Manombo data are from Rakotomalaza & Messmer (1999), except for forest height, which is from Helme & Rakotomalaza (1999). Manombo B data are from B. Rakotonirina, V. H. Jeannoda & E. G. Leigh Jr, unpublished. Ranomafana data are from Schatz & Malcomber (1995), except for the basal area which is from Rakotomalaza & Messmer (1999); Ambohitantely data are from Birkinshaw *et al.* (2000); Manongarivo data are from D'Amico & Gautier (2000); data for Kirindy, Analamazaotra and Ambohitantely are from Abraham *et al.* (1996) except for altitude of Kirindy, which is from Sorg & Rohner (1996). Celebes data from Whitten *et al.* (1987: 339). New Caledonia wet forest data are for slope forests on ultrabasic soil, from Jaffré & Veillon (1990), New Caledonia seasonal forest data are forest on schist, from Jaffré & Veillon (1995); Puerto Rico data are from Thompson *et al.* (2004) except for forest height (pre-hurricane), which is from Brokaw *et al.* (2004); Mauritius is for the sum of 100.1 ha plots in a relatively uniform forest, given by Vaughan & Wiehe (1941); La Réunion data is from Strasberg (1995) except for canopy height, which is from Strasberg *et al.* (1995).

spread, this invader cannot replace the hundreds of other tree species with which it coexists. On the other hand, a freshwater stream fish cannot invade a drainage occupied by another member of its genus or subgenus, although that other member was not excluded from this drainage by the many fish of other genera already present when it invaded (Reeves & Bermingham, 2006). Following Darwin (1859), Lack (1947), Diamond (1973, 1975, 1986), Schluter (1994) and many others, we conclude that diversification is driven by natural selection to avoid competitive exclusion.

TABLE IX

Monthly rainfall (mm), number S of species of trees > 10 cm dbh, and Fisher's alpha for seasonal forests at Barro Colorado Island, Panama (top), Manongarivo, Madagascar, Santa Rosa, Costa Rica and Kirindy, Madagascar (bottom)

Jan.	Feb.	Mar.	Apr.	May	Jun.	July	Aug.	Sept.	Oct.	Nov.	Dec.	Year	S	α
71	37	23	108	245	275	237	322	309	364	360	202	2551	91	35.5
37	40	50	90	200	380	470	430	280	150	60	45	2232	90	27.0
0	0	0	33	180	213	197	246	307	290	115	33	1614	56	18.7
1	2	5	23	42	149	254	188	108	22	5	0	799	45	10.4

Tree diversity data are from Table 8 except for Santa Rosa, where data are from Burnham 1997. Climate data for Barro Colorado are from Leigh *et al.* (2004b); climate data for Manongorivo are from Cours-Darne 1965, p. 38 for Hell-Ville, on nearby Nosy-Be; climate data for Kirindy are from Sorg and Rohner 1996, p. 59.

How does the limited area and degree of isolation of a land mass influence the diversity maintained thereon by the balance between immigration and adaptive diversification, and extinction? A species of bird, lizard or ant on a small island tends to occupy a wider range of habitats, and eat a wider range of foods, than conspecifics or congenerics on larger land masses (Crowell, 1962; MacArthur & Wilson, 1967: 105; Keast, 1968; Lack, 1976; Roughgarden *et al.*, 1983). Species on smaller islands are more likely to be wiped out by local catastrophes such as disease outbreaks or extremes of weather (Terborgh, 1973). On small islands, rare foods or rare habitats may be insufficient to support viable populations of animals specializing on them (Diamond, 1975). On small islands, moreover, extremes of weather are more likely to wipe out rarer or more specialized populations. Finally, smaller land masses provide less opportunity for speciation, while isolation reduces the frequency of immigrants that might replace extinct species (MacArthur & Wilson, 1967; Terborgh, 1973; Diamond, 1977). Therefore, on small, isolated islands, speciation and immigration balance extinction at a lower species diversity (MacArthur & Wilson, 1967). Accordingly, selection favors a yet greater generalization in diet and habitat use among those species present (MacArthur & Wilson, 1967). As "the jack of all trades is master of none" (MacArthur, 1961), the severity of competition among the species present should be less on smaller land masses, as we will show later in this paper.

Finally, predators are rarer than their prey, so predators, especially larger, more specialized ones, are less likely to persist on small, isolated islands. Thus, as we shall see later on, the pace of life will be slower on small, isolated islands.

WHAT FACTORS AFFECT THE PREDICTABILITY OF EVOLUTION?

Other worlds like our own, such as Madagascar, Australia or Miocene South America, prompt the question, how predictable is evolution? If limited area limits the variety of trophic levels, the intensity of competition and the pace of life on smaller land masses, should not the closest evolutionary convergence occur between biotas of similar-sized, long-isolated land masses? We can give only a cursory survey of these questions. After assessing what constitutes the best evidence of evolutionary convergence, we consider instances of convergence between Malagasy and continental biotas, discuss cases where the evolutionary potential of the biota on long-isolated land masses appear limited by their area, and provide examples of convergence among organisms on different long-isolated land masses of limited area.

HOW BEST TO DETECT EVOLUTIONARY CONVERGENCE

The most objective evidence for close evolutionary convergence between unrelated clades is when members of one clade are assigned to the other until molecular phylogenetic analyses reveal the mistake. For example, understory forest birds in Madagascar once classified, some

as bulbuls, some as babblers, actually belong to an endemic clade of Old World warblers, Sylviidae (Cibois *et al.*, 2001). Other Malagasy bird species formerly classified, one as a bulbul, another as a flycatcher, and perhaps others now classified as Old World warblers, are actually members of the endemic clade of vangas (Schulenberg, 2003a). *Cryptoprocta ferox*, Madagascar's largest predator (Fig. 2), was often classified as a cat (Garbutt, 1999: 129; Hawkins, 2003: 1360). After all, it has retractile claws, a cat-like skull and mode of killing prey, spotted kittens resembling small lion cubs, and it purrs during courtship (Albignac, 1984; Garbutt, 1999): captive animals even purr when caressed (Paulian, 1981: 76). *Cryptoprocta* has been likened to a miniature short-legged puma (Garbutt, 1999: 129). It bears a far closer resemblance to a jaguarundi, *Felis yaguarondi*, as described by Sunquist & Sunquist (2002: 113-119) Nonetheless, *Cryptoprocta* belongs to the mongoose family (Yoder & Flynn, 2003). Burrowing frogs in India, Madagascar and Africa, with feet adapted for burrowing and tadpoles that live in temporary ponds, were once classified as belonging to the same genus *Tomopterna*. In fact, Madagascar's burrowing frogs belong to the endemic family Mantellidae, and India's "*Tomopterna*" are now placed in the genus *Sphaerotheca* in the Ranidae (Vences *et al.*, 2000; Bossuyt & Milinkovitch, 2000). Malagasy tree frogs of the genus *Boophis* were classified in the same subfamily, Rhacophorinae, as look-alikes in India, but these *Boophis* belong to the Mantellidae (Bossuyt & Milinkovitch, 2000). Finally, Madagascar's Tenrecidae were long placed in the order Insectivora (now Lipotyphla), for tenrecs have many insectivore look-alikes. *Tenrec ecaudatus* resembles a Malay moonrat (Garbutt, 1999); *Setifer* and *Echinops* (Fig. 2) resemble European hedgehogs (Eisenberg & Gould, 1984: 160), some *Microgale* resemble shrews (Jenkins, 2003), *Oryzorictes* resemble moles or shrew-moles (Garbutt, 1999; Goodman, 2003b), and *Limnogale* resembles the desman or water-shrew (Eisenberg & Gould, 1984, p. 161). Nonetheless, the tenrecs are more closely related to elephants than to shrews or hedgehogs: they belong to an African clade, the Afrotheria that includes elephants, hyraxes, manatees, aardvarks, and golden moles (Stanhope *et al.*, 1998; van Dijk *et al.*, 2001; Douady *et al.*, 2002; Springer *et al.*, 2003).

Evolutionary convergence and non-convergence with continental biotas

Madagascar's biota shows many examples of convergence with continental inhabitants. Types of native vegetation in Madagascar are similar to those found in similar climates elsewhere in the tropics. In the rainforests of Madagascar's east coast, as in continental rainforests, the average leaf length in canopy trees decreases with the average temperature of the year's coolest month, while the proportion of woody plants < 3 m tall with leaves spiral or decussate around erect stems (as opposed to distichous along horizontal twigs) is higher in shorter forests (Leigh, 1988, 1999). In Madagascar, as in windward rainforests in other hurricane belts, such as Puerto Rico or Taiwan, canopy height is about 25 m, whereas the canopy is taller, 30 m or more, in rainforests closer to the equator, which are free from hurricanes (De Gouvenain & Silander, 2003). In tropical rainforests of both Madagascar and Australia, emergents are absent, as if hurricanes favor a smooth canopy (Smith & Ganzhorn, 1996: 34). Similarly, the hurricane-visited rainforest of El Verde, Puerto Rico has a smoother canopy than the hurricane-free forest of Barro Colorado Island, Panama (Brokaw *et al.*, 2004). In tropical evergreen rainforests of both Madagascar and Australia, leaf flush peaks in the rainy season, while fruit and seed production peaks late in the dry season, and a substantial proportion of the fruit and seeds produced in these rainforests consists of medium to large seeds and fleshy fruits (Smith & Ganzhorn, 1996: 34-35). The deciduous dry forest of Madagascar's west coast resembles Australia's deciduous dry monsoon forest in its dense understory, from which emerge numerous trees, many with bottle trunks, up to 25 m tall. In the dry forests of both countries, leaf flush is concentrated at the beginning of the rainy season while fruits, mostly fleshy, are available to some degree all through the year (Smith & Ganzhorn, 1996: 35). The spiny forest of southwest Madagascar resembles the caatinga of northeastern Brazil (Schnell, 1971: 752), and some plants of the family Didiereaceae, which are characteristic of southwestern Madagascar, resemble the Fouquieriaceae of Baja California and Arizona's Sonoran desert (Koechlin, 1972: 178).
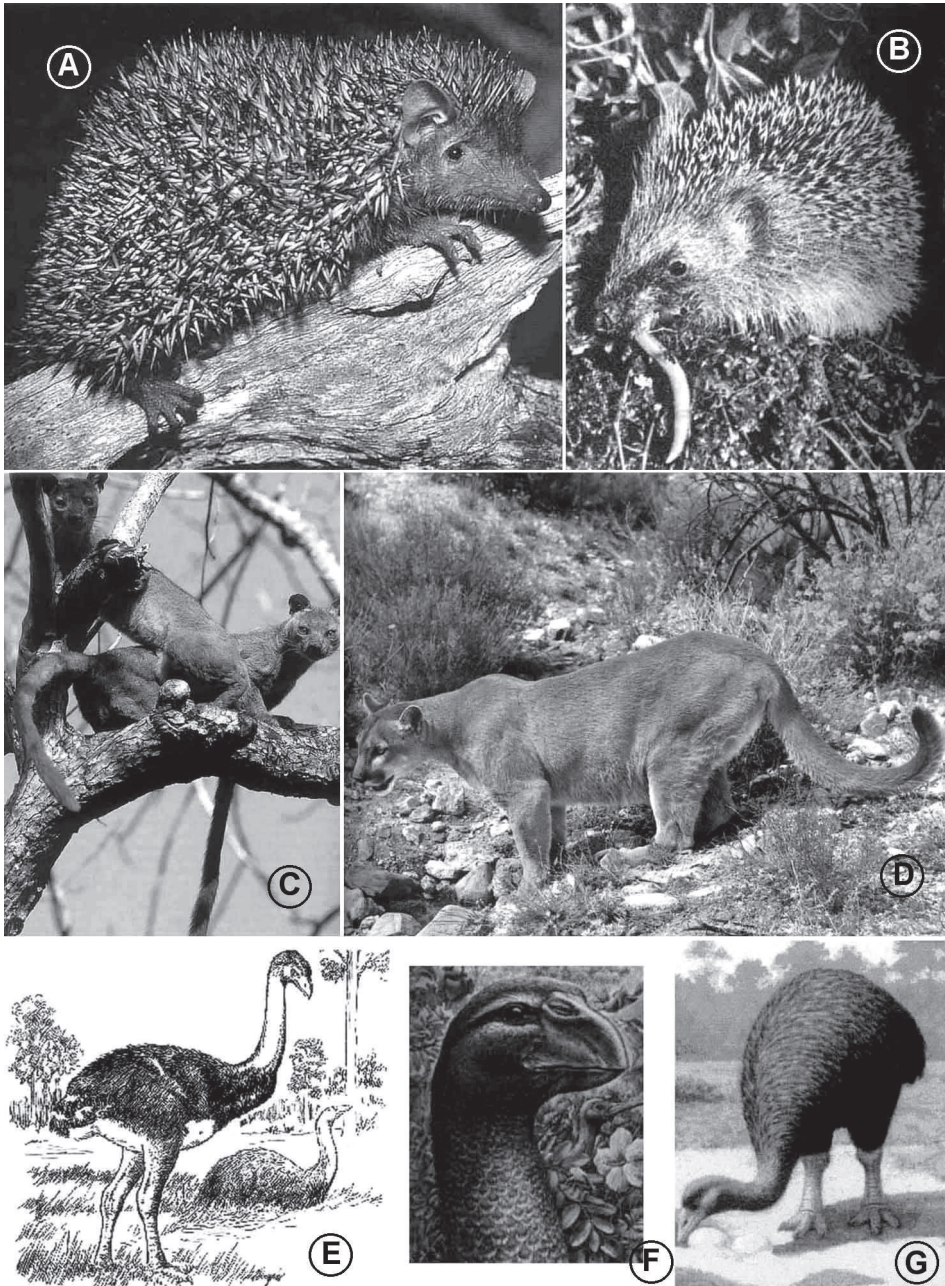
Figure 2. — Evolutionary convergence. The lesser hedgehog tenrec, *Echinops telfairi* (A; photo H. Schütz) was originally placed in the same order as the European hedgehog, *Erinaceus europaeus* (B), although they belong to different branches of the placental mammals. Similarly, *Cryptoprocta ferox* (C), Madagascar's largest predator, was originally placed with the puma, *Puma concolor* (D) in the cat family, although molecular phylogeny places it in the mongoose family. Before human settlement, the largest herbivores of our focal land masses were birds, including Madagascar's largest elephant bird, *Aepyornis maximus* (E), which weighed 270 kg, New Zealand's largest moa, *Dinornis giganteus* (G), which weighed 140 kg, and the moa-nalos of the Hawaiian Islands, such as Kauai's *Chelychelynechen quassus* (F), which may have weighed 7 kg.

Vertebrates in Madagascar also provide many examples of evolutionary convergence with continental counterparts. For example, small arboreal lemurs on Madagascar that eat fruit, nectar and gum and prey by sight upon big insects [even gut morphology is convergent for gum-eating species, *Phaner furcifer* and *Caluromys philander* (Fig. 3)], are similar to small arboreal primates with similar diets in Africa such as *Galago elegantulus*, and small arboreal marsupials in Australia such as the leadbeater possum, *Gymnobelideus*, and the pygmy-possum, *Cercartetus nanus* (Strahan, 1991) and small Neotropical marsupials such as *Caluromys*, (Charles-Dominique, 1977: 250-251; Charles-Dominique *et al.*, 1981; Steiner, 1981; Rasmussen, 1990). Frogs on Madagascar have a similar spectrum of reproductive modes, and similar relationships of tadpole to adult ecology, as do frogs in South America and India (Duellman, 1978; Blom-
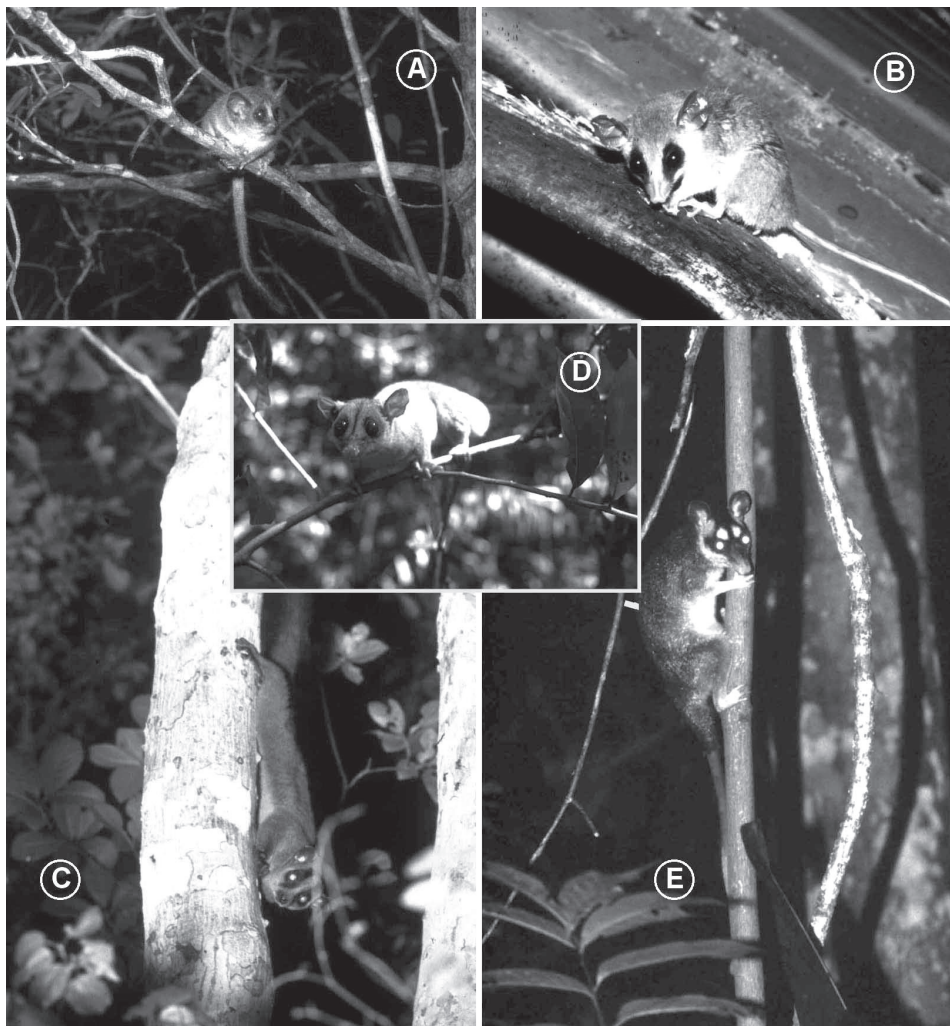
Figure 3. — Convergence between small nocturnal Malagasy lemurs and small nocturnal Neotropical marsupials. The 50 g lesser mouse lemur, *Microcebus murinus* (A), visual predator of insects that also eat fruit and tree exudates, resembles the 50 g mouse opossum, *Marmosa murina* (B) that likewise eats insects and fruit. The 300 g forked lemur, *Phaner furcifer* (C), which eats tree exudates (gums), insects and nectar, resembles the 250 g woolly opossum, *Caluromys philander* (D), which eats fruit, nectar, gums, and some invertebrates (even gut morphology is convergent for those gum eating species), and the 400 g four-eyedopossum, *Philander opossum* (E), which eats invertebrates, small vertebrates and some fruit (photos C.M. Hladik).

TABLE X

Number of mammal genera in different ways of life in Madagascar and Panama (from Table 1 in Leigh 1988, based on Table 2 of Eisenberg & Gould 1970)

Way of Life	Madagascar	Panama
Terrestrial anteaters	0	2
Arboreal anteaters	0	1
Arboreal insectivores that eat some fruit	4	3
Terrestrial insectivores that eat some fruit	4	2
Scansorial* insectivores that eat some fruit	1	0
Arborial carnivores** that also eat fruit and perhaps some insects	0	4
Terrestrial carnivores that also eat fruit and perhaps some insects	3	2
Scansorial carnivores** that also eat fruit and perhaps some insects	3	2
Arboreal carnivores	0	0
Terrestrial carnivores	2	3
Scansorial carnivores	2	1
Arboreal fruit and seed eaters that may eat insects	3	4
Terrestrial seed and fruit eaters that may eat insects	2	7
Arboreal herbivores that eat leaves and/or fruit	4	4
Terrestrial herbivores that eat leaves and/or fruit	2	5
Total number of genera	30	40

* Scansorial animals forage on the ground and in trees
** We classify *Eira* as a carnivore that also eats fruit (E. L. has seen one do so in the wild), whereas Eisenberg Gould classified it as strictly carnivorous.

mers-Schlösser & Blanc, 1993; Bossuyt & Milinkovitch, 2000). Eggs may be laid in ponds, or in tree holes, or on leaves overhanging water into which the tadpoles drop when they hatch, or on the ground; males may guard eggs, or even the tadpoles if they are living in confined spaces such as the water trapped in the axil of a large leaf, and so forth (Duellman, 1978; Blommers-Schlösser & Blommers, 1984). But a chance selection of particular examples does not comprehensively prove the predictability of evolution.

Indeed, convergence between Malagasy and continental biomes is by no means complete. Eisenberg & Gould (1970) showed that native mammals in Madagascar and Panama (which was entirely forested 10,000 years ago) occupied similar arrays of ways of life (Table X), but these ways of life were defined in rather general terms. Smith & Ganzhorn's (1996) more refined comparison between Madagascar's lemurs and the forest-dwelling possums and gliders of Australia found substantial differences (Table XI). Most species of possum and glider in Australian rainforest feed primarily on mature leaves, because in Australia most fruits are adapted to attract birds. In Madagascar, however, where there are relatively few fruit-eating birds, many tree species depend on lemurs for seed dispersal.

HOW EVOLUTIONARY OUTCOMES DIFFER ON LAND MASSES OF DIFFERENT SIZE

Limited area can restrict the degree of convergence of an island's biota to a continental one. Hawaii's endemic clade of lobeliads has invaded "nearly the entire range of light environments in moist to wet habitats in Hawaii" (Givnish *et al.*, 2004): the adaptation of their leaves to light converges to some degree on those of mainland forest plants. Just as with plants in continental settings, leaves of lobeliads in shadier habitats have lower photosynthetic capacity per unit leaf area, their leaf respiration is a smaller fraction of their photosynthetic capacity, and

Table XI

Mean number of mammal species per site with different diets in rainforests and monsoon forests of Australia and Madagascar (from Table 1 of Smith & Ganzhorn 1996)

Habitat and country	Leaves/fruit*	Frugivore/omnivore	Gum	Fruit/insects	Total
Rainforest, Australia	4.5	0.0	0.5	1.5	6.5
Rainforest, Madagascar	2.8	3.8	0.4	3.0	10.1
Monsoon forest, Australia	0.5	1.0	1.0	0.0	2.5
Monsoon forest, Madagascar	1.8	2.2	2.8	0.5	7.5

* Species with diets assigned to this category eat more leaves than fruit.

their photosynthesis increases faster when their light supply increases, than leaves of better-lit lobeliads (Givnish *et al.*, 2004). On the other hand, the range of leaf lifetimes among Hawaii's lobeliads − 4.1 to 10.1 months (Givnish *et al.*, 2004, Table III) − is far less than the range of leaf lifetimes among understory shrubs of the genus *Psychotria* in Panama − 4.0 to 40 months (Valladares *et al.*, 2000, Table V; Pearcy *et al.*, 2004, Table I). In rainforest of Gabon, leaves of sapindaceous shrubs, *Chytranthus*, live over five years (Hladik & Blanc, 1987: 222). In Panama, leaf lifetime is an integral part of a plant's adaptation to light level (King, 1994): are the different aspects of a plant less completely conformed to light level in Hawaii than in Panama or Gabon? Moreover, light levels in Hawaii's shadiest habitats are nine times higher than those of continental tropical rainforests (Givnish *et al.*, 2004: 239). Consequently, Barro Colorado has *Psychotria* whose leaves have lower photosynthetic capacity (2.62 and 2.85 µmol C m^{-2}s^{-1}, compared to 6.28 and 6.30 for Givnish *et al.*'s most shade-tolerant lobeliads) and lower leaf respiration (0.17 and 0.22 µmol m^{-2}s^{-1}, compared to 0.39 and 0.40 for the most shade-tolerant lobeliads; see Table 2 of Pearcy *et al.*, 2004 and Table 3 of Givnish *et al.*, 2004). Competition for light is less extreme in Hawaiian than in mainland rainforests, so adaptation to shade is less extreme in Hawaii.

Limited area also restricts the kinds of biomes that can evolve on a small island. Several subfamilies of grass appeared in India (and no doubt, in Madagascar too) by the late Cretaceous (Prasad *et al.*, 2005). Prasad *et al.* (2005) infer from their hypsodont teeth that the sudamericid gondwanatheres of India were specialized grass-eaters. Nevertheless, there is no evidence of Cretaceous grasslands anywhere in the world. Grasslands and grazing faunas evolved in South America by the Oligocene (Patterson & Pascual, 1972; Jacobs *et al.*, 1999), in Africa, North America and Europe by the middle Miocene, and in Australia by the late Miocene (Jacobs *et al.*, 1999; Retallack, 1992, 2001a, b). Grazers must have teeth adapted to the wearing task of eating grass, which leads to evolutionary convergence in shape of jaws and teeth among grazers on different continents. As grasslands are open spaces, devoid of hiding places, grazers small enough for the local predators to eat must have legs and feet that allow them to outrun their predators, which leads to evolutionary convergence between legs and feet such as that between horses and South America's lower Miocene litoptern *Thoatherium* (Simpson, 1980: 98-100).

How large must a land mass be to evolve grasslands and grazers? Central Madagascar is now covered by fire-maintained grasslands (Koechlin, 1972; Lowry *et al.*, 1997). Before people arrived, Madagascar appears to have lacked extensive grasslands and the variety of grazers that maintained them. In striking contrast to east Africa, with its extensive, spectacular grassland ecosystems (Sinclair & Norton-Griffiths, 1979; McNaughton, 1985), most of Madagascar's vegetation in prehuman times must have been forest, spiny bush, brushland, or open woodland with a grassy understory, all formations dominated by woody plants (Lowry *et al.*, 1997: 114). To be sure, before people arrived there was enough grassland in Madagascar (Burney, 2003) to support the pygmy hippopotamus *Hippopotamus lemerlei*, whose skull and tooth wear patterns resemble those of its larger African congener *H. amphibius* (Stuenes, 1989: 260), a grazer (Kingdon, 1979). These grazers, however, did not evolve in Madagascar: they were an import, probably during the Pleistocene, from Africa (Stuenes, 1989). Moreover, *H.*

lemerlei gave rise to *H. madagascariensis*, which, judging by the resemblance of its skull and tooth wear patterns to those of the browsing pygmy forest hippopotamus of West Africa (Stuenes, 1989), was a browser.

Before people arrived, New Zealand's South Island had native alpine tussock grasslands above tree line (Atkinson & Cameron, 1993). These grasslands, however, spread into the dry lowlands of South Island only as a result of Polynesian activities (Worthy & Holdaway, 2002). These grasslands were not maintained by grazers, although geese, *Cnemiornis*, may have grazed lowland grassy meadows bordering streams, ponds and coastal lagoons (Worthy & Holdaway, 2002: 477-478). New Zealand did not evolve extensive lowland grasslands: before people arrived, 78% of New Zealand was covered by forest (Atkinson & Cameron, 1993), and, except for the alpine meadows and grasslands, most of the rest was presumably shrubland.

Before people arrived, New Caledonia had native grasses, but lacked grasslands (Virot, 1956; Schmid, 1989). Then, New Caledonia was covered by forest, brushland, and maquis, which is rather like chaparral (Virot, 1956). Now, however, a third of its area is covered by grasslands and savannas created by human activity (Schmid, 1981). Similarly, a variety of grasses had colonized the Hawaiian Islands before people arrived (Sakai *et al.*, 1995), but these islands' savannas and grasslands were also created by human activity (Schmid, 1989). The native vegetation of the Hawaiian Islands is woody – rainforests, mesic forests, dry forests and woody shrubbery (Sohmer & Gustafson, 1987). In its lack of extensive grasslands before humans settled, Madagascar resembled other small long-isolated land masses.

Limited area may also limit the potential of certain evolutionary innovations. New Zealand inherited mammals from Australia. These mammals apparently belonged to a primitive stock that diverged like the multituberculates from placental ancestors before marsupials did (Worthy *et al.*, 2006). Descendants of primitive continental mammals became the dominant terrestrial vertebrates after the extinction of the dinosaurs. Dinosaurs died out in New Zealand, too, and New Zealand's mammals outlived them by at least 46 million years. Instead of becoming dominant, however, these mammals died out some time after the middle Miocene. Indeed, their niche may be partially occupied by descendants of the mystacinid bats that coexisted with them in the Miocene (Worthy & Holdaway, 2002; Worthy *et al.*, 2006). As we have seen, some groups stage spectacular adaptive radiations when freed from competition. Do other groups wither and eventually peter out when isolated on too small a land mass, failing of a spectacular potential for lack of the right kind of competition?

CONVERGENCE AMONG ORGANISMS ON SMALLER LONG-ISOLATED LAND MASSES

It is useful to ask, however, whether Malagasy organisms were more likely to evolve convergently with organisms on other long-isolated land masses. A rigorous answer to this question is not yet possible, but the available evidence is suggestive. The largest herbivore on Madagascar (Fig. 2), the 275 kg elephant bird, *Aepyornis maximus* (Worthy & Holdaway, 2002: 153), is strikingly similar to New Zealand's largest prehistoric herbivore, the 140 kg moa *Dinornis giganteus* (Worthy & Holdaway, 2002: 146). Moreover, New Zealand's suite of 11 species of moas, ranging in weight from 20 to 140 kg, parallels Madagascar's suite of eight species of elephant birds, ranging in weight from 60 to 275 kg (Worthy & Holdaway, 2002; Hawkins & Goodman, 2003). More generally, the largest herbivores living before human settlement on very distant oceanic islands such as the Hawaiian archipelago, or on very distant "land bridge" islands that have been isolated for many million years, such as New Caledonia, were birds, whereas on larger land masses this office was filled by a mammal (Burness *et al.*, 2001).

Malagasy frogs of the genus *Mantella* that live on the forest floor have evolved convergently with brightly colored poison-dart frogs, Dendrobatidae, that evolved in pre-Pliocene South America: *Mantella* and their dendrobatid counterparts are splashed with bright, even garish, colors; they are small, with a snout-vent length less than 50 mm, they have toothless jaws and lay terrestrial eggs; they move jerkily, and they are diurnal, foraging actively for ants and other arthropods of the leaf litter on the forest floor (Zimmerman, 1996; Clark *et al.*, 2005). Like poison-dart frogs, *Mantella* lace their skins with poisonous alkaloids, many of which, such as pumiliotoxins, are compounds also used by dendrobatids (Daly *et al,.* 1984,

1996). Again, like dendrobatids, and like the poisonous birds of New Guinea – the pitohui and the ifriti – *Mantella* derive their alkaloids from poisons in the ants and other arthropods they eat (Daly, 1995; Daly *et al.*, 1996, 2002; Saporito *et al.*, 2003, 2004; Dumbacher *et al.*, 2004; Clark *et al.*, 2005). Sequestration of poisonous alkaloids from their prey by colorful frogs and toads has evolved in Australia, South America and Madagascar: this phenomenon has yet to be recorded from larger continents (Daly *et al.*, 1984; Daly, 1995). The extraordinary similarity in the alkaloids sequestered by Malagasy *Mantella* and South American dendrobatids is driven in large part by convergence in chemical defenses among litter ants of the two regions (Clark *et al.*, 2005).

Madagascar's aye-aye, *Daubentonia*, has an elongated fourth finger with which it removes grubs from galleries in wood, rodent-like incisors, and a skull designed to withstand the stress of chiselling wood with its incisors. This combination of characteristics has also evolved in one other mammal, the smaller marsupial *Dactylopsila* of New Guinea and northeast Australia. Both *Daubentonia* and *Dactylopsila* have evolved on isolated land masses that lack woodpeckers (Cartmill, 1974).

The lemurs that humans extinguished were all larger than any living lemur, and most of them fed primarily on leaves (Godfrey & Jungers, 2003). Most of these extinct lemurs resembled animals that live, or recently lived, in New Guinea, Australia and South America. These extinct lemurs include the 20 kg *Archaeolemur*, which resembled the tree-climbing kangaroo *Dendrolagus* of New Guinea (Godfrey, 1988), but had strong jaws, and tooth wear patterns similar to those of *Cebus apella*, which crack hard nuts and chew up wood to reach woodboring grubs (Godfrey *et al.*, 2005; Terborgh, 1983); the 30 kg *Hadropithecus*, which was neither a baboon-like runner nor a grass specialist (Godfrey *et al.*, 2005); the 10 kg *Mesopropithecus*, the 15 kg *Babakotia* and the 50 kg *Paleopropithecus*, which resembled tree sloths in their suspensorial locomotion and herbivorous habits, the larger species being more sloth-like; the 200 kg *Archaeoindris*, which resembled a ground sloth (Jungers *et al.*, 1997; Simons, 1997); and the 50 and 75 kg *Megaladapis*, which resembled koalas in their folivory and style of locomotion (Godfrey & Jungers, 2003).

Why should Malagasy animals – and Malagasy vegetation – converge mainly on counterparts in other long-isolated land masses? One feature New Guinea, Australia and pre-Pliocene South America shared in common was the relative inefficiency of their larger carnivores. When a land bridge connected the Americas, the first South American mammals to disappear were its marsupial carnivores (Simpson, 1980; Webb, 2006: 251). A more complete answer requires closer examination of how the limited area of a long-isolated land mass influences evolution and diversification on that land mass, but it begins to look as if life is slower-paced on smaller land masses.

The Hawaiian archipelago, with its several islands in similar settings, offers more precise evidence on the predictability of (some aspects of) evolution. For example, an 8.6 kg herbivorous flightless goose evolved on Hawaii's big island during the last half million years from colonizing Canada geese (Paxinos *et al.*, 2002). This goose is convergent on similar-sized herbivorous moa-nalos that evolved from colonizing terrestrial dabbling ducks on Oahu and the other older islands (Sorenson *et al.*, 1999; Paxinos *et al.*, 2002). Two other examples of evolutionary convergence within these islands are provided by the spider genus *Tetragnatha*. One *Tetragnatha* clade has spiny legged spiders that actively hunt prey. These spiders come in four different morphs, each with a different ecological role: a green, leaf-dwelling morph that eats mostly small, flying insects, a moss-dwelling maroon morph that eats weakly flying insects, a slow-moving large brown morph that lives on bark and eats caterpillars, and an active small brown morph that occurs on twigs and eats very small flying insects. Ten of the 11 communities Gillespie (2004) studied in the Hawaiian Islands had at least three coexisting morphs of *Tetragnatha*, and two had all four. Three of these morphs have evolved more than once (Gillespie, 2004). Another clade builds webs. The webs come in three types: larger webs with a medium density silk spiral, larger webs with a low-density (less tightly-wound) spiral, and smaller webs with a medium-density spiral. Each web type was evolved independently by spiders on two of

the three islands examined. Sympatric spiders build webs of different types, but only one of the three rainforests studied had all three web types (Blackledge & Gillespie, 2004).

Other archipelagoes also provide evidence of evolutionary convergence. For example, lizards of the genus *Anolis* evolved, usually independently, large dwellers in tree crowns, smaller denizens of trunk and crown, and of trunk and ground, and perchers on twigs, in Cuba, Hispaniola, Jamaica and Puerto Rico. An "anole" is morphologically more similar to anoles of the same habitat on other islands than to anoles of the other three habitats on any island, including its own (Losos *et al.*, 1998).

SEVERITY OF COMPETITION

Darwin (1859: 106) predicted not only that "more new places will be formed ..." but also that "the competition to fill them will be more severe, on a large than on a small and isolated area". Here we ask how the severity of competition on a land mass varies with its area. There are several ways to gauge the severity of competition in a region. Where competition is less severe, one might expect to find "archaic groups" that have disappeared from regions where competition is more severe. Severity of competition is also reflected in the intensity of the "arms race" between the anti-herbivore defenses deployed by a region's plants and their herbivores' capacity to parry these defenses (Vermeij, 1987). The severity of competition in a region may also be gauged by the "pace of life" there: animals must be more active, and capable of responding to more kinds of stimuli, where competition is more severe (Vermeij, 1999, 2004). We will now compare these features on land masses of different sizes.

Shelter for archaic groups

Darwin predicted that old, long-isolated land masses would shelter "archaic" groups that are no longer competitive in mainland settings. For example, Australia shelters egg-laying mammals, monotremes, that once ranged as far as South America (Pascual *et al.*, 1992), and wollemi pines, *Wollemia nobilis* (Araucaceae) which were common and widespread when Australia was an integral part of the Gondwana continent (McLoughlin & Vajda, 2005). Cuba and Hispaniola shelter solenodons, basal Lipotyphla (insectivores) which diverged from other members of their order 76 million years ago (Roca *et al.*, 2004). To shelter an "archaic" group, a land mass must not only be old: it must be so large that the archaic group escapes "accidental" extinctions from vagaries of weather or disease, yet small enough that the group will not be wiped out by superior competitors or voracious consumers.

On Madagascar, "living fossils" plants include *Malagasia*, whose subfamily Proteoideae (Proteaceae) is most diverse in Africa and Australasia, and *Dilobeia*, whose subfamily Grevilleioideae (Proteaceae) is overwhelmingly concentrated in Australasia (Weston & Crisp, 1996). Both these lineages may belong to Madagascar's Gondwana heritage (Schatz, 2001). Other relict plants in Madagascar include the basal araliad *Melanophylla*, and the basal dioscoread *Trichopus sempervirens*, possessing a rhizome but no tuber, whose only congener is found in Sri Lanka, India and the Malay Peninsula (Leroy, 1996; Schatz, 1996, 2001; Caddick *et al.*, 2002; Jeannoda *et al.*, 2003). Perhaps the most striking relict animal in Madagascar is the dipluran *Heterojapyx* (Paulian, 1961: 132), which closely resembles the 300-million-year-old *Tetrajapyx* (Daugherty *et al.*, 1993). *Heterojapyx* also occurs in the Pamirs, and in New Zealand (Paulian, 1961). Madagascar's lack of driver and weaver ants has allowed some archaic groups of ants to survive there (Fisher, 1997). Although all Madagascar's living Neoaves belong to families that evolved after it became an island (Ericson *et al.*, 2006), and therefore can be presumed to descend from overseas colonists, Madagascar harbors relict lineages of birds. The most striking relict is the endemic non-passerine family Leptosomidae, which diverged from its sister clades about 60 million years ago (Ericson *et al.*, 2006; Fig. 2). Its sister clades are abundantly represented on all continents save Antarctica. They include bird families ranging from owls (Tytonidae and Strigidae), hornbills (Bucerotidae), barbets (Capitonidae), toucans (Rhamphastidae), woodpeckers (Picidae), puffbirds (Bucconidae) and jacamars (Galbulidae)

to rollers (Coraciidae), kingfishers (Alcedinidae), motmots (Momotidae), todies (Todidae), bee-eaters (Meropidae) and trogons (Trogonidae). One sister clade includes another bird family endemic to Madagascar, the Brachypteraciidae, with five species, which diverged from its sister family Coraciidae about 32 million years ago (Ericson *et al.*, 2006). The Coraciidae have 17 species spread over Africa, Asia and Australia. Madagascar's third endemic non-passerine family, the asities (Mesitornithidae), with three species, diverged between 55 and 65 million years ago from the ancestors of hoatzins (Opisthocomidae), tropicbirds (Phaethontidae), flamingoes (Phoenicopteridae) and grebes (Podicipidae). The last three families are now distributed around the world (Ericson *et al.*, 2006). Madagascar's most archaic passerines, its endemic suboscine family Philepittidae (Benson, 1984), with three species, diverged 43 million years ago from their continental counterparts (Barker *et al.*, 2004).

New Zealand's living fossils include the tuatara, *Sphenodon*, the only surviving representative of a Mesozoic order of reptiles, Acanthisittidae, the sister family to all other passerine birds (Barker *et al.*, 2004), the dipluran *Heterojapyx*, with congeners in Australia as well as Indo-Madagascar (Paulian, 1961: 132), and frogs, *Leiopelma* (Daugherty *et al.*, 1993). *Leiopelma*'s closest relative is the North American *Ascalaphis*, from which *Leiopelma* diverged when Gondwana split from Laurasia. Together, *Leiopelma* and *Ascalaphis* form the sister group to all other frogs (Roelants & Bossuyt, 2005).

New Caledonia shelters the endemic monotypic family Amborellaceae, which many consider the sister group to all other living angiosperms (Wikström *et al.*, 2001; Hilu *et al.*, 2003). The tree genus *Acmopyle* (Podocarpaceae), now restricted to New Caledonia and Fiji (Mabberley, 1997), ranged as far as west Australia, Antarctica and Patagonia in the middle Eocene, 45 million years ago (Hill & Brodribb, 1999: 657). New Caledonia's endemic bird family, the Rhynochetidae, diverged from the Neotropical sun bitterns, the monotypic family Eurypygidae, about 30 million years ago. The sister clade of kagus plus sun bitterns includes the asities (Mesitornithidae) and their sister clades, hoatzins, tropicbirds, grebes and flamingoes (Ericson *et al.*, 2006: Fig. 2).

PLANT DEFENSES AND HERBIVORE COUNTERMEASURES

On many small islands, herbivores are less well defended than in comparable continental settings, presumably because herbivore pressure is lower on these islands. Plant species endemic to the Channel Islands off the coast of southern California, are much less spiny, and some of them less well defended chemically, than their closest mainland relatives (Bowen & Van Vuren, 1997). Secondary compounds are less frequent in native rainforests of the small oceanic island of Mayotte than among the native plants of the Ampasikely forest in the far larger island of Madagascar (Simmen *et al.*, 2005). In the mainland neotropics, the pioneer tree *Cecropia* is defended against herbivores and encroaching vines by ants which the trees house and feed, but in the Antillean islands, *Cecropia* do not maintain ants, because they face fewer herbivores and vines there (Janzen, 1973; Rickson, 1977).

On the Hawaiian Islands, native Hawaiian vegetation is notoriously vulnerable to vertebrate herbivores (Carlquist, 1980; Vitousek, 1987), and native plants are less well defended against vertebrates than their mainland relatives. Carlquist (1995) remarked that "defenses of Hawaiian angiosperms have plummeted to the lowest levels seen on any oceanic islands". Very few of the native plants of the Hawaiian Islands are poisonous: nearly all the species of poisonous plants on these islands have been introduced by human beings (Carlquist, 1980). Some plants defend themselves with odoriferous oils, but plants in the most diverse clade of Hawaiian mints (*Phyllostegia* and its descendants) are nearly scentless, unlike most members of their family. The Hawaiian *Coprosma* (Rubiaceae) has odorless leaves, whereas on larger land masses, even New Zealand, *Coprosma* leaves are foul-smelling (Carlquist, 1980). Hawaiian members of the silversword alliance (Madiinae) appear less well defended than their closest continental tarweed relatives (Baldwin, 2003; Carlquist, 2003).

How well defended against insects are Hawaiian plants? The poisons and odoriferous oils Hawaiian plants lack could deter insect as well as vertebrate herbivores. Three indigenous, non-endemic plant species invaded Hawaii successfully even though, thanks to Hawaii's lack

of ants, these plants lack the extra-floral nectaries that conspecifics elsewhere use to attract herbivore-deterring ants (Keeler, 1985). Is pest pressure so low on Hawaii that these plants could invade even though one of their defenses, ant-attracting nectar, was useless? On the other hand, defenses of different Hawaiian plants are distinctive enough, and effective enough, that many of their insect herbivores are species-specific (Carlquist, 1980; Asquith, 1995; Gillespie & Roderick, 2002). Although over a third of the Hawaiian Islands' 8,100+ insect species have recently been introduced by human agency (Eldredge & Evenhuis, 2003), and although an introduced parasitic wasp is currently destroying the Hawaiian endemic *Erythrina sandwicensis* – and its introduced congeners – (Gramling, 2005), introduced insects do not usually figure on lists of herbivores damaging native Hawaiian vegetation, and are uncommon in intact native forests (Rosemary Gillespie, personal communication). Ants, however, are a conspicuous exception: some introduced ants eat seeds, with devastating effect (Hunt, 2006).

Leaves of many of New Caledonia's endemic plants, especially its Apocynaceae, have alkaloids, which presumably serve as defenses against herbivores or pathogens. Chemicals plants use to deter herbivores and pathogens are often useful in curing human ills (Coley *et al*., 2003). Some alkaloids of these endemic plants have promising medical applications (Schmid, 1981: 74).

In New Zealand, many plants have physical defenses that were presumably evolved to protect them from moas, such as spiny or fibrous leaves or a divaricating architecture that makes it difficult for moas to reach leaves (Cooper *et al.*, 1993). New Zealand plants are also much better defended chemically than their Hawaiian counterparts (Carlquist, 1995). Introduced mammals, such as deer, however, cope easily with the defenses of New Zealand plants (Cooper *et al.*, 1993).

Leaves of Malagasy plants seem to be as well defended as leaves of plants from continental tropical regions (Ganzhorn, 1992; Simmen *et al*., 1999; Hladik *et al.*, 2000). The higher occurrence of secondary compounds in the native plants of Ampasikely (Madagascar), compared to plants of the rainforest of Mayotte (Simmen *et al.*, 2005), can be related to the very different areas of these islands. There are spectacular examples in Madagascar of coevolution between plant defenses and herbivore countermeasures, most notably that between cyanide-making bamboo and cyanide-tolerant bamboo lemurs, *Hapalemur aureus* (Glander *et al.*, 1989). Madagascar periwinkle and other plants of Madagascar have contributed useful medicines (Jolly, 1980, ch. 8).

Is pressure from specialized pests less intense in Madagascar than in continental settings? Although seeds or seedlings of dry forest plants in both Madagascar and East Africa benefit from being further from their parents, the effect appears stronger in east Africa (Bleher & Böhning-Gaese, 2001).

THE PACE OF LIFE

In the world as a whole, diversity, productivity and severity of competition increased as organisms tapped more new sources of energy (including other organisms), exploited old energy sources more effectively, and recycled more different kinds of waste products (Leigh & Vermeij, 2002; Vermeij, 2004). These developments both permitted and were made possible by increased activity levels. Competition is inherently unequal, which is why different species must occupy different ways of life (Gause, 1935; MacArthur, 1958). A new dominant species is usually enabled to replace its predecessor by being larger, having faster metabolism, responding to more different kinds of stimuli, engaging in a greater variety of interactions and/or performing more functions, at a higher level, than does the loser (Vermeij, 1999; Leigh & Vermeij, 2002). The features that enable new dominants to replace their predecessors all enhance the severity of competition by stepping up the pace of life. Where there are more opportunities for innovation, and where competitive encounters happen more often, as happens on larger land masses, competition will be more severe, productivity (like diversity) will be higher, and the pace of life will be more intense (Darwin, 1859).

The pace of life is indeed slow on small islands. On smaller islands, smaller animals that eat less for their size can maintain larger populations on the resources available, thereby allow-

ing the maintenance of more genetic variation and enhancing the population's chances of surviving catastrophes inflicted by the vagaries of weather or disease (McNab, 1994b, 2002). On many small islands, ectothermic reptiles, which have far lower metabolic rates and can therefore maintain far larger populations on a given food supply, occupy roles played by mammals on larger land masses (McNab, 2002). Flight is expensive both as an activity and as an ability, and many insects have evolved flightlessness on small islands (Darwin, 1859; Carlquist, 1974), presumably to reduce energy expenditure (McNab, 1994a, 1994b). On small ($\leq 1,000$ km^2) Pacific islands, pigeons (McNab, 2000), flying foxes, Pteropodidae (McNab & Bonaccorso, 2001) and rails (McNab & Ellis, 2006) are smaller, and have lower basal metabolism for their size, than their continental counterparts (Table XII). In rails, at least, these developments are further favored by the low predation pressure characteristic of small islands. Rails evolve flightlessness on islands lacking placental carnivores — even if the islands have marsupial carnivores. A rail's basal metabolic rate declines with the proportion of its body weight devoted to its pectoral (wing) muscles (McNab & Ellis, 2006). Rails on islands average 84% of the basal metabolic rate predicted for rails of its size, and flightless rails, 71%, compared to 109% for rails from larger land masses (calculated from Table 2 of McNab & Ellis, 2006). Many other birds restricted to small islands evolve flightlessness (Carlquist, 1965), presumably because absence or ineffectiveness of their predators favors this mode of saving energy.

Indeed, students of small rodents describe an "island syndrome." Rodents on islands live longer, have shorter reproductive seasons and lower reproductive effort, and attain sexual maturity later in life than mainland conspecifics, because predators are far less common and diverse on the islands (Levins & Adler, 1993; Adler & Levins, 1994; Adler, 1996). *Anolis* lizards on a small West Indian island, Dominica, are far less likely to be preyed upon, and were therefore longer-lived and later-maturing, and invest less effort in reproduction than their mainland counterparts on Costa Rica (Andrews, 1979). The average ± standard deviation in clutch size for different species of island rails is 3.4 ± 1.35 (N = 19 species), and among flightless members of this set of island rails, 2.7 ± 0.53 (N = 11 species), compared to 6.4 ± 1.81 for rails on larger land masses (calculated from Table 2 of McNab & Ellis, 2006). The "island effect" therefore describes contrasts between island and mainland species, as well as between island and mainland populations of a single species.

The "island effect" is writ large on our smaller sites. Hawaiian land snails of the genera *Partulina* and *Achatinella* first reproduce only when six or seven years old, and produce relatively few young (less than 8 per year) once they mature, whereas their introduced predator *Euglandina* reproduces when less than a year old, producing over 600 eggs per year (Simon, 1987). New Zealand is noted for the slow pace of life of its indigenous animals, a feature that is attributed to the lack of nocturnal mammalian predators that can find prey by their odor (Daugherty *et al.*, 1993). New Zealand brown geckoes, *Hoplodactylus*, have the longest lifetime and lowest fecundity of any known lizard. Giant land snails, *Powelliphanta*, take 15 years to attain sexual maturity. Giant wetas, *Deinacrida*, orthopterans that play the ecological role of mice, and weigh up to 70 g, live for three or four years, and take two years to attain sexual maturity. Kiwis, *Apteryx*, flightless birds that weigh ≤ 4 kg, live over 30 years. New Zealand's

TABLE XII

Average percentage of expected basal metabolic rate for species of flying foxes, Pteropodidae, and pigeons, Columbidae, on land masses of different sizes

	Small islands (ca. 1,000 km^2)	Medium islands (ca. 10,000 km^2)	New Guinea and larger
Pteropodidae	80.0 ± 11 (N = 5)	92.3 ± 11 (N = 3)	113.3 ± 25 (N = 10)
Columbidae	67.5 + 9.2 (N = 2)	90.8 ± 2.6 (N = 4)	102 ± 9.1 (N = 9)

For a flying fox weighing g grams, ln (basal metabolic rate, oxygen consumption in cc/hr) = ln (2.14) + 0.806 ln g (McNab & Bonaccorso, 2001); for a pigeon or dove, ln (basal metabolic rate) is ln (6.95) + 0.606 ln g (McNab, 2000). Bat data are from Fig. 6 of McNab & Bonaccorso (2001); pigeon data are from Fig. 8 of McNab (2000).

tuataras, *Sphenodon*, with an adult weight of 1.2 kg, take 13 years to attain sexual maturity. Once mature, a female tuatara lays ≤ 19 eggs every 4 years (Table 2 in Daugherty *et al.*, 1993). In contrast, female iguanas, *Iguana iguana,* which weigh ≤ 3 kg when mature, first lay eggs when two to eight years old and lay an average of 41 eggs every year or two (reviewed in Leigh, 1999: 33).

How does the pace of life on other long-isolated land masses increase with their area? One might expect the pace of life to be more intense in regions with larger herbivores and larger carnivores. The largest herbivore and the largest carnivore are larger on larger islands (Table XIII). The weight W, kg, of the largest herbivore, and the weight w of the largest carnivore, on a long-isolated land mass of area A, km^2, are both roughly proportional to the square root of its landmass's area A (Burness *et al.*, 2001), that is to say, proportional to the length or width of its land mass. To be specific: $W \cong 0.47A^{0.52}$, $w \cong 0.05A^{0.47}$ (Burness *et al.*, 2001). Why the exponent should be so close to 0.5 is not clear. Nonetheless, it is clear that natural selection reduces the size of large animals that reach islands. Hippopotami in Madagascar were smaller than their African ancestors (Stuenes, 1989). Elephants, mammoths and hippopotami on small islands in the Mediterranean, and off the coasts of California, Southeast Asia and Siberia are smaller than their continental ancestors (Roth, 1992; McNab, 2002).

As the island syndrome suggests, the long-term evolutionary response to more intense consumption is higher productivity. If more plant matter is consumed per unit area where herbivores are larger, plant productivity should be lower where the largest herbivores are smaller. In the Hawaiian Islands, above-ground plant productivity is much lower than in comparable habitats in Borneo (Table XIV). As we shall see, plants of the Hawaiian Islands are less well adapted for efficient photosynthesis and fast growth than their continental counterparts (Pattison *et al.*, 1998). On Madagascar, plant productivity appears to be lower than on the mainland: Madagascar's trees grow more slowly and produce less fruit than their continental counterparts (Ganzhorn *et al.*, 1999). Wright (1999) attributes this phenomenon to Madagascar's poor soil,

TABLE XIII

Weights of largest homoiothermic herbivore, and largest homoiothermic carnivore, on long-isolated land masses* of different sizes in the late Pleistocene (data from Burness et al.*, 2001; weights of* Aepyornis *and* Dinornis *from Worthy & Holdaway, 2002)*

Landmass	Area, km^2	Largest herbivore	Largest carnivore
Eurasia	55,000,000	*Mammuthus*, Mammoth, 5,500 kg	*Panthera spelea,* cave lion, 380 kg
Africa	30,000,000	*Loxodonta*, elephant, 3,900 kg	*Panthera leo*, lion, 176 kg
South America	17,800,000	Gomphothere, 4,200 kg	*Smilodon*, sabertooth, 390 kg
Australia	7,700,000	*Diprotodon*, 1,150 kg	*Thylacoleo*, 73 kg
New Guinea	810,000	*Nototherium*, 200 kg	*Thylacinus,* Tasmanian wolf, 25 kg
Madagascar	587,000	*Aepyornis*, 275 kg	*Cryptoprocta spelea*, 17 kg
New Zealand	270,000	*Dinornis* (the biggest moa), 150 kg	*Harpagornis* (eagle), 13 kg
Celebes	190,000	*Bubalus* (lowland anoa), 225 kg	*Macrogalidia* (civet), 5.1 kg
Cuba	110,000	*Megalocnus*, ground sloth, 150 kg	*Ornimegalonyx*, big owl, 8.3 kg
Hispaniola	76,000	*Megalocnus zile,* ground sloth, 150 kg	*Titanohierax*, big hawk, 7.6 kg
New Caledonia	16,648	*Sylviornis*, 40 kg	
Hawaii	10,434	Large Hawaii goose, 7.5 kg	*Haliaeetus albicilla*, eagle, 4.8 kg
Puerto Rico	9,000	Large rodent, 50 kg	*Caracara*, Caracara, 1 kg
Mauritius	1,894	*Raphus*, Dodo, 19 kg	*Circus,* Harrier, 0.6 kg

*a land mass may be connected by a narrow isthmus to another, as in the case of North and South America, or by an intermittent corridor of harsh climate, as are New Guinea and Australia.

TABLE XIV

Above-ground net primary production (ANPP, g dry matter per square meter per year) at different altitudes on Mt. Kinabalu, Sabah, Malaysia and Mt. Haleakala, Maui, Hawaii

	Sabah	Sabah	Sabah	Sabah	Maui	Maui
	Zonal soil	Zonal soil	Ultrabasic soil	Ultrabasic soil	P = 2,200 mm	P = 2,450 mm
Altitude	650 m	1,560 m	700 m	1,860 m	1,370 m	1,370 m
ANPP	1,900	1,300	1,700	800	900	1,100

Data for Sabah from Kitayama & Aiba (2002), data for Maui from Schuur & Matson (2001). P = pluviometry.

not its limited area, a proposition that can be tested by comparing Malagasy rainforest ecosystems with those of central Amazonia, where soils are also very poor.

In general, productivity differences are most evident in early succession (Janzen, 1974). Successional stands of invasive pioneers in Puerto Rico are two to seven times more productive than successional stands of native pioneers (Lugo, 2004). Plant ecologists have remarked that, although Madagascar suffers from frequent cyclones, it lacks an aggressive secondary vegetation (Koechlin, 1972; Koechlin *et* al., 1974; Phillipson, 1994). Is this because Madagascar's forest never had to cope with herbivores that can knock down trees, such as the elephants as Africa or Asia?

Even in Madagascar, the pace of animal life seems slower than in comparable mainland settings. Like rails or pigeons on small islands, lemurs have lower basal metabolism than continental monkeys of comparable size and way of life (Kappeler & Ganzhorn, 1993; Wright, 1999; Schmid & Stephenson, 2003). Like New Zealand reptiles, female *Propithecus* at Beza Mahafaly in southwest Madagascar reproduce later and live longer than mainland counterparts (Richard *et al.*, 2002). At least in the more seasonal regions of Madagascar, tenrecs have lower basal metabolism than comparable lipotyphlans in continental settings (Schmid & Stephenson, 2003). Again like New Zealand reptiles, lemurs and many other Malagasy mammals, even small ones, have fewer young per year than continental counterparts (Eisenberg, 1981; Goodman *et al.*, 2003), although a few exceptions have oddly large litters, *Tenrec ecaudatus* setting the mammalian record with a litter of 32 (Nicoll, 2003).

Wright (1999) and Richards *et al.* (2002) argue that the slow pace of animal life on Madagascar reflects the low above-ground plant production on Madagascar's poor soil. Probably of greater importance, many parts of Madagascar suffer an erratic climate, with periodic drought and frequent hurricanes. They conclude that the long life and slow reproduction of most lemurs (and other mammals) is a bet-hedging strategy adapted to cope with the catastrophes imposed by an erratic climate on an infertile world. Is the pace of life slow on Madagascar, not because predation pressure is less intense, but because these animals must parry other threats as serious as predators?

It is, however, very likely that Madagascar's lack of big carnivores also contributed decisively to the slow pace of animal life there. Before people arrived, Madagascar's largest carnivore was the 17 kg *Cryptoprocta spelea*, which is far smaller than the largest continental carnivores (Table XIII). It is true that *Cryptoprocta* on Madagascar eat plenty of lemurs, and is the chief source of adult mortality for some; no doubt *Cryptoprocta* and its larger congener ate more and larger lemurs in the past (Ganzhorn & Kappeler, 1996; Wright *et* al., 1997; Goodman, 2003c; Pochron *et al.*, 2004). *Cryptoprocta* are cathemeral, hunting by day but mostly at night (Hawkins, 2003). Group defense is the chief defense of larger lemurs: it pays these animals to be alert and active when *Cryptoprocta*, an ambush predator that often takes sleeping lemurs, is on the prowl (Colquhoun, 2006). Indeed, diurnality and cathemerality of Malagasy lemurs appear to be ancient adaptations (Curtis & Rasmussen, 2006), not adjustments to the recent extinction of large predators or competitors, as suggested by Kappeler (1997). Various hawks also take lemurs as large as *Eulemur*; the harrier hawk, *Polyboroides radiatus*, sometimes even takes adult white sifaka, *Propithecus verreauxi* (Karpanty & Goodman, 1999).

Nonetheless, predation pressure on monkey-sized vertebrates (as measured by the size, skill and abundance of the predators they face) is more intense in Africa (see Cheney & Seyfarth, 1990) than in Madagascar. African monkeys face a wider variety of predators: even leopards and chimpanzees include some monkeys in their diets. Are African monkeys more skilled than their Malagasy counterparts in avoiding predators? In prehuman times, moreover, Madagascar's larger lemurs and its elephant birds, all now extinct, faced far milder predation pressure than that imposed by lions, leopards, and their allies impose on African animals in the size range of Madagascar's extinct megafauna. Indeed, Madagascar's largest mammals and birds, all now extinct, are convergent, as we have seen, on those of other land masses with small or inefficient carnivores, such as Miocene South America, Australia, New Guinea, and New Zealand.

EVOLUTIONARY INNOVATIONS

Darwin (1859: 106) predicted that:

"although small isolated areas probably have been in some respects highly favorable for new species, yet ... the new forms produced on large areas, which have already been victorious over many competitors, will be those that spread most widely, will give rise to the most new varieties, and will thus play an important part in the changing history of the organic world."

As Darwin predicted, oceanic islands seldom generate evolutionary innovations that can succeed in mainland settings. In the Galapagos, the woodpecker finch *Camarhynchus pallida* has evolved the ability to use a cactus spine in the place of an ordinary woodpecker's long tongue to probe for grubs after "trenching" the wood with its bill (Lack, 1947). In the Hawaiian Islands, the akiapolaau, *Hemignathus munroi*, of the honeycreeper radiation, uses its short lower mandible to "trench" the wood, and its longer, decurved upper mandible to play the role of a woodpecker's tongue (Lack, 1947: 154; Freed *et al.*, 1987: 197). These are both makeshifts: a cactus spine is less easily controlled than a tongue, and one mandible delivers a weaker blow than a closed bill. Thanks to the lack of effective competitors, Hawaiian honeycreepers have radiated into various ways of life, many never occupied by its finch-like ancestors – some eat nectar, some also eat insects, others eat only insects, yet others eat fruit and/or hard seeds (Freed *et al.*, 1987). Thanks to Hawaii's lack of effective pathogens, and its birds' resulting lack of resistance to disease, introduced bird malaria was able to wipe out all of Hawaii's lowland honeycreepers (Carlquist, 1980; Vitousek, 1987). There are two basic reasons why small islands have not evolved innovations capable of succeeding in mainland settings. First, favorable mutations are rare. Less populous ecosystems offer fewer opportunities for favorable mutations to occur (Darwin, 1859; Fisher, 1930). Secondly, a successful mainland innovation has been far more thoroughly tested than an island innovation could be: the mainland innovation has "faced down" a far greater variety of competitors, predators and parasites than counterparts on oceanic islands would ever experience (Darwin, 1859: 106).

New Zealand has produced an evolutionary innovation that has proven successful in a mainland setting: a New Zealand flatworm, *Artioposthia triangulata*, was accidentally introduced to the British Isles and is now destroying the native earthworms of Great Britain and Ireland (Daugherty *et al.*, 1993, p. 441). New Zealand, however, has not evolved effective nocturnal carnivorous vertebrates (Daugherty *et al.*, 1993) despite being endowed with a diverse set of birds and Mesozoic reptiles, including dinosaurs (Cooper & Millener, 1993), and even mammals (Worthy *et al.*, 2006).

Madagascar has produced evolutionary innovations capable of successfully invading mainland settings. The plant genus *Kalanchoe* (Crassulaceae) radiated in Madagascar, evolved crassulacean acid metabolism there (as many other plant lineages have done elsewhere), diversified into a variety of settings and ways of life in Madagascar, and invaded, and diversified in Africa (Gehrig *et al.*, 2000). The subfamily of chameleons evolved in Madagascar, from whence it invaded Africa three times (Raxworthy *et al.*, 2002). Yet Madagascar seems to have been unable to evolve effective carnivores: Madagascar has effective carnivores because their

carnivorous ancestors crossed over from Africa twenty million years ago (Yoder & Flynn, 2003). Thus Darwin's (1859) prediction is fulfilled: successful innovation is most likely in competitive continental settings. Indeed, land masses as large as Australia and Miocene South America did not evolve efficient placental mammalian carnivores although, like the far smaller island of Madagascar, these continents were quite large enough to support them. In both these continents, the larger mammalian carnivores were marsupials. No marsupial has a basal metabolic rate 10% higher than the average for placental mammals of their size, whereas the basal metabolism of placental carnivores that eat vertebrates is much higher (McNab, 2005).

INVASIBILITY

In accord with Darwin's (1859: 337, 390, 393, 394) prediction, biotas on smaller land masses are changed more by invading species. Invading plants have little impact on intact mainland rainforests (Rejmanek, 1996). For example, *Clidemia hirta*, a Neotropical shrub that has wrought havoc in Hawaii (DeWalt *et al.*, 2004), occurs in light gaps of Pasoh Reserve, Malaysia, that have been heavily disturbed by wild pigs (Peters, 2001), but it does not appear to threaten the integrity of this forest. Intact Malagasy rainforests have suffered rather few invasions, but a few Malagasy habitats have been devastated by invading plants. The vine *Cissus quadrangularis* is smothering trees and blocking regeneration in gallery forests near Berenty, in the far south of Madagascar (Binggeli, 2003). When the cactus *Opuntia monacantha* was introduced to Fort Dauphin in 1770, it spread rapidly in the spiny bush of Madagascar's southwest, where it replaced large expanses of native vegetation. Only after cochineal scale insects, *Dactylopsius*, were introduced to control this cactus was it reduced to a rare and scattered plant (Guillaumet, 1980: 40-41; Binggeli, 2003b). In New Zealand, an ornamental herb imported from Brazil, *Tradescantia fluminensis*, forms a dense ground cover in some native forests, blocking regeneration; browsing by feral goats is changing the species composition of some native lowland forests; and deer are dangerously depleting the understory of some montane forests (Atkinson & Cameron, 1993). In New Caledonia, sclerophyllous forests, but not the island's other types of vegetation, are invaded by aggressive exotic plants such as *Lantana camara*, *Psidium guajava* and the vine *Cryptostegia grandiflora* (Lowry, 1998). In the Hawaiian Islands, and other oceanic islands, introduced plants and pigs are disrupting and transforming intact rainforest (Lorence & Sussman, 1988; Strasberg, 1995; Sohmer & Gustafson, 1987), while an introduced species of predatory land snail, *Euglandina rosea*, is wiping out native Hawaiian land snails (Vitousek *et al.*, 1987).

In this section, we first document that smaller land masses are more readily invasible. We begin by reviewing some of the pre-human evidence on the subject, and then we consider the responses of land masses of different sizes to a standardized battery of common invaders. We end by considering what makes the ecosystems of smaller land masses more invasible, and more easily disrupted by invasion.

Smaller land masses are more invasible: prehuman evidence

Malagasy plants and animals have colonized continental settings without human help. The gentian genus *Exacum* evolved in Madagascar about 30 million years ago from a species that colonized Madagascar from overseas. Madagascar now has 38 species of *Exacum*. Like the chameleons and *Kalanchoe* of Madagascar mentioned in the last section, *Exacum* has successfully colonized continental settings. *Exacum* dispersed from Madagascar to Asia roughly twenty million years ago, giving rise to 24 species, concentrated in India but ranging from Socotra to north Australia. Another species of *Exacum* dispersed about five million years ago from Madagascar to Africa, giving rise to two living species (Yuan *et al.*, 2005).

Nonetheless, an island as large as Madagascar is much more easily invaded than Africa, even if it is far less easily invaded than much smaller islands. Of ten indigenous species of Asclepiadoideae (Apocynaceae) shared between Madagascar and Africa, nine originated in Africa, and only one in Madagascar (Meve & Liede, 2002). More generally, although Mada-

gascar was already separated from Africa when flowering plants evolved, whereas its land connection via India to Antarctica, South America and Australia was only severed less than 90 million years ago, the generic composition of Madagascar's flora resembles Africa's far more than that of any other continent (Leroy, 1978).

Similarly, several genera of alpine plants have dispersed successfully from New Zealand to larger land masses. *Myosotis* (Boraginaceae), *Gentianella* (Gentianaceae), *Chionohebe* (Scrophulariaceae) and *Ranunculus* (Ranunculaceae) have colonized Australia from New Zealand; *Myosotis* and *Hebe* (Scrophulariaceae) have colonized South America from New Zealand, and *Myosotis, Anaphelioides* (Compositae) and *Parahebe* (Scrophulariaceae) have colonized New Guinea successfully from New Zealand (Winkworth *et al.*, 2002). Nonetheless, New Zealand's flora is composed very largely of descendants of overseas immigrants from Australia (Pole, 1994).

The story is similar for animals. One of the best-studied examples of relative invasibility is the interchange of mammals following the joining, three million years ago, of long-isolated South America to North America, which was frequently connected to Eurasia (Webb, 2006). Soon after the two continents were joined, 17 families of North American mammals had invaded South America, and 20 families of South American mammals had invaded the north (Webb, 2006: 251), not what Darwin's theory predicts. North American invaders, however, diversified rapidly in South America. Nowadays, over half South America's mammal genera descend from North American invaders (Webb, 2006: 251), whereas only four genera of invaders from South America now survive in North America north of Mexico. On the other hand, tropical Mesoamerica was an isolated habitat of limited area, which was very different from North America's vast expanses of temperate zone habitat. Bats, monkeys, rodents and edentates that descended from inhabitants of South America's vast expanses of tropical forest now form a major part of the mammal fauna in places like Panama and Costa Rica (Webb, 2006: 254).

The asymmetry between invasions of islands from continents and invasions of continents from islands has been most carefully analyzed for Australia, New Guinea and Northern Melanesia (Mayr & Diamond, 2001). Although the Bismarck Islands have 142 species of land and freshwater birds compared to New Guinea's 550, no more than three Bismarck Island species have successfully invaded New Guinea, whereas 130 species from New Guinea have colonized the Bismarcks, providing the overwhelming majority of the Bismarck Island bird fauna. Similarly, the New Hebrides (Vanuatu) have 56 species of land and freshwater birds, compared to the Bismarcks' 142, but only one New Hebrides bird species has successfully colonized the Bismarcks, whereas 16 species from the Bismarcks have successfully colonized the New Hebrides (Mayr & Diamond, 2001: 110).

SMALLER LAND MASSES ARE MORE INVASIBLE: RESPONSES TO HUMAN INTRODUCTIONS

Now we compare susceptibility of different-sized land masses to human-introduced invaders. Many factors could confound the comparison. Invasive plants, which favor open, well-lit sites, most readily colonize disturbed habitats (Fine, 2002), and appear first where human traffic carries them. Our land masses have suffered different amounts and types of human disturbance. Invasive plants colonize fertile places most readily (Fine, 2002): most of Madagascar, and much of New Caledonia, is infertile. It may take a seemingly unpredictably long time for a species, once introduced, to become aggressively invasive. Invaders may facilitate other invaders, so a region's number of aggressive invaders depends in part on the frequency of human introductions.

On the other hand, the recent histories of our four focal sites are rather similar, lending some trustworthiness to the comparisons. People settled all four rather recently, reaching New Caledonia 3,000 years ago, New Zealand 750 years ago, and the other two sites between 1,500 and 2,000 years ago. All four sites were colonized by Europeans or North Americans a century or two ago: these colonists introduced a great variety of domestic and commensal animals and ornamental plants, and drastically changed land use in many areas. Nonetheless, their four histories are far from identical. Cattle reached Madagascar far earlier than any of the other sites, and Madagascar has been connected to networks of international trade for over 500 years,

much longer than the other sites (Wright & Rakotoarisoa, 2003). Madagascar, unlike the other sites, has had small European enclaves on its shores for almost as long (Brown, 2000).

The set of invaders whose impacts on different-sized land masses we compare are (1) the invasive shrubs *Psidium cattleianum* (Myrtaceae) and *Clidemia hirta* (Melastomataceae); (2) pigs, Suidae; (3) rats, *Rattus*; and (4) invasive ants, particularly crazy-ants, *Anoplolepis gracilipes*, big-headed ants, *Pheidole megacephala*, and little fire ants, *Wasmannia auropunctata*. The comparison is not complete: among our focal sites, responses to all four categories of invaders are published, to our knowledge, for only Madagascar and the Hawaiian Islands.

(1) Psidium cattleianum *and* Clidemia hirta

In Madagascar, *Psidium cattleianum*, introduced from Brazil, invades clearings and disturbed areas. It also invades tree fall gaps in the rainforest near Ranomafana, delaying natural regeneration (Phillipson, 1994; Binggeli, 2003). Similarly, *Clidemia hirta*, introduced from the neotropics, is common in Malagasy second growth, and invades light gaps even in remote evergreen rainforests, but shows no sign of taking over or adversely affecting these forests (Binggeli, 2003).

In the Hawaiian Islands, introduced plants are invading large tracts of native forest (Pattison *et al.*, 1998). *Psidium cattleianum* is rapidly invading undisturbed native rainforest there (Huenneke & Vitousek, 1990) and *Clidemia hirta* is also spreading rapidly (De Walt *et al.*, 2004). Introduced plants are invading and replacing native forest in yet smaller islands, such as Mauritius and Réunion (MacDonald *et al.*, 1991). *Psidium cattleianum* is the single most threatening invader of rainforest in Mauritius (Lorence & Sussman, 1988) and Réunion (Strasberg, 1995). Walking into the Black River Gorges National Park of Mauritius on 22 September 2005, one of us (EGL) passed by 2-m tall thickets of *Psidium cattleianum* so dense that a cat could hardly pass between the stems, with a scattering of surviving emergent native trees.

(2) *Pigs (Suidae)*

Bush pigs, *Potamochoerus larvatus*, were probably introduced to Madagascar by early settlers (Paulian, 1961: 338, n. 1): they pose no noticeable threat to its forests (Andrianjakarivolo, 2003). In New Zealand, goats, deer and chamois are far more damaging than pigs to the native forest (Atkinson & Cameron, 1993). On the other hand, "the feral pig *Sus scrofa* is considered to be one of the most damaging agents in Hawaiian forests ... Through trampling, rooting and preferential feeding across a broad spectrum of habitats, pigs have impacted almost every native plant community in the Hawaiian Islands" (Aplet *et al.*, 1991: 55-56). By exposing the ground, pigs in the Hawaiian Islands also facilitate colonization by some invading plant species, notably *Myrica faya*, whose nutrient-rich leaf litter increases earthworm numbers, attracting further visits from pigs to eat these earthworms. Finally, pigs also disperse the seeds of some of the most aggressive plant invaders of the Hawaiian Islands (Aplet *et al*., 1991).

(3) *Rats*, Rattus *spp*.

"Domestic" rats, *Rattus* spp., cannot invade intact rainforest in East Africa (Goodman, 1995). On Madagascar, introduced *Rattus* were almost never found in native Malagasy rainforests before 1890 (Goodman, 1995), even though they had reached Madagascar by 1400 (Goodman *et al.*, 2003). Since then, rats have spread rapidly. They are now found in every one of Madagascar's forests. *Rattus* represent up to 14% of the rodents caught in the undisturbed rainforests of Andringitra, in southeastern Madagascar. *Rattus* are the most common rodent caught in dry forest at Zombitse, in Madagascar's southwest, and in lower montane rainforest at Analamazaotra, east of Antananarivo, and the only rodent caught in the plateau forest at Ambohitantely (Goodman, 1995). *Rattus* may be replacing some native rodents (Goodman 1995), but they do not appear to be a serious threat to the rest of Madagascar's biota. In New Zealand however, rats have caused many extinctions. They eliminated tuataras, several species of birds, a species of bat, several large species of frogs, *Leiopelma*, the region's largest species of gecko, its four largest species of skinks, *Cyclodina*, and a variety of large invertebrates from the main

islands of New Zealand, and those satellite islands they reached (Worthy & Holdaway, 2002). In the Hawaiian Islands, introduced rats wiped out some native birds (Steadman, 1995). Rats prevent the reproduction of some native plants by eating all their seeds (Sohmer & Gustafson, 1987: 10). Indeed, by blocking regeneration, Polynesian rats are thought to have deforested parts of Hawaii that Polynesians had not yet reached, and to have prevented forest regrowth on Easter Island (Hunt, 2006).

(4) *Invasive ants*

In Madagascar, exotic ants are most common in open and disturbed areas. Some introduced ants, including *Technomyrmex albipes*, have begun to invade undisturbed rainforest in eastern Madagascar. So far, however, the presence of exotic ants has been correlated with reduction of native ant populations only in fragmented and disturbed sections of the littoral rainforest along Madagascar's east coast (Fisher, 2003). Although Fisher (2003) records the presence in Madagascar of *Pheidole macrocephala*, he does not mention its impact. In New Caledonia, the little fire ant, *Wasmannia punctata*, is eliminating all native ants from a rainforest that it is invading (Le Breton *et al.*, 2005). In the Hawaiian Islands, crazy-ants, *Anoplolepis*, and big-headed ants, *Pheidole macrocephala*, have eliminated the diverse native spider fauna where they have invaded. Exotic ants are also reducing or eliminating the native crickets in invaded areas (Holway *et al.*, 2002).

The situation is worse on smaller islands. Exotic ants, particularly *Pheidole macrocephala* and *Technomyrmex albipes*, have restricted the native ants of Mauritius to a few isolated tracts of relict forest (Ward, 1990). Finally, on the 134 km^2 Christmas Island introduced crazy-ants, *Anoplolepis gracilipes,* which had been introduced around 1900, began forming huge, multi-queened supercolonies just before 1990. Ants of these supercolonies are eliminating the island's dominant consumer, the red land crab, which is the island's main defense against invading plants and mollusks. By "cultivating" scale insects for the honeydew they produce, these ants have increased the abundance of scale insects and sooty molds tenfold in invaded areas, causing dieback and some mortality in canopy trees. The result may be a destroyed ecosystem (O'Dowd *et al.*, 2003).

Why are smaller land masses more invasible?

Was Darwin (1859: 106) right to argue that smaller land masses are more susceptible to invasion because their inhabitants are less competitive than those of continental ecosystems? To answer, we consider what features make an introduced species a successful invader.

Some invaders do what their local counterparts did, only much better. The little fire ant, *Wasmannia auropunctata*, is replacing native ants in a New Caledonian rainforest because the invading ant exploits available opportunities so much more effectively (Le Breton *et al.*, 2005). The invader finds food placed by experimenters on tree trunks far faster, and recruits additional workers to these food sources far more quickly and abundantly, than do the native ants. The invader nests in nearly all trees of the two understory species that offer the most favorable nest sites, whereas in the invader's absence, native species occupy only about half of them. Finally, an understory palm in this rainforest, *Basselinia*, shelters giant scale insects, from which ants derive honeydew, under its dead fronds. Where fire ants have prevailed, scale insects occupy one third of the *Basselinia* palms, compared to one quarter where fire ants are absent, and fire ants increase the number of scale insects per occupied palm five-fold. The honeydew of these scale insects supports a higher density of fire ants, allowing these ants to consume more prey, and recruit more abundantly to other foods. The fire ants are replacing native ants because the invaders are far more effective in securing food than the 30+ species of native ants they are replacing. In its native Neotropical forest, however, dominant territorial ant species keep *Wasmannia punctata* from monopolizing food sources, and this fire ant coexists with up to 100 other ant species (Le Breton *et al.*, 2005).

In the Hawaiian Islands, Pattison *et al.* (1998) found that, on the average, plants of five invading species grew much faster than four comparable native species, gaining 25% of their

weight per week in full sun and 17% in partial shade, compared to 9% and 6% for the natives. Even in full shade, the invaders grew 40% faster than the natives. Pattison *et al.* (1998) compared the physiological characteristics of these nine species and found that, in sun and in partial shade, the invaders could fix far more carbon per unit weight, and per unit area, of leaf. Moreover, leaf respiratory costs comprised a far smaller proportion of the carbon fixed in the invaders than in the natives. The advantages of an invasive species of *Bidens* over its native congener were as substantial as the average advantage of invaders over natives (Pattison *et al.*, 1998).

Some invaders gain their advantage by escaping a "handicap," a predator, pest or pathogen that limited their populations in their continental homeland, without wiping them out. For example, *Clidemia hirta* is restricted to clearings in its native Costa Rica, but it readily invades tropical forests in Hawaii. Spraying *Clidemia* planted in Costa Rican forest understory with fungicide, and protecting these plants from insect herbivores, enabled them to survive there, but similar treatment did not affect the survival and growth of *Clidemia* in Hawaiian forest understory (DeWalt *et al.*, 2004). For an example concerning larger land masses, ecologically similar trees from South Africa's fynbos and a section of Australia with a similarly Mediterranean climate were introduced to each other's habitats. Each did far better in the other's habitat, suggesting that each species had escaped the specialist pests that limited its numbers in its native land (Fine, 2002: 692). Indeed, escaping the pests that limited them in their homeland allows plants to invade continental habitats. Cappucino & Carpenter (2005) compared nine species of invasive exotic plants with nine species of non-invasive exotics in an area stretching from Ontario to Massachusetts. They found that leaf damage averaged 97% lower in the invasive species.

Some invaders fill empty niches. In some cases, these niches were never filled before, as happens when an island can support a predator that it was too small to evolve. Guam had no nocturnal arboreal carnivores before the brown tree snake, *Boiga irregularis*, was introduced: this snake has spread and multiplied with devastating results (Fritts & Rodda, 1998). In other cases, human hunters emptied the niche. In the Hawaiian Islands, vertebrate herbivores were introduced to a paradise where large geese and ducks, these islands' only native vertebrate herbivores, had been hunted out. The introduced herbivores, pigs, goats and the like accordingly spread and multiplied (Carlquist, 1980).

WHY ARE HUMAN-INTRODUCED INVADERS MORE DISRUPTIVE ON SMALLER LAND MASSES?

A land mass's ecosystem evolves to resist or accommodate invaders of the types they normally encounter, as was shown for birds by Lack (1976) and *Anolis* lizards of the West Indies by Roughgarden *et al.* (1983) and Losos (1998). Judging by the long list of terrestrial species that visit the Hawaiian Islands without breeding there (Pyle, 2002), even those islands can resist colonization by most of the bird species that arrive there without human help. We may view the plants and animals that reach isolated land masses as innovations, analogous to those that evolve on mainland settings. A few of these innovations are fruitful: they establish viable populations, some even give rise to adaptive radiations. Most potential invaders, however, like most mutations in organisms, are doomed to failure. Species diversity in an island ecosystem is set by the balance between speciation and successful immigration, on the one hand, and extinction, on the other (Lack, 1976). This balance is in turn greatly influenced by the island's size. As we have seen, this balance governs the level of specialization in diet and habitat among an island's species (MacArthur & Wilson, 1967; Lack, 1976), how many trophic levels the island supports, the sizes of its largest herbivore and largest carnivore (Burness *et al.*, 2001) and therefore the severity of competition and pace of life on that island. Before the recent rash of human introductions, the most disruptive invasions occurred when land bridges connected long-separated land masses, as when the Americas were joined three million years ago (Simpson, 1980; Webb, 2006). Is there a trade-off between ability to disperse over large expanses of sea and the capacity to disrupt an island ecosystem?

Human introductions, however, have a wide range of impacts. Some of these invaders are benign. The lower productivity of smaller land masses may be most evident in secondary vegetation, just as the poor soil of the Malay Peninsula relative to Costa Rica is most evident in

the much higher growth rate of Costa Rica's roadside pioneers (Janzen, 1974). In Puerto Rico, a 9,000 km^2 oceanic island much less severely isolated than, say, New Caledonia, introduced tree species, including the African tulip tree *Spathodea campanulata*, which grow several times faster than native pioneers, dominate successional vegetation, but they have not invaded intact rainforest (Lugo, 2004). Most of Puerto Rico's exotic pioneer species provide a habitat where native species readily become established (Lugo, 2004). In Madagascar, exotics invade secondary vegetation, even in the most remote rainforests (Lowry *et al.*, 1997: 112, 118). Phillipson (1994: 280) commented that: "Natural vegetation on Madagascar appears mostly to have a low regenerative ability. Disturbed areas rapidly become colonized by alien plant species, which hinder or prevent regeneration of indigenous vegetation. However, introduced species do not often colonize or invade undisturbed native vegetation."

On larger islands, invading plants are especially common in forests of secondary succession from abandoned fields. In a secondary lowland forest in New Guinea, an island larger than Madagascar, *Spathodea campanulata* and *Piper aduncum* jointly provide 31% of the stems over 1.5 m tall and 36% of their basal area (Novotny *et al.*, 2004). If, however, the invaders exceed the effectiveness of their native counterparts by a sufficient margin, disaster can follow (see below).

Human-introduced invaders may be incompatible with the integrity of the native ecosystem, just as, when individuals of two species hybridize, the young may die because the genes of their parents function incompatibly. In some cases, the competitive techniques of the invader clash with the ecosystem it is invading. For example, the European knapweeds *Centaurea maculosa* and *Centaurea diffusa* are spreading widely and monopolizing open space on the North American plains, becoming far more abundant than in their native European habitats. These invaders spread because their roots exude substances that poison neighbouring plants of other species – substances that do not affect their neighbours in Europe (Callaway & Ridenour, 2004). The European herb *Alliaria petiolata*, garlic mustard, is invading closed-canopy forest in much of the United States and Canada, suppressing native understory plants including canopy tree seedlings. Garlic mustard, which is non-mycorrhizal, spreads because its roots exude chemicals that prevent neighbouring plants of other species from becoming infected by the arbuscular mycorrhizal fungi they need to take up nutrients from the soil. In Europe, garlic mustard is common in disturbed areas, but does not invade closed forest (Stinson *et al.*, 2006).

Such novel forms of chemical warfare have not yet been discovered in invaders of oceanic islands. The difference between the severity of competition and the pace of life between continental and small-island ecosystems, however, can generate destructive incompatibilities. On islands as small as Mauritius and Réunion, aggressive continental successional species are replacing native forest because competition for light there is so lax that enough light reaches the forest floor to support the invaders. The Hawaiian Islands had herbivorous birds before people arrived (Sorenson *et al.*, 1999; Paxinos *et al.*, 2002), but the rather minimal defenses that allowed Hawaiian plants to coexist with herbivorous geese and ducks do not suffice to prevent destruction by continental herbivores such as pigs and goats (Carlquist, 1980).

The problem is most extreme when an invader is a predator of a sort that the island is big enough to support, but not big enough to evolve. Hawaiian land snails suffered little predation before people arrived. Their low reproductive rate does not permit these snails to maintain their populations in the face of significant predation. Since Europeans arrived, rats and greedy shell collectors have wiped out many species of land snails (Hadfield, 1986). The pace of life of Hawaiian achatinelline snails, which first reproduce when six or seven years old and produce fewer than eight eggs per year, is utterly incompatible with the pace of life of the predaceous snail, *Euglandina rosea*, which eats them. Thus, when *Euglandina* were introduced to Hawaii, they proceeded to wipe out the remaining species of achatinelline snails that they can reach (Hadfield, 1986), just as wiped out all seven species of the land snail genus *Partula* from Moorea after being introduced to that island (Clarke *et al.*, 1984; Murray *et al.*, 1988). The introduced brown tree snake, *Boiga irregularis*, Guam's first nocturnal arboreal carnivore, wrought similar devastation. Guam's native species, unlike its introduced ones, are defenseless

against this snake. This snake has wiped out three of Guam's four species of native seabirds, nine of its 12 species of native forest birds, and three of its 11 native lizard species. This snake is also wiping out Guam's one remaining bat species, and has severely restricted the distributions of its three remaining forest bird species (Fritts & Rodda, 1998). New Caledonia lacked efficient predators before European settlement, so introduced dogs and cats pose a threat to native bird species such as the kagu, *Rhynochetos* (Letocart & Salas, 1997).

Isolation plays a role in enhancing the disruptiveness of invaders. Although Australia evolved large carnivores from ancient marsupial stock, they were not efficient. The largest Australian carnivore that survived the aboriginal human settlement, the "Tasmanian wolf" *Thylacinus*, was quickly replaced by feral dogs, dingoes, when they reached Australia sometime during the last ten thousand years (Strahan, 1991: 483). Neither marsupial carnivores nor dingoes "prepared" Australia's biota to cope with the retractile claws of feral cats: wounded prey that escape the cats quickly die of infections transmitted by the claws (David Watson, personal communication). In contrast, *Cryptoprocta*, descended from mongooses that invaded Madagascar twenty million years ago (Yoder & Flynn, 2003), has retractile claws: thanks to this relatively recent invasion of efficient carnivores, Madagascar's biota could cope with introduced cats.

In sum, invaders reveal much about how the size of an oceanic island shapes the characteristics of its ecosystem, and suggests the role coevolution among this ecosystem's species shapes this ecosystem's features.

CONCLUSIONS

Isolated islands and archipelagoes large enough to permit resident populations to speciate represent a series of evolutionary experiments. The Galapagos archipelago showed David Lack (1947) what factors were required for speciation to occur. Long-isolated land masses show how a land mass' area and degree of isolation affect both its macroevolutionary potential and the major features of its ecosystem.

As Darwin (1859) predicted, innovation is more likely on larger land masses. Australia and all larger continents but Antarctica evolved grasslands and grazers. Madagascar's grazer, a hippopotamus, crossed the sea from the continent where it evolved. No smaller island evolved a grazing ecosystem.

As Darwin (1859) also predicted, the area and degree of isolation of a long-isolated island govern its species diversity. On small islands, populations are more liable to extinction. They have fewer individuals, and are more likely to be wiped out by episodes of catastrophic weather that would be too local to wipe out more widespread continental populations. A species on a small island uses a wider range of resources and occupies a wider range of habitats than a continental counterpart, features that reduce the island population's chances of extinction. Diversity, total and local, is higher on larger islands where extinction is less likely and there is more scope for speciation and diversification. Isolation, however, reduces the frequency of colonization, so diversity is lower for more isolated islands, especially small islands where extinction risks are high and opportunities for speciation are few. Even Madagascar's diversity of birds and bats, however, is lowered by its degree of isolation.

Thanks to the higher diversity and greater potential for innovation of biotas on larger land masses, their species face a greater variety of competitors and predators. Therefore, competition is more intense on larger land masses, favoring specialization to reduce competition with similar species for limiting resources, a feature that confers more advantages and fewer risks than on smaller islands. In general, dominant animals tend to be replaced by competitors that are more active and versatile, and respond to a greater variety of stimuli (Vermeij, 1999). Small islands lack the resources needed to evolve such active dominants. In particular, the largest herbivores, and the largest carnivores, are larger on larger land masses (Burness *et al*., 2001). Even Madagascar is not large enough to evolve herbivores big enough to knock down trees, so Madagascar never evolved an aggressive secondary vegetation. Similarly, even Madagascar

did not evolve a top carnivore weighing over 17 kg: even a large *Cryptoprocta* does not bear comparison with a lion, leopard or chimpanzee. Several conclusions follow:

Because plant productivity is usually higher where herbivore pressure is greater, plant productivity is lower in the Hawaiian Islands, and perhaps even in Madagascar, than in comparable mainland settings, because these islands' herbivores are smaller and less efficient.

Because predation pressure is lower on smaller islands, animals are longer-lived and less fecund than counterparts of continental settings. Even on Madagascar, mammals are usually longer-lived and less fecund than ecological counterparts on the mainland. Indeed, intensity of predation plays a crucial role in an ecosystem's evolution. Many of the most striking examples of evolutionary convergence, such as between elephant birds and moas, and even moanalos, sloth lemurs and sloths, and the like, occur on land masses that had small or inefficient carnivores.

Because predation pressure and the intensity of competition are lower on small islands, and these islands' resource base is more limited, animals on small islands have lower basal metabolic rates than ecological counterparts on the mainland (McNab, 1994b, 2002). Even Madagascar's lemurs and tenrecs generally have lower basal metabolism than similar-sized mainland counterparts.

Therefore, ecosystems on larger land masses, with greater diversity, more intense competition and faster pace of life, tend to be less invasible. Moreover, they tend to be less disrupted by the invaders that do succeed than ecosystems of smaller islands. Small-island ecosystems can be disrupted by introduced predators more voracious than the natives' limited reproduction can support, or by predators or competitors that use techniques which these islands' inhabitants have never encountered before.

Isolation also profoundly affects the evolutionary potential and ecosystem characteristics of a land mass. As Darwin (1859) predicted, isolation allows some successful colonists of islands to found striking adaptive radiations by protecting them from more efficient mainland invaders, even though extensive adaptive radiations also can occur on large, less isolated islands whose biotas are diverse and competitive enough to deter invaders.

A land mass's degree of isolation also affects its intensity of competition and its invasibility. Although isolation does not prevent a small continent like Australia from evolving large carnivores, even early Pliocene South America was too small to evolve efficient mammalian carnivores (Webb, 2006). Although Australia evolved much larger carnivores than did Madagascar, Madagascar's carnivores were far more efficient. Australia's carnivores were locally evolved marsupials. The largest Australian carnivores that survived human settlement could not compete with dingoes, and Australia's biota was vulnerable to introduced cats. Madagascar's carnivores, on the other hand, descend from mongooses that colonized from Africa twenty million years ago. These carnivores have survived the advent of dogs, cats and rats, and thanks to their presence, the rest of Madagascar's fauna, unlike Australia's, suffered little from human-introduced carnivores. Although a land mass's size seems to be the dominant influence on the diversity, level of competition, pace of life, and invasibility of its ecosystem, isolation plays an important role, too.

Competition, scale and degree of isolation can be expected to interact in roughly similar ways for any complex system whose parts compete for resources to grow and reproduce. This analogy has no moral: it simply results, as does evolution by natural selection, from the interplay of chance and necessity. Human economies share striking analogies with ecosystems. Economies, like ecosystems, are shaped by competition for the means to live and grow or multiply. Competition favors diversification, for new (unexploited) or underexploited opportunities yield the easiest profit (Kauffman, 2000). Because the jack of all trades is master of none (MacArthur, 1961), competition also favors specialization, for being a master at exploiting some resource or opportunity renders displacement by another competitor for that way of life less likely. Indeed, different species, like different business firms, often coexist by exploiting different resources or opportunities.

Specialization lays the foundation for cooperation and interdependence. Flowering plants provide food to bribe mobile animals to convey pollen to the flowers of distant conspecifics

(Corner, 1964) and carry seeds far from their parent tree and its load of specialist pests and pathogens (Howe & Smallwood, 1982). Productive coral reefs evolved because corals found a way to attract symbiotic algae, zooxanthellae, which they provide with mineral nutrients and a relatively safe, well-defended home in return for the carbohydrates their guests synthesize (Goreau *et al.*, 1979). Just as organisms provide services for others in the course of, and as a way of, pursuing their own self-interest, so in human society, "it is not from the benevolence of the butcher, the brewer and the baker that we expect our dinner, but their regard for their own interest" (their desire to earn their own living) (Smith, 1776, Book I, Chapter II). Therefore, economies and ecosystems are simultaneously competitive arenas and webs of interdependence.

In both economies and ecosystems, productivity and diversity are essential, interrelated characteristics. In both, productivity is enhanced by technological innovation: tapping new sources of energy or income, using old ones better, recycling others' wastes, and the like (Fischer, 1984; Vermeij, 1995). In both, productivity also increases when entities with different abilities join together to compete more effectively against third parties (Vermeij, 1995; Leigh & Vermeij, 2002; Vermeij, 2004). Small economies support a low diversity of occupations. "As it is the power of exchanging that gives occasion to the division of labor, so the extent of this division must always be limited by the extent of that power, or, in other words, by the extent of the market. When the market is very small, no person can have any encouragement to dedicate himself entirely to one employment, for want of the power to exchange all that surplus part of the produce of his own labour, which is over and above his own consumption, for such parts of the produce of other men's labour as he has occasion for" (Smith, 1776, Book I, Chapter III.)

Larger economies, like ecosystems on larger land masses, support a higher diversity of occupations, thereby providing more opportunities for both competitive and cooperative interactions. Consequently, larger economies have a faster pace of life (greater resource turnover), more intense competition, a greater frequency of technological innovation, and higher productivity. The same is true for ecosystem on large continents.

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