GUEST EDITORIAL

The mismeasure of islands: implications for biogeographical theory and the conservation of nature

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ABSTRACT

The focus on *place* rather than space provides geography with a powerful *raison d'être*. As in human geography, the functional role of place is integral to the understanding of evolution, persistence and extinction of biotic taxa. This paper re-examines concepts and biogeographical evidence from a geographical rather than ecological or evolutionary perspective. Functional areography provides convincing arguments for a postmodern *deconstruction* of major principles of the dynamic Equilibrium Theory of Island Biogeography (ETIB). Endemic oceanic island taxa are functionally insular as a result of long-term island stability, confinement, isolation, and protection from continental invasion and disturbance. Most continental taxa persist in different, more complex and open spatial systems; their geographical place is therefore fundamentally distinct from the functional insularity of oceanic island taxa. This creates an insular-continental *polarity* in biogeography that is currently not reflected in conservation theory. The focus on the biogeographical place leads to the development of the *eigenplace* concept defined as the *functional spatial complex of existence*. The application of still popular ETIB concepts in conservation biology is discouraged. The author calls for the integration of functional areography into modern conservation science.

Keywords

Functional areography, geographical place, eigenplace concept, island biogeography, insularity, continentality, conservation biology, nature conservation.

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The importance of islands for our understanding of evolution, ecology, and biogeography cannot be overstated. Although MacArthur & Wilson's (1967) classic monograph and foundation for the Equilibrium Theory of Island Biogeography (ETIB) has been largely invalidated and superseded by new field data and more realistic concepts, there are still key aspects of the ETIB paradigm that continue to influence basic biogeographical thinking and its application in conservation science today. It is the purpose of this paper to re-examine the concept of insularity and its use and application in recent biogeographical literature as well as in contemporary conservation biology.

The specific objectives are (1) to evaluate the interpretation of biogeographical data from an island-centric rather than from a taxon dispersal perspective, (2) to propose the application of functional geographical criteria to distinguish islands from spatial entities on mainlands, and (3) to reflect on the application of biogeographical concepts in conservation science. My aim is to reconceptualize the field of island biogeography. In particular, I wish to add evidence on the nature of oceanic islands, to contrast oceanic life to that of continents, and to discourage the application of ETIB concepts to the increasingly triage-pressured field of conservation biology.

DEFINING ISLANDS

In this paper, a terrestrial island is defined as land separated from a much larger mainland or other islands by a water barrier reducing accessibility and linkage but also protecting island biotas from certain mainland impacts such as predation, competition, and disease.

The ETIB model was originally developed for and confined to the Indo-Australian oceanic islands. But it was soon extended to all kinds of islands and even mainland 'islands' (MacArthur & Wilson, 1967; Diamond, 1975, 1981; Diamond & May, 1976; Soulé *et al.*, 1979; Higgs, 1981; Newmark, 1995, 1996). What then constitutes a biogeographical island?

Rosenzweig (1995) asked this question and came up with the definition 'an island is a self-contained region whose species originate entirely by immigration from outside the region' (p. 211). The first part of this definition is acceptable because it underlines the uniqueness and isolation of many island ecosystems. The second part is only valid where there has been no *in situ* evolution of taxa which is true for almost all recently formed land bridge islands (British Isles, Elba, Dalmatian islands) but not for thousands of oceanic islands. In fact, for Rosenzweig all regions 'whose species originate entirely by speciation within the region' (p. 212) are considered mainlands. He insists that Hawaii is a mainland; logically then, so should most other islands with endemic taxa. It would be more useful to term such islands as novel centers of diversity. From the perspective of functional areography, Rosenzweig's approach fails to acknowledge the all-important biotic community and physical geocoenosis context in which species evolve and persist on islands (see below).

Alfred Russel Wallace (1869, 1880) remains, of course, the patron of island biodiversity studies. The current renaissance of Wallace's works (Berry, 2002) and a new biography (Raby, 2001) will surely lead to greater appreciation of insular biotas and of the diversity of physical, climatic, and cultural island environments. Brown & Lomolino (1998) and Whittaker (1998) review island geography and distinguish several types of oceanic and continental islands. Mayr (1941) had noted that there has been some confusion over the term *oceanic island*. There is a geologic definition (an island not situated on a continental shelf) and there is a zoogeographical definition: 'an island which has received its fauna across the sea and not by way of land bridges' (Mayr, 1976, p. 604). The latter will be used for the purposes of this paper.

BACKGROUND ON ETIB

In the first chapter of MacArthur & Wilson's monograph (bearing the title 'The Importance of Islands') the authors stress the advantages of island studies. 'In the science of biogeography, the island is the first unit that the mind can pick out and begin to comprehend.' The second paragraph begins with the sentence 'insularity is moreover a universal feature of biogeography' and proclaims that 'many of the principles graphically displayed in the Galapagos Islands …apply in lesser or greater degree to all natural habitats'. They mention the 'insular nature of streams, caves, gallery forest, tide pools, taiga as it breaks up in tundra, and tundra as it breaks up in taiga'. Then they link basic science with real world application by stating that 'the same principles apply, and will apply to an accelerating extent in the future, to formerly continuous natural habitats now being broken up by the encroachment of civilization' (MacArthur & Wilson, 1967, pp. 3–4).

The theory was introduced as a 'more precise zoogeographic theory' of the Indo-Australian bird faunas (MacArthur & Wilson, 1963) and fully developed in the classical monograph (MacArthur & Wilson, 1967). It quickly attained the status of a paradigm and has maintained its magnetic attraction for researchers to the present day. In recent years, it has gained wide popularity among students and natural history buffs who read the Pulitzer Prize-winning book 'The Song of the Dodo' (Quammen, 1996). Repeated failures to prove the major hypotheses have not led to their rejection 'but rather to attempts to fault the deductive logic or experimental procedure' (Simberloff, 1976; see also Gilbert, 1980).

The ETIB postulates that the species–area relations (SAR) of island archipelagoes are driven by immigration and extinction rates of species; although island area and isolation play pivotal roles in the determination of island diversity (species richness) it is the interplay between immigration and extinction that leads over time to an equilibrium number of species residing on a given island.

Island biogeography changed 'in a decade from an idiographic discipline with few organizing principles to a nomothetic science with predictive general laws' (Simberloff, 1974). Supporting evidence accumulated with papers by Diamond (1969, 1971, 1972), Simberloff & Wilson (1970), Wilcox (1978), Lomolino (1986), and many others [Simberloff's review paper (1974) cited 121 references]. Much of the ETIB support literature focused on species turnover rates, on island 'saturation', on the 'relaxation' of faunas towards equilibrium levels, and on application to mainland habitat islands and nature reserves. ETIB has retained its paradigmatic dominance in ecological theory because the model's predictions could be 'tested rigorously with quantitative data', and – ironically – because 'they have frequently been falsified unequivocally' (Brown, 1986). In fact, the greatest value of ETIB has remained its position as a well understood anchor for floating alternate theories and scenarios of island biogeography. Substantive criticism came from F. S. Gilbert who scrutinized every part of the theory and its supposed validations; it is worthwhile to reread this paper even today. The exhaustive, fair, and careful scientific analysis of this author yielded the conclusion that 'quantitatively, however, it would seem that the model has little evidence to support its application to any situation' (Gilbert, 1980). The serious erosion of support for ETIB continued at a 1987 symposium in Rome where critics focused on new biological evidence from island investigations (Minelli, 1990; Olson, 1990; Solem, 1990).

Human impact on islands

Olson (1990) reviewed the prehistoric impact of humans on island birds and concluded that 'analysis of the fossil record has repeatedly shown that prehistoric man has had an extremely adverse effect on insular ecosystems on a global scale'. He documented that on many Pacific islands (from New Zealand, New Caledonia, Oahu, Maui, Managaia, to Huahine in the Society Islands) some 40–80% of the native land bird species had gone extinct in prehistoric and/or historic times (Steadman, 1997b). Olson showed that current distribution patterns have been unnaturally modified by man-caused extinctions 'and have thus led to many fallacious systematic and biogeographic conclusions'. He argued that 'at this point,

the only safe generalization in island biogeography is that it is not safe to make generalizations' (Olson, 1990). Similar effects of prehistoric and historic human agency have been discovered in the West Indies (Woods & Sergile, 2001).

The severe species and habitat loss experienced by many island ecosystems has been accompanied (and possibly accelerated) by intentional and accidental invasions of exotic biota. Sax *et al.* (2002) have shown that the species richness of vascular plants has approximately doubled on oceanic islands as a result of recent human impact.

Species–area relationships and turnover

Minelli (1990) reviewed the species–area relationships on islands. He found that area was often less important for the observed species diversity than habitat diversity, elevation, climatic diversity, floristic diversity, and habitat disturbance regimes. Species diversity is positively increased by speciation given suitable conditions of size, time, and isolation. The classical ETIB model operates in ecological time omitting speciation processes. Minelli then scrutinized the sampling procedures used to assess equilibrium and turnover states (see also Gilbert, 1980; Brown & Lomolino, 1998; Whittaker, 1998). He questioned the census accuracy and species selection of published case studies (what is a proper census interval, what is the exact source pool of species, do we count only within or between habitats, taxon levels, guilds, native and/or introduced species?). The conclusion reached was that the available evidence is riddled with uncertainty because of inappropriate or non-comparable sampling procedures and taxon selections. Thus, there is a high probability of crypto-turnovers and false equilibrium assessments.

Land snails: a different universe

Solem (1990) applied the model in its widest sense to the island biogeography of land snails. The result comes close to a contradiction of the ETIB paradigm. First, he investigated Preston's (1962) and MacArthur & Wilson's (1967) belief in the concept of community saturation, that 'there is a maximum number of species that can exist in a given area'. How much space do land snails need? Solem found that non-relictual snail species may persist in ranges as small as 0.01 km^2. This means that even very small islands can have *in situ* land snail speciation events; an island of 50 km^2 could support a snail fauna of 60 to > 300 allopatric species. Secondly, he analysed the SAR of Pacific land snails. He found that islands with areas of 13–585 km^2 average the same number of species, low islands have fewer species than high islands, and snail diversity is greatest on small, high, and isolated islands. He observed no saturation of land snails anywhere and concluded that land snail faunas do not exhibit equilibrium situations, as rare colonization events are followed by extensive *in situ* speciation processes. Moreover, in the Mediterranean, recently introduced land snails have sympatrically added themselves to the native fauna (meaning: there is

ecological space for the newcomers); similar evidence was documented by my student Christian Albrecht at a coastal site in southern California (Albrecht, 2001). Solem (1990) concluded that (a) most equilibrium and species–area studies have been concerned with organisms that are both vagile and require large areas for long-term survival, (b) 'mostly it will be found to be an ornithological or vertebrate pattern', and (c) 'a refocus of biogeographic thought is desirable'.

Northern Melanesia: ETIB update

The new and astonishingly detailed book on the birds of northern Melanesia (Mayr & Diamond, 2001) offers a textbook-like update of and support for familiar ETIB themes. This elevates it to a must-read lesson on ETIB. It contains a richness of abundance, dispersal, and speciation data on 195 bird species spread over some 200 ornithologically well surveyed islands. It focuses heavily on the importance of water barriers for colonization and different degrees of endemism and allopatric speciation of numerous superspecies complexes. The authors have devised new indices for the effects of vagility and abundance on geographic variation (p. 138), for community endemism as a function of island area and distance from the nearest major colonization source (p. 198), as well as for pairwise differentiation of nearby island avifaunas (p. 208). They postulate about supersaturated island numbers, differences between volcanic and fragmented Pleistocene islands, and the role of generalization in island biogeography. However, because northern Melanesia is ecologically and climatically unusually homogenous, it lacks a diversity of habitats (particularly xeric ones) found on many other oceanic islands. Hence the absence of sympatric speciation and of intra-island radiation among Melanesian birds (p. 307). In spite of its commendable detail and explanatory power, it remains doubtful that this updated model of tropical ETIB can find applications beyond its regional geographical and ornithological context (see below).

New ecological and biogeographical paradigms

Island biogeography offers a fascinating case study on the dialectics of science. Over a time span of 40 years there have been often surprising yet permanent paradigmatic shifts and reversals in our understanding of the world around us. Much of the progress in science can be understood in a Hegelian philosophical framework of thesis development and establishment followed by critique, increasing irrelevance, and formulation of alternate or opposing theses. I still grew up with a *weltbild* of permanent continents and climax ecosystems. Since the 1960s, plate tectonics, chaos theory, new succession models, vicariance, disturbance, disequilibrium, and species-based concepts in biogeography (Lomolino, 2000a, b; Whittaker *et al.*, 2001) as well as Hubbell's (2001) 'unified neutral theory of biodiversity and biogeography' have created an entirely different playing field for the natural sciences (detailed discussions in Brown, 1995; Brown & Lomolino, 1998;

Whittaker, 1998). None of these intellectual endeavours has, however, focused on the central *geographic* content and objective of biogeography although Maurer (1999) and Rhodes *et al.* (1996) emphasized the spatial factor in the dynamics of ecological populations. Stoddart (1986) was a lone voice when he critiqued studies in island biogeography and lamented 'that the data once collected are handled in a completely aspatial manner. Island area has become a statistic divorced from location, as do other attributes of islands' (p. 280). He called for a 'putting the geography back in the bio-' to provide once more 'that comprehensive view of the distribution of life on earth, pioneered by Humboldt and established by Darwin' (p. 305).

ISLANDS REVISITED

Robust and stable oceanic islands

Oceanic islands have been favorite objects of island biogeography since the days of Darwin and Wallace. Island biotas have generally been depicted as impoverished, depauperate, disharmonic, prone to turnover, and possessing 'notorious fragility' (Mayr, 1965; Carlquist, 1974; Simberloff, 1974; Williamson, 1981). This perception of island life resulted from (1) a lack of solid information on the actual, historic, and prehistoric biodiversity and true geological age of many tropical oceanic islands (which have only come to light in the last two decades), and (2) the fact that most published island studies dealt with the generally small continental land bridge islands of the North and Baltic Sea, the eastern Atlantic and the Mediterranean (Lack, 1942, 1969; Haila & Järvinen, 1983; Russell *et al.*, 1995)

which are indeed impoverished etc. but often populated by metapopulations from the nearest mainland, and usually are anthropogenically modified biotic samples (Walter, 1988) of their much larger neighboring mainland regions.

In contrast to many islands of the central and western Pacific (Steadman, 1997a, b), the oceanic islands and archipelagoes of the central eastern Pacific (Galapagos, Cocos Island, Revillagigedo) were pristine at the time of the Columbian conquest around 1500 AD. This has facilitated the historic chronicling of their recent human impact, landscape change, and biodiversity loss and turnover. An example is Socorro Island (140 km^2, 1040 m above sea level), largest of the four Revillagigedo Islands in the Mexican Pacific. Socorro remained pristine until 1869 when sheep were introduced. A few years earlier (1865), the American naturalist Grayson discovered its small but entirely endemic terrestrial avifauna (Table 1). Neither extinction nor immigration of any bird taxon was documented on Socorro (Grayson, 1871) until the Mexican Navy constructed a military settlement there in the 1950s. The endemic elf owl subspecies (*Micrathene whitnei graysoni*) vanished for unknown reasons and an endemic pigeon, the Socorro dove (*Zenaida graysoni*), became extinct in the wild by 1972 – a victim of documented direct human persecution, probable feral cat predation, and (perhaps) landscape change.

Although over 75 non-breeding land birds have visited this island, no viable population of an immigrant taxon has established itself on the still pristine NW side of Socorro in 135 years. Two continental birds (mourning dove *Zenaida macroura* and northern mockingbird *Mimus polyglottos*) have, however, invaded the overgrazed and largely deforested SE side

Table 1 Resident breeding land birds of Socorro Island (Mexican Pacific)

A. Status at time of discovery, 1865 (Grayson, 1871)

Yellow-crowned night-heron	*Nyctanassa violacea gravirostris**
Socorro red-tailed hawk	*Buteo jamaicensis socorroensis*
Common ground-dove	*Columbina passerina socorroensis*
Socorro dove	*Zenaida graysoni*
Green parakeet	*Aratinga holochlora brevipes*
Elf owl	*Micrathene whitneyi graysoni*
Socorro mockingbird	*Mimodes graysoni*
Socorro wren	*Troglodytes sissonii*
Tropical parula warbler	*Parula pitayumi graysoni*
Spotted towhee	*Pipilo maculatus socorroensis*

B. Status in 1997 (Walter, 1998)

1. Colonizations

Mourning dove	*Zenaida macroura* (self-invader since *c.* 1970)
Northern mockingbird	*Mimus polyglottos* (self-invader since *c.* 1970)
Barn owl†	*Tyto alba* (self-invader, arrival probably as early as 1958)

2. Extinctions

Elf owl	*Micrathene whitneyi graysoni* (not observed since 1932)
Socorro dove‡	*Zenaida graysoni* (extirpated in the wild by 1972)

*This heron population is land-based, feeding on scorpions, land crabs and other invertebrates.
†Regular breeding awaits confirmation.
‡Repatriation of small captive population planned by 2005.

of Socorro (details in Walter, 1998). This history of Socorro's avifauna is similar to that of the Galapagos, Cocos Island, and Mexico's Tres Marias' Islands: the resident endemic island bird communities appear very stable with no or low turnover rates except after disturbance. Again, this is not what ETIB models predict. The colonization, evolution *in situ* and persistence of life on Socorro and similar oceanic islands appear to be strongly dominated by physical resource factors supporting the 'ecological poverty' concept of Lack (1976).

Further evidence for a lack of an immigration-extinction driving force comes from the West Indies. The mtDNA analysis of the resident native birds of Barbados has revealed a history of intermittent invasion and colonization over a time span of 700,000 years. 'Each island population represents the descendents of a single founding maternal lineage' (Lovette *et al.*, 1999). Another molecular phylogenetic analysis of the colonization of all the Lesser Antilles by small land birds (Ricklefs & Bermingham, 2001) revealed that the number of lineages in the Lesser Antillean avifauna appears to be limited only by the rate of colonization, and the archipelago is not close to saturation. A paucity of pre-human extinction events among small birds was detected.

There can be little doubt that many tropical oceanic islands have maintained tropical climates and continuous tropical vegetation over time spans of millions of years (Mueller-Dombois & Fosberg, 1998). Islands such as Réunion, Mauritius, Guam, and the Hawaiian chain of islands are 5–50 Myr old. This time period was long enough to account for the evolution and persistence of endemic taxa, including entire families as well as extensive radiations.

Natural disturbance factors and successional processes have also been found to be responsible for the turnover and species accumulation of recently formed volcanic islands. The long-term empirical investigation of the re-establishment of plants and animals after the catastrophic eruptions of Krakatau island in 1883 has given us an abundance of data and successional sequences that do not fit MacArthur & Wilson's ETIB model. The data come from ferns, higher plants, reptiles, butterflies and birds (Bush & Whittaker, 1993; Whittaker & Jones, 1994; Whittaker, 1995; Thornton, 1996; Whittaker *et al.*, 1997). A continuing dynamic disequilibrium has existed for well over 100 years. The Krakatau data also point to the importance of natural disturbance regimes on islands in 'structuring colonization patterns and turnover' (Whittaker, 1995). A new study

of Long Island and Motmot Island provides evidence for a much slower colonization rate for these islands compared with Krakatau (Thornton *et al.*, 2001); extinction rates and turnover are very low after more than 350 years of existence.

The Motmot and Krakatau model of invasion and colonization differs from that of Socorro. Whereas the former are still at the early stage of island succession and colonization, and lie close to source areas with rich biodiversity of the tropical rainforest biome, the latter is old and quite isolated from a distant source region of the dry tropical forest biome on the Mexican west coast. The avifauna of Socorro can only be called *robust* and *stable* and has – with high probability – persisted as an entirely endemic community for millennia. The terms *robust* and *stable* should be understood as reflecting the status of the biotic community; I am well aware of the many physical changes and dynamics of volcanic islands. As long as the endemic taxa survive such changes with little turnover, the terms are justified. Life on such a small and xeric island is challenging for any bird species and colonization followed by speciation processes has only been possible for taxa that can tolerate the harsh physical and seasonal environment (Walter, 1998).

Lack of turnover and colonization

In order to examine the relevance of another aspect of ETIB – its focus on turnover ratios (Diamond & Jones, 1980) – I reanalysed the avifauna of the California Channel Islands (Walter, 2000) which lie close to the mainland but are not classified as recent land bridge islands. I divided the breeding land birds into three groups: endemic taxa (including single island- and archipelago-endemics) and their populations on eight different islands, non-endemic regular breeders and occasional breeders. Where did the turnover occur, and what might be responsible for it? Table 2 contains a summary of the data for the eight islands (Howell, 1917; Diamond & Jones, 1980). The overall persistence of the endemic and non-endemic land birds over at least 100 years has been remarkable considering the immense anthropogenic transformation and degradation of most of the islands. Both extinctions of endemics are directly related to habitat loss (one an island-wide wildfire on Santa Barbara Island). Only three other non-endemic regular breeding populations have disappeared out of 136 different island populations. Two exotic species (house sparrow *Passer domesticus*, starling *Sturnus vulgaris*) have not

Table 2 Populations of land bird taxa of the eight California Channel Islands

Occurrence	Single island endemic	Archipelago endemic	Non-endemic
Regular breeders	Six pop. of six taxa	40 pop. of 10 taxa	81 pop. of 25 taxa
Occasional breeders	0	Four pop. of two taxa	34 pop. of 19 taxa
Disappeared breeders	0	Three pop. of three taxa	Three pop. of three taxa
Extinct breeders	Two pop. of two taxa	0	0
New regular breeders	0	Two pop. of two taxa	18 pop. of 12 taxa
Total	Eight populations	49 populations	136 populations

Modified from Walter (2000) and Table 1 in Diamond & Jones (1980).

only colonized the California mainland but also some of the Channel Islands. The high turnover ratio originally reported by Diamond (1969) was mainly caused by the disappearance of raptors and seabirds because of human persecution and pollution of the marine food chain as well as by 19 species classified as occasional breeders (Table 2).

Does the latter group really matter as support for a basic principle of ETIB? As the islands are within easy reach of these bird species, are they not part of regional metapopulations and subject to their interannual population fluctuations in response to weather and resource variables? If a few blackbirds or robins are resident breeders 1 year and absent the next ('winking in and out'), can that tell us anything important about insular colonization processes?

Turnover studies of British islets (Diamond & May, 1977; Russell *et al.*, 1995) have analysed similar satellite island populations near large mainland source pools. The observed occasional breeding events resemble a weather station's recording of a trace of rain now and then that has no meaningful effect on soil moisture and vegetation growth.

In his review of ETIB case studies, Gilbert (1980) exempted the famous experimental zoogeography of the fumigated mangrove 'islands' of Florida (Simberloff & Wilson, 1970) from his critical evaluation. A brief comparison of the invertebrate reoccupation of defaunated mangrove patches to the short- or long-term colonization of Krakatau or Socorro shows that this experiment has little if any appropriateness and relevance to the functional processes of organic life on real islands. First of all, the mangroves were not cut down; their branches and leaves, indeed their biomass and resources, remained largely if not completely intact except for the sudden absence of all invertebrates. Then, the authors recorded gradual arrival and presence of invertebrate species from surrounding unaffected mangrove patches. If this were a simulation of island life and its dynamics, it would be akin to removing all birds, bats, or other island life forms from an island without disturbing its vegetation and other resources. The mangrove experiments are simply not applicable to oceanic and slowly evolving island ecosystems in general.

Species–area relationships

Islands – oceanic islands in particular – should probably not be a priority for species–area studies. Area size per se is obviously of great importance (but not necessarily the cause) for biotic diversity because a larger area – in all probability – increases space availability for higher abundance of populations, more resources, more habitats, more microclimates, etc.). However, differences among equal-sized islands in elevation, freshwater sources, habitat quality, geologic and human history complicate the relationship between area and species richness except in fairly uncommon circumstances where all factors other than area size are more or less identical. A key and still unresolved problem for all researchers is the human inability to fully understand and measure how different taxa evaluate and classify habitats in the landscape.

There are many exceptions to the typical species–area curve. The species richness of small islands may be relatively independent of area and isolation (Lomolino & Weiser, 2001; Lomolino & Smith, 2003). On larger islands, one of the most atypical datasets concerns the avifauna of the Canary Islands (Lack, 1976). An arid climate and volcanic soil and surface have drastically depressed bird and plant richness of Lanzarote and Fuerteventura compared with the other islands. Among land snails (see above, Solem, 1982, 1990) SAR are inverted on some oceanic islands. Differences in species–area relationships may provide important clues on the composition, history, and function of biotic communities on continents. An example is Keeley's (2003) comparison of Australian and Californian shrub communities.

Relaxation?

The term *relaxation* (Diamond, 1972) describes the process of biotic reduction to a readily predictable number in response to areal decrease; it is inextricably linked to ETIB and the equilibrium concept. Relaxation occurs when extinction rates outnumber immigration rates resulting in a lower dynamic equilibrium number. Recent land bridge islands have provided the bulk of the relaxation literature. I have avoided the term for three reasons: (1) the term conveys a positive process, even in its physical meaning, of attaining a point of balance although it results in the loss of species; (2) real islands, particular oceanic islands, lose and gain taxa for many reasons not directly linked to area (succession, disturbance, catastrophes, human impacts); and (3) the long time period required for an ideal natural relaxation regime exceeds thousands of years and is meaningless in triage-concerned conservation applications.

The new paradigms of a biotic world in disequilibrium and frequent disturbance (Brown & Lomolino, 1998; Whittaker, 1998) have no use for this concept. In my opinion, there is a neutral and perfectly adequate term available for all kinds of actual species loss in island and mainland landscapes: the corporate management process of *downsizing* the company and its employees seems to be a process analogous to areal shrinking as well as habitat loss and degradation resulting in lower biodiversity richness.

The rich and unique oceanic island

Steadman (1997a) estimates that the most abundant family of birds was the rail family (Rallidae) with possibly thousands of now extinct endemic and mostly flightless island species in the Pacific before human dispersal to Oceania. Current species lists from Hawaii and other Pacific islands represent therefore amputated remainders of once more diverse and richer island avifaunas. It is essential and logical that avifaunal turnover studies attempting to confirm a stated rule or theory of nature avoid all datasets potentially or actually modified by human impacts, and, in particular, recognize the full magnitude of direct and indirect anthropogenic landscape change and of

Table 3 Richness of selected bird orders and families on islands and continents

		Strigiformes	Psittaciformes	Falconiformes	Columbidae	Rallidae
A	Species richness, global	208	353	310	309	134
B	Monotypic, global (no subspecies)	105	197	187	154	79
C	Endemic, on single island only	34	32	22	31	19
D	Endemic, on more than one island	12	42	24	56	8
E	Polytypic, global (two or more subspecies)	103	143	123	155	55
F	Endemic, on single island only	0	14	2	5	5
G	Endemic, on more than one island	20	56	11	71	9
H	Subspecies richness, global	512	553	512	593	235
I	Endemic, on single island only	81	135	77	81	51
J	Endemic, on more than one island	86	137	107	224	59
K	Taxa occurring on mainland and island(s), global	49	31	102	64	36
Total taxon richness (B + H)		617	750	699	747	314
Total endemic monotypic species on islands (C + D)		46	74	46	87	27
Total endemic island species (C + D + F + G)		66	144	59	163	41
Total taxa endemic to single islands (C + I)		115	167	99	142	70
Total taxa endemic to more than one island (D + J)		98	179	131	280	67
Total endemic island subspecies (I + J)		167 (32.6%)	272 (49.2%)	184 (35.9%)	335 (56.5%)	110 (46.8%)
Total taxa endemic to islands (C + D + I + J)		213 (34.5%)	346 (46.1%)	230 (32.9%)	422 (56.5%)	137 (43.6%)
Total taxa occurring on islands (C + D + I + J + K)		262 (42.5%)	377 (41.6%)	332 (47.5%)	486 (50.2%)	173 (55.1%)

Compiled from data in Clements (2000) and checklist updates; data on non-endemic island occurrence of many taxa probably underreported in the literature.

other habitat disturbance on colonization and extinction processes (Whittaker, 1995, 1998; Haila, 2002).

A surprisingly large percentage of extant bird taxa belong to insular endemics. As an example, I offer relevant global statistics for owls (Strigiformes), raptors (Falconiformes), parrots (Psittaciformes), doves (Columbidae), and rails (Rallidae) using a recent checklist (Clements, 2000). A total of 213 (34.5%) of 617 owl taxa (105 monotypic species and 512 subspecies) are endemic to islands; of these, 115 taxa are confined to a single island (Table 3). The order Psittaciformes has 353 species with 553 subspecies; 346 taxa (46.1%) are only found on islands. Pigeons and doves are even richer on islands: 422 or 56.5% of 747 taxa are confined to islands around the world (Table 3). Islands in general contribute a more significant share of global biodiversity than commonly recognized: the importance of islands for mammals compared with the biodiversity of the Amazon lowlands can be shown with these figures: true islands only represent about 1.97% of the earth's surface but have 697 (14.1%) mammal species while the Amazon has 3.54% of surface area and only 8.8% of the world's mammal species (Alcover *et al.*, 1998).

Insular radiations of many plant and invertebrate taxa are well known. They contribute unique and substantial diversity lacking on the mainland. The attribute of impoverishment given to many islands has to be qualified and complemented with the abundant evidence of their extraordinary contribution to global biodiversity.

FUNCTIONAL ISLAND SPACE

The reappraisal of islands has emphasized biotic attributes and processes on islands that cannot and should not be squeezed into the statistical straitjacket of ETIB concepts. I will now approach life on islands from a functional and island-centric perspective in order to examine and highlight the difference between oceanic islands and mainland isolate patches.

Most of the endemic taxa of oceanic islands are not aware of the existence of anything else such as other islands or a huge mainland. Their universe is absolutely bounded by the island perimeter: the island is their ancestral and current home or place! Turnover without human disturbance would only be of minor importance considering the fact that it has probably taken at least a million year or so of island ecosystem stability to facilitate the evolution of most island endemics. Endemic island taxa have been selected for and are adapted (only) to the unique functional environment of the biocoenosis and the physical landscape existing on their island or archipelago. Such taxa are truly *insular* because they exhibit *functional insularity*; obvious examples are Hawaiian land snails and crickets, flightless birds such as Pacific rails, ducks, geese, and the extirpated dodo (*Raphus cucullatus*) of Mauritius. They can only survive in their insular geographical space where they are isolated, confined to small terrestrial land areas, exposed to island and maritime climate factors, co-existing with a unique assembly of other insular taxa including aerial (owls, hawks) but often no native mammal predators and carnivorous ants; most of all, they are protected from many continental abiotic and biotic factors. As a general definition, functional insularity exists wherever a taxon's persistence does not require immigration from outside its island range.

Functionally insular taxa are not 'sink' species (Rosenzweig, 1995, p. 211). Unique selective forces and reproductive strategies of insular life are commonplace; they have been dealt with in great detail [for plants, see Carlquist (1974) and

Table 4 Major factors of biotic existence on oceanic islands

Evolution on oceanic islands
  Isolation
  Small size
  Protection
  Natural selection in island 'theater'
  Adaptation to island environment
Functional insularity
  Limited landscape diversity
  Disharmonic biotic communities
  Survival of old relict taxa
  Depauperate species richness
  Lower predator diversity
  Lower disease and parasite diversity
  Generalist habits and niches
  Modified morphologies
  Unique radiations
  Endemic taxa, unique life forms
  Restricted range

Mueller-Dombois & Fosberg (1998); for animals, see Williamson (1981) and Lack (1971)]. Table 4 summarizes some of the key factors of insular existence that are shared by many but not necessarily all oceanic islands.

The *Eigenplace* concept

The foregoing discussion of the functional role of confined and bounded insular existence provides a characteristic example of functional biotic space; I will use it as the cornerstone for a new biogeographical concept. The biotic space of a single taxon (usually a species, but applicable also to subspecies, populations and even individuals), is called its *eigenplace* defined as *the functional spatial complex sustaining a taxon*. The eigenplace of a species is more than the species-specific *Arealsystem* of Müller (1977, 1981) and earlier areographic definitions of the species *area* (de Lattin, 1967; Rapoport, 1982). The eigenplace of a taxon includes every *spatial pattern and process* as part of its functional relevance for persistence. For example, climatology, landscape heterogeneity, current dispersion and dispersal (vagility), historic dynamics of local, regional and global distribution area, metapopulation structure, and reliance on particular substrates or mutualism are some but certainly not all factors defining an eigenplace. The latter is the spatial component of the *ecological niche,* probably close to but more explicitly functional than the structural niche of Grinnell (1917, 1928), as defined and discussed by Shugart (1998).

It makes sense to separate and amplify the functional spatial complex of a taxon's ecological niche for several reasons: (1) place as a physical reality is a real evolution, existence, and survival factor – widely ignored in evolution and ecology, (2) geographers study the nature and function of place; (3) real-life mappable distribution factors acquire real meaning for planners and decision-makers while other niche dimensions

usually do not; and (4) large-scale spatial components (islands, climate zones, biomes) have played a dominant role in the development of conservation biology and global biodiversity classifications.

The composite noun *eigenplace* means: (1) The German prefix *eigen-* confers the notion of belonging to, of being owned or produced by a particular person or object (which is exactly the intended meaning). Examples are *Eigenheim* (one's homestead, your own house), *Eigentum* (one's property) and *Eigentor* (a self-goal in soccer). (2) *Place* is a key concept in geography, particularly in modern regional, cultural, and behavioural geography (Livingstone, 1992); it is not a synonym for space – this was beautifully expressed by my former Berkeley mentor *James J. Parsons* who is said to have exclaimed: 'Place, that's it. Place not space' [...is what geographers study] (Denevan, 2000).

Each taxon has and creates its own eigenplace because no two taxa will function in an identical way in a particular spatial arena composed of physical, biotic and cultural properties, processes, and histories. Anything of spatial relevance to the taxon may be part of its eigenplace. The endemic bird taxa of the Galapagos and Hawaii are classic examples of island-defined eigenplaces as are those of all endemic island taxa. By contrast, the spotted owl (*Strix occidentalis*), California condor (*Gymnogyps californianus*), white stork (*Ciconia ciconia*), and grizzly bear (*Ursus arctos horribilis*) are continental and quite different examples of well known eigenplaces. This includes the access to landscape resources such as terrestrial and water habitats, breeding places, resting and refuge locations, dispersal routes, migration corridors, wintering regions, etc. An interesting eigenplace is that of the Swainson's hawk (*Buteo swainsoni*): its modern breeding range is confined to only a part of western North America where it prefers open habitats of grassland and agricultural landscapes. It migrates to northern Argentina in the austral summer feeding on insects in similar habitats (Canavelli *et al.*, 2003). This hawk is currently exposed to and increasingly dependent on highly modified and often chemically enriched lands managed by agribusiness interests.

Measurement and rank of eigenplace

Important components of the eigenplace are well known for many wildlife taxa. Wildlife management students have carried out exhaustive studies on many game and endangered species resulting in very elaborate and quantitative measurements of wildlife-habitat relationships (Morrison *et al.*, 1998). Population-level responses to landscape factors and the modelling of these relationships can provide valuable information on the spatial complex sustaining a taxon (McCullough, 1996; Bissonette, 1997). The 'biodiversity hypercube' model of Hollander *et al.* (1994) goes far in integrating spatial and ecological niche components into a regional planning scenario. The use of spatially explicit population models (SEPMs) may assist in a better understanding of taxon space use and dispersal (Macdonald & Rushton, 2003) while response surface

models can display intraspecific adaptations of plants such as *Pinus ponderosa* to varying environmental conditions across its range (Humphries & Bourgerou, 2003). Finally, more and more phylogeographical analyses include a reconstruction of the historic areographic dynamics of taxa; a fine example concerns the California thrasher (*Toxostoma redivivum*) using nested-clade analysis of mitochondrial-DNA variation (Sgariglia & Burns, 2003).

What is of interest here is the interface between place and taxon: how does it differ between taxa, and how place-dependent is a taxon in its entirety? This means looking at the global distribution area independent of state and country boundaries. As a first order estimate of eigenplace I have selected six spatial taxon variables that contribute to a geographical expression of the eigenplace: the history of distribution, current distribution area, dispersion within the area, vagility, isolation, and location reliance. We can assign five attributes or values to each of these variables and rank a taxon in comparison with other taxa at the same taxonomic level or ecologic function. This constitutes a basic qualitative index of eigenplace parameters that confers a notion of the survival importance of the geographical place occupied by the taxon. A high ranking of this *eigenplace index* indicates a strong dependence on specific meso- and macroscale landscape variables present within its area for the persistence of the taxon; a low ranking generally means that the taxon possesses some spatial independence, habitat flexibility, and adaptability in its survival quest. *Appendix A* contains a detailed explanation of the six spatial variables, the calculation of the index, and examples of the ranking of selected bird species.

THE MAINLAND DIFFERENCE

Continental taxa have evolved in a different spatial 'theater': they are immersed in a dynamic and pulsating physical and biotic landscape setting that is vastly more complex, variable, and rich in potential mortality factors than insular space at similar latitudes. The isolation of the island – serving as a powerful shield against continental invaders and other factors of change – is absent thereby exposing mainland populations and communities to a multitude of within-habitat, edge, and 'matrix' factors unknown on pristine oceanic islands. Climatic and other environmental extremes create higher environmental uncertainty than found on most islands. Higher species richness includes more predators, disease organisms, mutualisms, and direct competitors. On the contrary, the continental expanse offers significantly enhanced survival opportunities. Faced with this complexity of continental life what functional geographical space is needed by a mainland taxon for viable persistence?

Functional continentality

Many, perhaps a majority of continental taxa have used the large or even vast continental surface. Since the last Ice Age, many European species have moved their range margins between 200 and 2000 km (Huntley, 1998). Some North American mammals that had overlapping ranges just a few thousand years ago often have non-overlapping ranges today. Large territories, low densities, long-distance migrations, and extensive spacing behaviours are other spatial characteristics of a typical continental taxon (Table 5). Even in ecological time there is a lot of movement of species ranges and reshuffling of communities as evidenced by European and American bird breeding census data. Berthold (1993) analysed the changing avifauna of Central Europe over the last 120,000 years. He documented dramatic changes caused by a massive inland glaciation pattern, the subsequent warming and deglaciation, the settlement and transformation of natural landscapes by humans, and the recent warming of regional climates in the twentieth century. Many partial migrant birds have ceased migration altogether or have shifted their migration routes and winter quarters to take advantage of milder winter climates. European and North American tree species have also completed continent-wide migrations since the last glaciation (Huntley & Birks, 1983; Sauer, 1988; Hengeveld, 1990).

The evolution and allopatric distribution of North American songbird species goes back millions of years. Klicka & Zink (1997) studied the mitochondrial DNA divergence values of 35 songbird species pairs. They found that 25 of them diverged at least 2–5 Ma, and the most recent split or taxon divergence occurred some 300,000 years ago in the myrtle and Audubon warbler pair (*Dendroica coronata coronata* vs. *D. c. auduboni*). This means that the ranges of these species are likely to have moved about the continent multiple times during glacial and interglacial intervals. A sample study area of 100 km² in Pennsylvania, Iowa, or Oregon must have seen a dramatic succession of different biomes, dominant plant species, and invertebrate and vertebrate fauna since the last Ice Age – a time span of a relatively short period of only 18,000 years. Compare that to the relative constancy of climate, vegetation and fauna of most tropical oceanic islands during glacials and interglacials.

Table 5 Major factors of biotic existence on continents

Evolution on continents
No or temporary geographic isolation
Huge connected area
Exposure to diffuse *physical* extinction factors of mainland
Exposure to diffuse *biotic* extinction factors of mainland
Natural selection in mainland environment
Adaptation to mainland 'theater'
Functional continentality
Mainland taxa, characters, niches, diversity, rarity, and complexity
Highly dynamic geographic area over time
High connectivity or linkage (source-sink, meta, contiguous)
High competition
High predation
Often large territories
Often huge range size
Considerable environmental uncertainty possible

Continental communities are also spatially less stable and more turnover-prone at a given location (not necessarily over their entire range) than corresponding insular biotas because they can dynamically respond to a changing regional and global environment. Central to continental distribution is a strong need for connectivity of populations and habitat linkages that allow taxa to survive and maintain their genetic and demographic identity in a generally open and essentially borderless mainland setting. These attributes add up as a definition of *functional continentality* (Table 5).

THE INSULAR-CONTINENTAL POLARITY

We can now attempt a general comparison between the functional areography of islands and continents. MacArthur & Wilson (1967) had proclaimed the validity of their insularity concept on both islands and mainlands without any clarification or elaboration of a difference between the nature of island insularity and mainland insularity. In fact, they argued that 'the same principles apply …to formerly continuous natural habitats…' on continents (pp. 3–4).

First, we use a basic model of taxon distribution in time and space. It focuses on three components: the area *occupied* (O) by the taxon (the entire distribution area at specified points in time), the potentially *occupiable* area (P) that the taxon does not occupy at this time for one reason or other, and the area on earth that is *unavailable* or unoccupiable by the taxon (U). The dimensions of the latter two components are often unknown because only the taxon's past or future expansion or contraction processes can demonstrate the magnitude of the potential distribution area. The relationship between the three spatial components can be displayed as a histogram; this *OPU* model is dynamic as the relations between the three components may change over time because of biotic and abiotic driving or limiting factors (Fig. 1). The histogram serves as a general answer to Müller's (1977) question: 'Where is the species present, and where is it absent?' Many of the new grid-based bird atlases contain detailed presence–absence information and may even offer data on species abundance in central and peripheral range areas (Devillers *et al.*, 1988; Hagemeijer & Blair, 1997).

Continental taxa may show much P that they cannot occupy because of barriers preventing colonization, temporal constraints, or other reasons; they may also show considerable O and P variability over time as a result of range expansions and contractions prompted by glacial advances and other driving factors of global change. By contrast, endemic island taxa possess *OPU* components that often occupy the entire available island space over evolutionary time; they have essentially no P at all and a huge U as the rest of the earth constitutes an unavailable area. Endangered taxa commonly show an *OPU* histogram with vastly declining P and O sectors. The success of many exotic species in their secondary area on newly invaded continents, such as house sparrow *Passer domesticus*, starling *Sturnus vulgaris,* and various pine (*Pinus* sp.) and acacia (*Acacia* sp.) species,
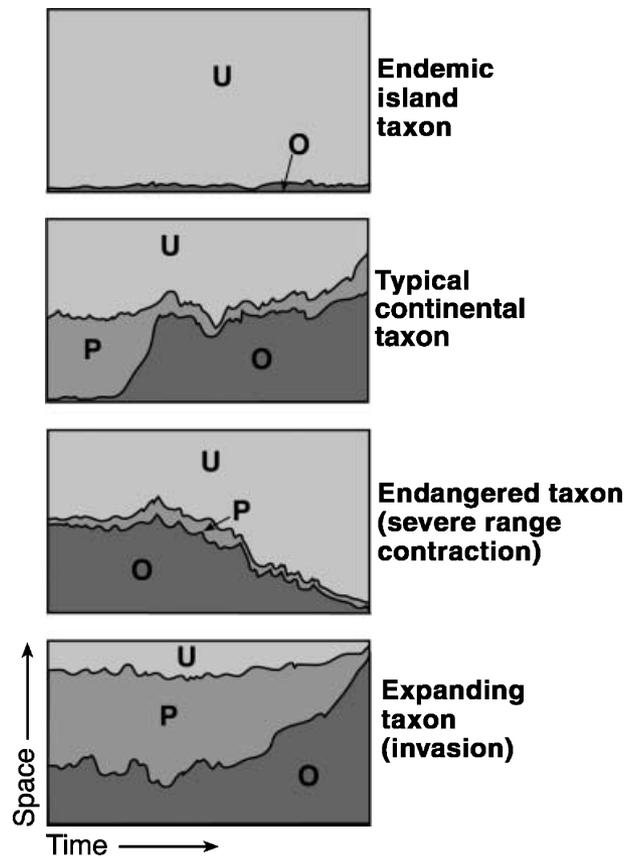

Figure 1 Areographic histogram of spatiotemporal dynamics of biotic space. Note that a typical small island endemic taxon lacks the P sector (potential distribution area) because of its functionally confined persistence on its island.

Table 6 Functional polarity between oceanic islands and continents

	Undisturbed* insular biotic communities	Undisturbed* continental *local* biotic communities
Stability	High	Low/variable
Turnover	Low	High
Colonization	Low	High
Extinction	Low	High
Resistance	High	Variable
Evolution	High/variable	Low/variable

*Prior to human impact of any kind.

offers excellent lessons about the temporal dynamics of O, P and U.

Secondly, when assessing commonly used parameters of evolutionary and community ecology (Pimm, 1991) from an areographic perspective, a strong difference emerges between oceanic islands and continents when we compare relevant data from undisturbed (!) island systems to mainland biodiversity (Table 6). The contrasting parameters appear to justify the

emphasis placed here on functional insularity and continentality. For an understanding of the planet's biodiversity this functional biogeographical contrast existing between islands and continents is of fundamental importance and relevance.

There is a gradient of eigenplace sets from isolated oceanic islands to strictly continental or cosmopolitan distribution areas. In between are taxa that occur both on some islands and continents as well as continental relics occupying restricted isolate mainland areas. The functional areographic perspective therefore establishes a pronounced *functional polarity* gradient between insular and continental taxa.

APPLICATIONS OF ETIB AND EIGENPLACE CONCEPTS

We shall now apply the knowledge gained from the re-analysis of ETIB and from the functional spatial concept of insular-continental polarity to real world problems endangering the conservation of nature. The still popular transfer of the insularity concept of ETIB to mainland environments (Quammen, 1996) has probably greatly contributed to the development and long persistence of the ETIB paradigm. We will assess the suitability of fragmented habitats and of parks and nature reserves for ETIB application; in addition, continental islands as well as areas with relict or otherwise restricted taxa will be scrutinized for features of insularity.
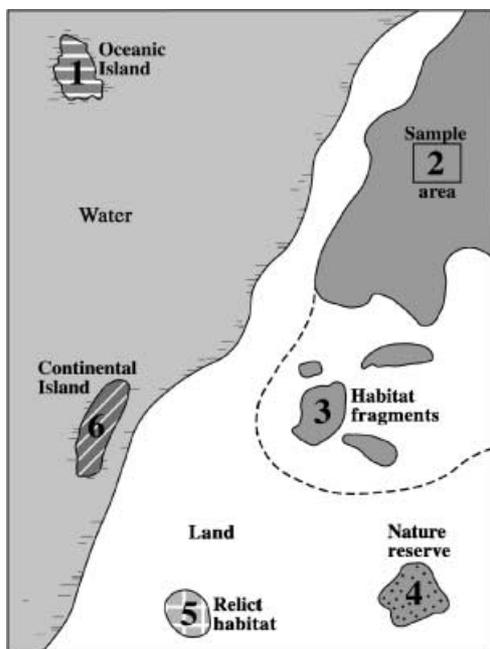

Figure 2 Generalized map of six terrestrial study sites of similar size with different biotic spaces: (1) an entire oceanic island, (2) a sample landscape patch within a contiguous unfragmented habitat, (3) a landscape with fragmented habitat isolates, (4) a nature reserve or national park, (5) an isolate patch with unique properties supporting a relict habitat and taxa, and (6) a continental (land bridge) island.

Figure 2 depicts six landscape patches containing terrestrial biotas. The persistence and eigenplace characteristics of patch no. 1 (pristine oceanic island) and patch no. 2 (sample study area in a contiguous mainland habitat landscape) have been discussed above as examples of the I-C polarity. The probability of long-term survival of their biotas remains high in the absence of disturbance and catastrophic events because they maintain functional insularity and continentality. Can the same be said for the biotas of the remaining landscape patches (nos 3–6)?

Biota in habitat fragments and remnants

Because of widespread habitat loss and degradation more and more taxa are confined to fragments of grassland, chaparral, or forested landscapes. ETIB has been applied to many fragmentation studies. Of particular prominence has been the first of a series of publications on the avifauna of chaparral fragments in urban San Diego (Soulé *et al.*, 1988). It attempted to relate fragment size and time since isolation to a small set of 'chaparral birds' without looking at habitat history (last fire, last major disturbance?), edge effects, species-specific dispersal potential, etc. In other words, it was a classical non-functional assessment of the urbanized landscape and its birds. Subsequent papers on the same subject (Kraus *et al.*, 2003) have been more circumspect; Crooks *et al.* (2001) include population density estimates and observations of fragment recolonizations. They concede that 'given the ecological heterogeneity of these birds, idiosyncratic autecological features of individual species must be considered in the design of conservation measures for these species in fragmented landscapes'. A recent and comprehensive study of the urban bird fauna of Vancouver, British Columbia, has confirmed the complexity of individual species responses to the interdigitated habitat patches and gradients of urban and suburban landscapes (Melles *et al.*, 2003). ETIB concepts including area and isolation variables failed to model and predict the size of colonies ('towns') of black-tailed prairie dogs (*Cynomys ludovicianus*) in Oklahoma (Lomolino & Smith, 2003).

Any habitat-dependent continental population trapped in habitat isolates faces oblivion unless it can remain viable with a minimum of available resources provided by the isolated habitat and/or maintain connectivity with subpopulations in adjacent fragments or patches. All other populations, particularly large-sized, naturally rare and widely dispersed ones are likely to vanish from small fragments because of their inability to maintain connectivity with other populations. Figure 3 illustrates the potential diversity of spatially defined avian territorial occupants that can be expected in and around mainland habitat fragments, a far more complex spatially-defined community than would be found on an undisturbed oceanic island. Some of the principal differences between oceanic islands and habitat fragments are listed in Table 7.

Quite a few studies have insisted all along that habitat *fragments are in fact not islands*. Considerable insight into the complexity of biotic fragmentation is shown by Schelhas &
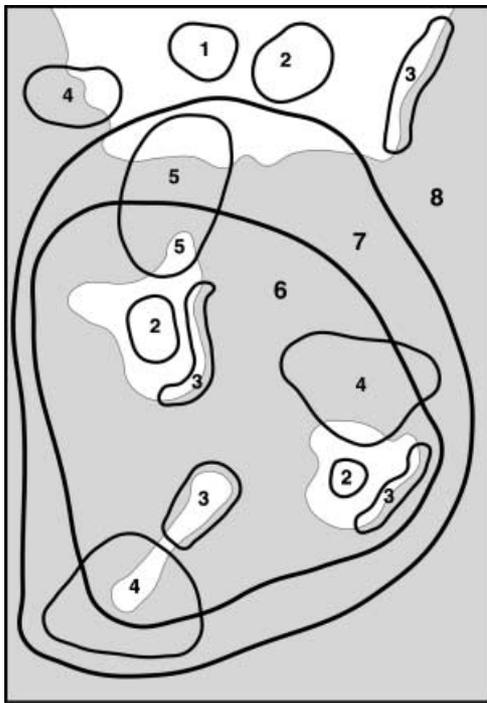
Figure 3 Functional avian territorial or home range sets which may occur in and near habitat fragments: 1 = interior habitat specialist, 2 = habitat specialist, 3 = edge specialist, 4 = environmental *matrix* specialist and edge intruder, 5 = habitat linkage-dependent taxon, 6 = metapopulation-dependent taxon, 7 = interior habitat-avoiding generalist, and 8 = habitat generalist.

Greenberg (1996) and Laurance & Bierregaard (1997) who focused on tropical forest remnants. A broad review of avian habitat fragmentation effects can be found in Newton (1995). An excellent collection and review of European case studies focusing on fragmented plant and insect populations can be found in Amler *et al.* (1999). All of these studies and datasets are consistent with the island-derived eigenplace concept and the I-C polarity. Anthropogenic fragments and remnants may constitute a survival threat for many taxa, lead to non-viable population levels, and exceed historical adaptations of the spatially dynamic mainland eigenplace to naturally changing environments.

Summarizing, the biota found in continental habitat fragments do not possess *functional insularity*. Rather, populations of various continental taxa have been spatially isolated so that their functional continentality is impaired or curtailed because required linkages and spatial elasticity have been threatened or already lost. *Remnant habitats* are the terminal stages of fragmentation processes and habitat loss; they are by definition continental isolate patches without their former connectivity to similar habitats. As Haila (2002) points out 'forest remnants, as remnants, have no evolutionary history at all'. For conservation biology, typical continental biota reduced to existence in such remnant habitats must be given a high priority status for protection since they are unlikely to persist for long in tiny geographical isolates (Laurance & Bierregaard, 1997; Stattersfield *et al.*, 1998).

National parks and nature reserve isolates

It has become fashionable to apply island biogeography to the design and development of natural reserves and national parks. Wilson & Willis (1975) formulated geometric principles for the design of natural reserves in a paper entitled 'applied biogeography'. Diamond (1981) suggested that East African montane forest reserves function like oceanic island analogues. Soulé *et al.* (1979) developed a model of 'faunal collapse' for the game reserves of East Africa based on ETIB. Faaborg (1979) proclaimed that the application of island principles to conservation practices and the design of nature reserves constituted a 'crowning achievement'. He proceeded to compare neotropical land-bridge islands avifaunas to mainland patterns and drew 'lessons for conservation'.

Newmark (1995, 1996), applied the ETIB model to continental situations, particularly national parks in North America and East Africa. He found an inverse correlation between park size and the extinction of some mammals over a relatively brief historic time span. This statistical analysis neglected to account for with-in park anthropogenic disturbance, climatic variables, edge problems, and other mainland variables that might have affected the park ecosystems and individual mammal populations. If a mammal population disappears from a western North American National Park it may not because that park is an 'island' as perceived by Newmark; rather it may be because it has become a *continental isolate* and some of its taxa have lost their functional continentality because of barriers, loss of linkage, etc. Woodroffe & Ginsberg (1998) show that large carnivores in reserves suffer from higher mortality in the border areas: 'The species most likely to disappear from small reserves are those that range widely – and are therefore most exposed to threats on reserve borders – irrespective of population size'. Another problem facing any comparison with historical range maps is the potential inaccuracy of these maps (Habib *et al.*, 2003).

Natural reserves and national parks in mainland landscapes are usually administrative land parcels that function as continental isolates for their biotic communities. They are similar to fragments and remnants in the functional context; they are neither homologues nor analogues of oceanic islands and their biota as Janzen (1983) emphatically declared: 'No park is an island'. As Pain & Donald (2002) point out, 'reserves cannot be viewed in isolation, as many activities and population processes taking place outside protected areas can adversely affect conditions for species within protected areas'.

Rather than using ETIB concepts as a predictive baseline for the fate of reserve-limited biota, insights from fragmentology and landscape ecology (Forman, 1995) are more likely to improve the understanding and management of biotic communities isolated in nature reserves and national parks. In the

Table 7 Differences between an oceanic island and a continental habitat fragment

Property or process	Island	Fragment
Geography	Isolated piece of land surrounded by 1000 km of water in all directions	Broken off piece of a once large habitat or land unit on the mainland
History	Millions of years old	Several decades old
Areal dynamics	Stable in ecological time	Sudden shrinkage or gradual contraction and separation from other habitat patches
Edge	Saltwater matrix	Uniform or diverse types of habitats surround the fragment that differ from it
Ecotone	None: you are either on the island or in the water	One or many depending on landscape composition
Predation	Low: most predators absent (non-volant mammals, carnivorous ants)	High: most predators are present (easy access from edge)
Stability	High except after disturbance event (from outside or volcanic eruption)	Low because of downsizing of community: large, rare, and specialist species likely to vanish from fragment
Evolution	Endemic taxa, even unique radiations possible	None: fragment may contain viable and non-viable populations of continental taxa
Invasibility	Negligible except with human support; water barrier highly protective	High because of edge effect and proximity of surrounding matrix
Robustness	High: supports all of its insular biodiversity over long-term	Low: cannot support animals with large home range; ecological decay of habitat because of edge effect
Succession	Normal stages within island ecosystem	Arrested succession: old growth will die out

end, the preservation of nature in parks will, however, be determined not only by science but by social, cultural, and political means and strategies (Terborgh *et al.*, 2003).

Restricted range species and relict habitats

Taxa *endemic to restricted areas* on continents (narrow endemics) often co-occur with other endemics in the same restricted, rare or relict landscape patch (Fig. 2). Again, ETIB does not apply here. The eigenplace of these taxa exhibits a unique functional continentality that has evolved and survived on a particular substrate or some other spatially limited resource. Thus, connectivity may be unimportant or irrelevant to their survival; the taxa have successfully coexisted with a host of continental extinction factors. As long as their particular eigenplace – however small it may be – remains intact, these taxa are likely to persist (as they have over the millennia). Many tropical bird species exist only in EBAs (Endemic Bird Areas) of < 50,000 km^2 (Stattersfield *et al.*, 1998). Many plant taxa are endemic to particular soils and substrates such as those found on serpentine soils and ultramafic rocks (Kruckeberg, 1984; Chiarucci *et al.*, 1995). Unfortunately, recent anthropogenic disturbance, degradation, and outright habitat loss have become a nearly universal problem for these taxa.

Continental islands

Continental (land bridge) islands have often been compared with habitat fragments. They resemble the latter in some respects: their limited size and disconnection from the mainland will result in similar biodiversity losses and downsizing over time as can be experienced in continental remnant habitats. ETIB proponents have used the 'relaxation' of land bridge islands since the end of the last Ice Age as a key argument for applying ETIB principles to nature reserves (Faaborg, 1979; Soulé *et al.*, 1979). However, the different nature of the surrounding matrix – the seawater barrier – keeps many continental mortality factors affecting mainland fragments off the island, potentially lowering the extinction rate compared with what might occur at the place–taxon interface of a mainland remnant isolate. In addition, there is no terrestrial edge effect. Often, there are no endemics on such islands but some island populations may have become independent from their mainland conspecifics thereby achieving full functional insularity. In other cases, continental islands may harbour relict taxa already extinct on the mainland or taxa that only exist on islands regardless of their connection to a mainland (white-crowned pigeon *Columba leucocephala* in the Gulf of Mexico). Thus, continental or near-shore island biotic space must be considered separate from that of oceanic islands as well as from any mainland isolate patch.

DISCUSSION

MacArthur & Wilson (1967) were correct in stressing the importance of islands. The wealth of new studies and theories on island biodiversity that have recently been published is astounding [see the special issue of the *Journal of Biogeography*, **29** (5/6), 2002]. Islands around the world offer and demand much more from biogeography than a simplistic ETIB model can accomplish. In a post-modern sense, the evidence of the past 40 years amounts to a multi-level deconstruction of traditional island biogeography and its *mismeasure* of islands.

Limited validity of island concepts

An important element of the deconstruction of the ETIB paradigm is the increasing evidence for the *limited applicability* of the biogeographical database. First of all, there is the taxonomic conundrum, mentioned above. A pattern or process may be statistically highly significant for birds but not for frogs or butterflies; a look at the world from the point of view of a Pacific land snail confined to the island of Rapa in the remote Austral Islands (14.2 km^2, 100 species; see Solem, 1982 & 1990) would show that many continental regions (large desert areas, boreal regions) appear highly impoverished compared with the Polynesian snail fauna.

Secondly, there has been a tendency to generalize findings from local and regional environments and to accord them universal validity or significance. For instance, much of our knowledge on island birds comes from excellent field work conducted on temperate islands near Britain. As the interface between place and birds is inherently diverse and complex in different parts of the world we should look at both the birds *and* the places in order to understand the interface. In terms of birds, Britain has approximately 191 breeding bird species (Peterson *et al.*, 1983). Australia has 581 breeding birds (Simpson & Day, 1984), and tropical countries such as Kenya and Venezuela have 1084 and 1381 recorded species respectively (Zimmerman *et al.*, 1999; Hilty, 2003). Britain is clearly impoverished, lacking a substantial number of mainland European birds (Sweden has 250 breeding species) as well as many important tropical bird families. In terms of place, Britain itself and the surrounding minor isles are continental land bridge islands that are so fundamentally different from tropical Socorro, Montserrat, Réunion, or Maui – they lack long-term *in situ* evolutionary processes and unique taxa, and may have been impacted by severe glaciation – that we would be well advised to label as limited or partial biogeographical knowledge what we have learned from them. MacArthur (1972, pp. 199–226) was keenly interested in the tropical-temperate/arctic differences of island and mainland biotas. My own island experience, particularly on Socorro Island, has strengthened my conviction that a study of a few temperate bird populations on a tiny North Sea island cannot accomplish much for our understanding of tropical island biosystems. First, the birds themselves are just too different, and secondly, the island ecology and geography is rather non-comparable. In order to attain a broader understanding of latitudinal and longitudinal differences it might help to use a place-centric approach: the biota of islands at different latitudes or hemispheres, and with different historical spatiotemporal complexes, have unique characteristics that over time have added up to the existing diverse reality of inter-island biodiversity.

My intention here is not to roll back island biogeography to the nineteenth century but to recognize that ETIB and similar simplistic concepts of global island biogeography have missed their mark; thanks to intensive exploration, improved range maps, and computerized datasets we can document today that island biodiversity is richer and more complex than classical biogeography told us: while there are sets of islands exhibiting similar patterns and processes (each of which can be modelled) there are also numerous exceptions and unique eigenplaces that do not fit into simplistic models of the taxon–place interface.

Inappropriate models and data

The definition of functionally insular oceanic islands subject only to natural physical and biotic forces over space and time provides an unerring baseline against which all other distribution systems can be compared. Ingenious yet inappropriate has been the attempt to simulate the biotic dynamics of islands and archipelagoes through short-term and small-space experimental zoogeography of mangrove patch defaunation (Simberloff & Wilson, 1970, see above). Inappropriate as well has been the tendency of ecologists to treat island taxa as numerical units only (from eagles to hummingbirds) as if we were dealing with golf balls differing only in color or texture (see Sauer, 1969). Counting how many species are present, irrespective of size, guild, age, taxon uniqueness etc., can only be a first step in assessing the biodiversity of an area. A functional approach to biogeography has to deliver more than comparisons of species numbers.

The problem of incomplete or compromised datasets is serious as well. There are only very few islands left on earth without major impacts on their pre-human physical and biotic nature. We have replaced the natural landscape in most parts of the earth with the cultural landscape (how natural is Britain?) that is often rather similar to but sometimes profoundly different from a pristine and human-free environment. For all practical and theoretical purposes biogeography today and tomorrow takes place in an anthropogenic setting everywhere.

Küster (1995) shows great insight and breadth in analysing and explaining the many historic impacts on the landscapes of Central Europe where the landscaping effects of Roman and medieval land use practices are still visible today. Similarly, the Mediterranean maquis landscape developed and has maintained itself because of logging, burning, and livestock-browsing activities (Walter, 1970). In South America, vast areas of now treeless slopes of the western Andes were forested prior to western colonization (Gade, 1999). Thus, significant environmental change has been a strong natural as well as a human-generated attribute and process of continental lands over significant time scales.

Even dispersal cannot be considered a purely natural phenomenon anymore. The oceans are filled with ships serving as rest stops or passive dispersal vehicles; on land, automobiles and planes move biota around at ease. We may never again study a pristine and complete dataset. Biogeographical concepts and analyses will have to be modified for this new playing field; it will be of critical importance to understand the role cultural landscapes play in the taxon–place interface. Modern landscape ecology (Forman, 1995) can assist with this task.

Loss of eigenplace

The functional polarity between insular and continental eigenplace provides a focus of considerable relevance for basic research and for application in conservation science. On many islands, functional insularity has been lost because the protective barriers to dispersal and invasion have been breached or removed. Effectively, most islands today have been connected to continents, even to the entire biosphere. This has already resulted in thousands of documented vertebrate extinctions in historic and prehistoric times. 'Too many alien species have been introduced and too many pieces of the puzzle are missing to ever restore it to the way it was' is a statement on the current status of the biodiversity of Guam (Conroy, 2001). In Polynesia, current island diversity patterns and processes are very different from natural. They have been 'altered irreversibly' by 3500 years of human presence (Steadman, 1997a). This is particularly true for pigeons and rails who are so richly represented on islands (Table 1). A total of 52 of 61 globally threatened pigeons and doves are island endemics (Stattersfield & Capper, 2000). The human-caused downsizing of insular biota extends to mammals as well. Anthropogenic extinction events 'affected at least 27% of autochthonous mammal species on the world's oceanic and oceanic-like islands' (Alcover *et al.*, 1998). ETIB cannot provide any guidance for this significant threat to island biodiversity. In general, the restoration and maintenance of *functional insularity* should be the ultimate objective of island conservation efforts. In practice, this is an extremely ambitious and difficult goal considering the current status of most islands today.

The *loss of functional continentality*, i.e. the inability to adapt occupied space to the multiple physical and biotic limiting factors of a continental environment, can be considered a fundamental conservation problem of mainland biodiversity today. Although some scientists and agencies have applied ever more sophisticated conservation strategies (from MVP, Gap Analysis, metapopulation, bioreserve concepts to adaptive management and coarse filter approaches) the complexity of dynamic continental space for individual taxa and entire communities appears to have been widely ignored and under-researched so far. It is therefore laudable that a major conservation initiative ('The Wildlands Project') has developed scientific foundations for Regional Reserve Networks that aim at restoring and preserving the continental connectivity of natural ecosystems across North America (Soulé & Terborgh, 1999*)*.

It is likely that the increasing loss, degradation, and fragmentation of biotic space on islands and continents pose far more serious extinction risks than could have been predicted by ETIB. The latter's focus on area and distance (1) minimizes the profound functional differences between islands and continents as places of biotic evolution and persistence, (2) for mainland biotas, ETIB does not account for numerous powerful mainland extinction factors that must be added to area and isolation factors, and (3) for island biotas, extinction threats from exotic invaders (Guam), deforestation (Mauritius, Cape Verde Islands), disease (Hawaii) and other anthropogenic factors appear to be operating quicker and more effectively as extinction factors than shrinking island size or increasing isolation. The loss of functional insularity shared by so many island taxa today is better understood and documented than its mainland counterpart because we have solid zoo-archaeological evidence of prehistoric and recent extinctions that serve as proof for the efficacy of extinction factors operating on islands. On the mainland, local extinction factors appear to be often and temporarily compensated for by regional range dynamics and new habitat creation (often with human assistance such as forest plantation projects) thereby masking ongoing extinction processes.

Application of the eigenplace concept

We have defined eigenplace as the functional spatial complex sustaining a taxon. What does this mean for biogeographical theory, and how can it be applied to the conservation of nature? In terms of theory, it forces the biogeographer to pay full attention to the geographical place that constitutes the totality of its occurrence on the earth. The concept is less concerned with evolutionary questions and perspectives that have dominated biogeography; rather, it employs a forward-looking perspective that asks: If I understand the functional spatial complex (really the place–taxon interface) today where will this taxon be in the near or far future? One of the benefits is the holistic approach to species conservation. For example, it may provide a much-needed unbiased counterweight to conservation measures for species that do not require such human assistance for taxon survival. Currently, many species and subspecies receive substantial financial and manpower support in some countries where they are rare although they are not threatened in a global sense at all. Examples are the osprey (*Pandion haliaetus*) in parts of Europe and the grizzly bear (*Ursus arctos horribilis*) in the Greater Yellowstone Ecosystem of the USA.

The eigenplace concept can also be used to develop and progress into a body of derived principles that can be used to address the critical conservation problems faced by invasive species and the associated globalization of the biosphere. In order to stimulate further thought on this very subject, I have distilled pertinent elements for an *eigenplace theory* in the hope that they may serve as building blocks for 'putting the geography back in the bio-' (Stoddart, 1986). Each of the following statements is accompanied by a brief comment, prediction, or application.

1. *Functionally insular taxa and communities evolved and have persisted because of protection from continental variables and invasions provided by long-term isolation.* The conservation of insular eigenplaces and ecosystems depends on the continuance of the insular complex. Increased linkage of islands to mainland environments constitutes an incompatible breaching of insular isolation leading to the continentalization of island biotas and high extinction rates of insular endemics.

2. *Isolate taxa on continents are adapted to biotic space that differs from that of true insular taxa.* Continental isolates may expand or contract their occupied area in ecological and evolutionary time thereby maintaining their eigenplace on a changing continent.

3. *Continental physical and biotic systems are spatially dynamic and unstable.* Continental taxa depend on the vast linkage and areal potential of their continental existence. They depend on functional continentality and have historically been able to adapt to changing landscapes. Functional continentality buffers against the instability and stochastic dynamic changes experienced by local and regional landscapes on continents. Anthropogenic linkage barriers and permanent areal shrinkage create dysfunctional continental areas threatening eigenplace persistence.

4. *Fragmentation of continental taxa does not create insular taxa.* Only deep lakes and extensive cave systems on continents meet the physical and biotic requirements for functional insularity. Fragmentation of continental taxa is a serious extinction factor if it results in the disturbance or loss of functional continentality.

5. *Many continental taxa are adapted to high environmental impacts and interactions. There is often a prominent difference between edge and interior habitat space.* Continental habitat fragments are surrounded by diffuse components and processes of their spatial environment (matrix) creating predictable, severe, and adverse survival problems.

6. *Some continental taxa have an eigenplace with a naturally narrow or restricted range.* Localized endemics are still functionally continental except for connectivity dynamics; this fact makes them highly vulnerable to habitat degradation and loss.

7. *Tropical eigenplace characteristics differ from temperate ones; obvious differences are found in seasonality, migration, and prehistoric phylogeographical variables.* Separate conservation models and programs are needed for different latitudes.

8. *Regional characteristics of insular and continental eigenplaces (and models thereof) cannot be automatically applied at global or interregional scales.* Careful comparative analysis and evaluation is necessary before assigning the validity of eigenplace variables across regional boundaries.

9. *Different taxon groups (such as birds, bats, land snails, ferns, pines, etc.) often do not share the same areographic patterns.* It is imprudent and risky to develop general conservation plans for a region or environmental gradient based on one taxon group only.

10. *Climatic change at the end of the Ice Age resulted in asymmetric biome loss, gain, and zonation on the northern continents.* Mammal megafauna disappeared because of synergy between habitat and resource shrinkage as well as invasion by human hunters. Future climate change may also result in asymmetric geographical biome change.

11. *Phylogeographical data can provide pertinent historic data for functional areography.* Phylogeography provides a window to a taxon's former occupied area and spacing behaviour; this may identify at least a portion of its adaptive areal potential in the future.

12. *The human factor has embedded itself in earth biodiversity; the ongoing globalization process poses a grave threat to local and regional biodiversity.* There can be no future eigenplace determination that excludes human impact variables.

CONCLUSION

This paper has not attempted to downgrade the importance of species–area relationships in island biogeography. The message that I have tried to formulate is that ETIB is insufficient, misleading, and inappropriate as a foundation principle for conservation biology. A key problem of ETIB was its elegant simplicity and claim of universality. ETIB cannot explain, however, the observable patterns and processes of many islands around the world, and it should not be applied to mainland isolate complexes. The functional areographic approach offered here addresses the fundamental difference between island-evolved and mainland-evolved taxa as well as the importance of the complexity and relevance of the *geographical place*. It promises to yield a more differentiated appreciation and understanding of island biotas and opens the door for assessing the biogeography and conservation of mainland biotas from the perspective of functional continentality. In terms of the 'ontology of biogeography' (Ebach & Humphries, 2003) ETIB appears to have attempted to address some of the *how* question of taxon distribution, colonization, and extinction while the eigenplace concept encompasses the *why* question of distribution in time and space before and after human arrival.

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BIOSKETCH

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APPENDIX A

The *eigenplace* index

This index represents a qualitative estimate of the spatial importance of the occupied taxon distribution area compared to that of any related taxon (part of same genus, family, order,...). It is composed of the sum of the rankings (from 1 to 5 each) of six factors playing a key role in the functional spatial complex of taxon persistence. The value of the index ranges therefore from a minimum of 6 to a maximum of 30.

H – *History:* distribution record over time (dynamics of expansion and contraction over Holocene time scale established through fossil or historic evidence). This variable will often be difficult to establish because of the lack of any historic and prehistoric data; in such a case, the better known spatial dynamics of its biome affiliation may provide clues to the taxon's historical dynamics.

1 = highly variable, significant episodes of major range contractions and/or expansion, 2 = variable with significant episodes, 3 = important range dynamics, 4 = minor range dynamics, 5 = very stable or static occupied area (like 'taxon has always been here').

A – *Area:* space occupied by the taxon (contiguity, disjunction, size, seasonal migration and wintering area; established through museum records and /or direct observations).

1 = cosmopolitan, largely contiguous continental, 2 = large continental area, 3 = part of continental area or extensive island archipelago, some disjunctions possible, some seasonal area possible, 4 = limited or restricted continental or on large island, 5 = insular only.

D – *Dispersion:* criteria within the occupied area, including evenness or clustering, density, etc. (established through sampling, mapping, inventories).

1 = evenly and densely spread out, 2 = evenly spread throughout range at lower density, 3 = some unevenness or clustering, 4 = unevenness and low density, 5 = highly uneven and sporadic or rare.

V – *Vagility:* criteria such as natal, seed or adult dispersal, seasonal movements, irruption frequency (established through marking and tracking methods).

1 = very high dispersal rate (active or passive), 2 = high dispersal, 3= medium dispersal, 4 = low dispersal and/or seasonal movements, 5 = no dispersal, extremely sedentary.

I – *Isolation*: degree of ecosystem or bio-landscape isolation (oceanic island, continental island, montane habitat, wetland patch, etc.; measured with GIS tools).

1 = high connectivity and/or embedded in global or continent-wide biomes or ecosystems, 2 = area connected to or part of significant continental bio-landscapes, 3 = good linkage to ecosystems with rich representation of biodiversity, 4 = continental isolate with poor linkage to nearest continental biodiversity patch, 5 = isolated insular place protected from continental biodiversity factors.

L – *Location reliance*: degree of taxon persistence depending on the availability of its specific place, including required habitats, other landscape features, and geographic parameters (established through qualitative data on location-related niche factors).

1 = taxon area is independent of particular places, taxon can persist in most regions, 2 = low reliance on particular climatic, habitat, soil, other factors, 3 = medium reliance on particular bio-landscape complex, 4 = reliant on specific place at regional scale, 5 = absolute reliance on restricted or unique place.

Examples of eigenplace index assessments[*]:

Pigeon and doves (Columbidae):

Namaqua dove, *Oena capensis* – sub-Saharan Africa except equatorial lowlands in West Africa and Congo basin, Madagascar; avoids forests: H4, A2, D3, V3, I1, L2 = 15

Nicobar pigeon, *Caloenas nicobarica* – Andaman and Nicobar Islands west to Indonesia, Philippines, and Salomon Islands: H2, A3, D3, V1, I4, L3 = 16

Spinifex pigeon, *Geophaps plumifera* – Western and central Australia: H4, A3, D3, V4, I1, L2 = 17

Southern crowned-pigeon, *Goura scheepmakeri* – S New Guinea: H5, A4, D4, V5, I3, L4 = 25

Socorro dove, *Zenaida graysoni* – Socorro Island endemic: H5, A5, D5, V4, I5, L5 = 29

Turacos (Musophagidae):

Ross's turaco, *Musophaga rossae* – Angola to S Sudan: H3, A2, D2, V2, I2, L1 = 12

Great blue turaco, *Corythaeola cristata* – equatorial Africa from Guinea Bissau to W Kenya: H4, A2, D2, V3, I1, L2 = 14

White-bellied go-away bird, *Corythaixides leucogaster* – Somalia to Tanzania: H4, A3, D2, V3, I1, L1 = 14

Ruwenzori turaco, *Ruwenzornis johnstoni* – E Congo to SW Uganda: H4, A4, D3, V4, I3, L2 = 20

Bannerman's turaco, *Tauraco bannermani* – Cameroon highlands: H4, A4, D4, V5, I4, L4 = 25

*Assessed from species accounts of Vol. 4 of *Handbook of the birds of the world* (del Hoyo *et al.*, 1997).