Biogeographic Crossroads as Priority Areas for Biodiversity Conservation

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Abstract: Threats to biodiversity outpace the resources of the conservation community and necessitate careful prioritization of conservation actions. I suggest that targeting the regions where biogeographic assemblages intersect—"biogeographic crossroads"—is a strategy that may achieve significant conservation economy by focusing on areas that satisfy many conservation criteria. I used a combination of data on Scarabaeine beetles in Bolivia and on other taxa and locations from the literature to consider the short- and long-term benefits of conserving these biogeographic crossroads. Biogeographic crossroads are areas of high species richness and beta diversity, often across many taxonomic groups. They are also regions where representativeness can be achieved with relative efficiency. Recent evidence that ecotones may be loci of evolution suggests that evolutionary processes such as speciation and coevolution may be conserved at biogeographic crossroads. Biogeographic crossroads appear to be areas of high conservation priority and opportunity in both the short and long term and require increased attention in the process of setting conservation priorities.

Introduction

The magnitude of the threats to biodiversity, coupled with the limited financial, technical, and physical resources available for biodiversity conservation, requires careful prioritization of our efforts. Previous efforts to formalize the process of setting conservation priorities have been concentrated at two scales: global (or continental) and local. Global efforts have focused on documenting worldwide patterns of biological diversity to identify biodiversity "hotspots" (Mittermeier et al. 1998; Myers et al. 2000) or delineate ecoregions (Dinerstein et al. 1995; Olson & Dinerstein 1998) with important biodiversity elements so that conservation efforts can be con-
centrated there. Despite some criticism (Prendergast et al. 1993), the strategy seems to be achieving positive results, at least terrestrially (Balmford & Long 1995). At more local scales, a variety of algorithms have been developed for computing the optimum area and configurations of reserve networks (McKenzie et al. 1989; Davis 1996; Freitag et al. 1997; Rodrigues et al. 1999; Rothley 1999). The algorithms are used to find the minimum area and most feasible spatial arrangement of reserves so as to protect a specific proportion of the region’s species or populations (Pressey et al. 1995).

Recently, conservation practitioners have begun filling the “mesoscale” gap in our ability to identify areas of high conservation priority. An increasing focus on conserving large, connected landscapes and regions of rapid species turnover (high beta diversity) is evident in conservation planning efforts (Dinerstein et al. 1995; Wikramanayake et al. 1998; Foreman et al. 2000). I suggest that targeting the regions where biogeographic assemblages intersect—“biogeographic crossroads”—is a strategy that complements this new mesoscale approach.

Biogeographic crossroads present conservationists with opportunities to achieve significant economy of effort by focusing on relatively narrow areas that simultaneously satisfy many of the major criteria for establishing conservation priority (for more extensive treatments of priority-setting criteria, see Margules & Pressey 2000; also see Vane-Wright et al. 1991; Pressey et al. 1993; Mittermeier et al. 1998; Prendergast et al. 1999). Large biogeographic intersections create regions of rapid turnover (or high beta diversity) of species and habitats, leading to exceptionally high levels of species richness and creating the opportunity to meet the goals of representativeness and complementarity in protected-areas systems. Protection of biogeographic crossroads may also provide long-term biodiversity benefits by conserving evolutionary processes such as speciation and coevolution.

I illustrate the benefits of conserving biogeographic intersections with data from a series of surveys of a widely proposed rapid biodiversity assessment group, scarabaeine beetles (Coleoptera: Scarabaeidae: Scarabaeine) (Halffter & Favila 1993; Kremen et al. 1993; Spector & Forsyth 1998) in South America. I emphasize in particular one biogeographic crossroad region in eastern Bolivia that is currently protected within Parque Nacional Noel Kempff Mercado (PNNKM) (Fig. 1). Of the Huanchaca region where the 1.4 million-ha park is situated, Killeen (1998:83) states that “In no other part of [South America] can one find five such dramatically different ecosystems in a single region.” Four years of work in PNNKM by this author and others have yielded a nearly complete picture of the scarabaeine fauna and the habitat associations of each species (information on collecting methods and sampling localities in PNNKM are provided by Forsyth et al. 1998 and Spector & Forsyth [1998]). Thus, the park is an ideal area for examining biogeographic crossroads and their conservation implications.

I have also included data on additional taxa at other biogeographic crossroads that I encountered in the literature to emphasize that the high conservation value of biogeographic crossroads is a broader phenomenon than my own geographically and taxonomically restricted data can demonstrate. A number of these additional biogeographic crossroads are the sites of globally important protected areas. Although these parks were declared for a variety of reasons, their common position at biogeographic crossroads highlights the potential for conserving similar regions elsewhere.

Potential Benefits of Biogeographic Crossroad Parks

Species Richness and Beta Diversity

Species richness is a commonly utilized criterion for assigning conservation priority (Johnson 1995; Kerr 1997; Mittermeier et al. 1998). The total richness of any given area is a function of site richness (alpha diversity) and the rate at which species replace one another between sites (beta diversity) (Whittaker 1972). Previous authors have noted the role of biogeographic intersections in producing high beta diversity and consequently species richness (Fjeldså & Rahbek 1997), and recent approaches to designing conservation strategies have begun to emphasize zones of high beta diversity (Wikramanayake et al. 1998).

The high levels of beta diversity at biogeographic crossroads should be the characteristic most attractive to conservationists. Naturally, the zones where two or more biogeographic assemblages come into contact have high beta diversity. And, by concentrating large numbers of species in a single region, biogeographic crossroads present us with the opportunity to protect the species of two or more biogeographic zones within a single protected area.

For example, the known scarabaeine fauna of PNNKM currently holds at least 143 species. This is the highest known scarabaeine richness of any Neotropical area of its size—a full 12% of the approximately 1188 species known from South America (Hanski & Cambefort 1991) in <0.1% of the continent’s land area. One tribe in particular, the Phanaeini, a group of large, diurnal, colorful species, exhibits extremely high richness in the park, with 18 of the 74 species restricted to South America (W. D. Edmonds, personal communication) occurring in the park (24%).

Beta diversity is clearly the diversity component driving the overall high levels of richness in PNNKM. Any given sampling site (a roughly 500-m transect) in the park contained only a small subset of the park’s entire
fauna: on average, 29.4 (±9.8) of the total 143 species were found at a single site. Species in the tribe Phanaeini showed a similar pattern, with only 4.8 (±2.1) of the 18 species in the park occurring in any given site. Existing data on the biogeography of the Phanaeini (Edmonds 1972, 1994) indicate that Phanaeine species in the park are drawn from either the Amazonian Basin or the Cerrado Complex biogeographic assemblages; no species occur in both regions. In fact, exactly half of PNNKM’s 18 phanaeine species are associated with each biogeographic assemblage. Thus, inclusion of both assemblages within PNNKM effectively doubles the number of Phanaeine species under protection.

Located at another biogeographic crossroad, the Manu Biosphere Reserve lies along the Andes-Amazon confluence in Peru. The reserve is almost the same size as PNNKM (1.53 million ha) and protects the entire watershed of the Rio Manu and parts of the Rio Alto Madre de Dios watershed, encompassing a full complement of the biological communities from the grassy Andean highlands at 4000 m to the lowland Amazonian forests at 240 m (Dallmeier et al. 1996). The Manu Biosphere Reserve contains the highest known richness of carabid beetle species in the world (Erwin 1996).

Another Bolivian park, Parque Nacional Madidi, protects the entire elevational gradient from altiplano to lowland forest. As in PNNKM, high levels of beta diversity produce high overall richness of scarabaeines (S.S., unpublished data). The lowland forests of the park contain a fairly unremarkable Amazonian community of approximately 45 species. If the series of habitats found along the elevational gradient of the Andes is included, however, the number of scarabaeine species nearly doubles. Similarly, scarab richness nearly doubles when the

Figure 1. Partial map of North and South America, showing the positions of the biogeographic crossroad areas discussed: 1, Parque Nacional Noel Kempff Mercado (Bolivia); 2, Parque Nacional Madidi (Bolivia); 3, Parque Nacional Manu (Peru); 4, Sky Island/Sierra Madre Region (United States and Mexico).
Andean fauna is combined with the Amazonian lowland fauna in Manu Biosphere Reserve (A. Forsyth, personal communication).

**Cross-Taxon Correspondence**

One of the crucial questions faced in the prioritization process is assessment of the degree to which a proposed area will benefit multiple taxa, not just the focal or indicator taxon (or taxa) used to assign conservation priority. Prendergast (1997) and others (Pearson & Cassola 1992; Oliver et al. 1998) have shown that, locally, the patterns of richness and rarity across taxa are nonoverlapping biotas within a single protected area.

This is certainly the case in PNNKM, where, in addition to scarab beetles, species richness is also high for birds, reptiles, fishes, and mammals. The park protects the richest assemblage of canids in South America (four or possibly six species) (Bates et al. 1998; Emmons 1998; Harvey 1998; Sarmiento 1998), and there are currently more than 2700 species of vascular plants known in the park (Killeen 1998).

In southern Peru, the Tambopata–Candamo Reserved Zone protects an Andean–Amazonian gradient similar to that of Alto Madidi National Park and Manu Biosphere Reserve but has an added advantage of being situated at the boundary of Holdridge’s (1967) tropical and subtropical life zones. Tambopata-Candamo is the most species-rich site in the world for spiders, odonates (dragonflies and damselflies), cicindelids (tiger beetles), asilids (robin flies), and tabanids (horse flies) (Pogue 1996).

Another biogeographic crossroad, the Sky Island/Sierra Madre region of Arizona, New Mexico, and northern Mexico, is situated at the intersection of the subtropical Sierra Madre assemblage and the temperate Mogollon Highlands (Foreman et al. 2000). The Sky Islands are “the northern limit of 14 plant families and four bird families and the southern limit of seven bird families” (Warshall 1994, as cited by Foreman et al. 2000). All of these colliding ranges combine to produce high beta diversity and species richness across multiple taxa. Over half the bird species in North America occur in the region (Felger & Wilson 1994, as cited by Foreman et al. 2000), and it contains the greatest bee species richness in the world. The greater Sky Island region is also known to have the most diverse assemblages of ants, reptiles, and mammals in North America (Foreman et al. 2000).

**Representativeness**

Many efforts to set conservation priorities have incorporated the concept of representativeness into the ranking process (Johnson 1995). Representativeness seeks to include all the different species or ecosystem types of a given area within a protected-area system (Kitching 1996; Williams et al. 1996a, 1996b). Biogeographic crossroads are regions where representativeness can be achieved with relative economy, because beta-diverse biogeographic crossroads should permit greater numbers of species, communities, or ecosystem types to be conserved in a concentrated area. Moreover, the greater the fidelity of species to their respective biogeographic assemblages, the greater the opportunity to conserve complementary, nonoverlapping biotas within a single protected area.

In PNNKM scarabs, habitat fidelity is high. More than 80% of the park’s 143 scarab beetle species are entirely restricted to either the Amazonian forests or the Cerrado Complex shrublands and grasslands. Thus, the park is conserving at least two distinct faunas and including both major assemblages. Further, PNNKM is the only Bolivian park in which many of the cerrado specialist species are found, so the cerrado habitats of the park have a high complementarity within the system of Bolivian protected areas.

**Evolutionary Hotspots**

Another strongly argued conservation priority is the need to preserve evolutionary processes (Erwin 1991; Vane-Wright et al. 1991; Brooks et al. 1992). It has been difficult to translate this into direct conservation action, perhaps because it is difficult to identify evolutionary processes in space and time. Which evolutionary processes concern us? What sorts of landscapes harbor important evolutionary processes? What areas are “hotter” than others evolutionarily?

Interestingly, biogeographic crossroad parks may hold promise for conserving the dynamic processes of speciation, cladogenesis, and coevolution. Ecological heterogeneity, the essential feature of biogeographic crossroad parks, is the root of the variety of selective regimes to which species adapt. But classical evolutionary theory maintains that gene flow between populations effectively counters the effects of divergent selection on connected populations (Mayr 1963). Recent evidence suggests, however, that ecological heterogeneity and strongly differing selection pressures across ecotones may drive rapid evolutionary changes in populations even in the face of gene flow, perhaps driving evolution and speciation at...
the edges of habitats and enriching biotas (Enserink 1997; Smith et al. 1997; Schneider et al. 1999). Thus, at large scales the intersections of biogeographic zones may be evolutionarily active zones—the origination sites of new taxa or adaptations in existing taxa.

There is some evidence that speciation and divergence has occurred among the scarabs of PNNKM. Several congeneric pairs of ecological analogues exist across the boundaries of the Amazon-Cerrado complex in the park, suggesting that the close association of two such disparate habitats might have played a role in the diversification of Scarabaeines in the region. For example, *Oxysternon silenus* and *O. conspicillatum*, forest species, are closely juxtaposed with *O. palaemo* in the savannas and cerrados. Similarly, *Phanaeus chalcomelas, bispinus*, and *altaevidal* are all forest-restricted species, whereas their congeners *P. kirbyi, palaeno*, and *meli-baeus* are all limited to the nearby the savannas and cerrados (S. S., unpublished data).

Higher taxon evolution at biogeographic crossroads may have also played a role in generating the regional richness. *P. palaeno* and *O. palaemo* share a unique character, setae on the metasternum (Edmonds 1994). The two species are certainly correctly placed in their respective genera, but the shared character brings up the question as to whether the more derived genus *Oxysternon* may have diverged from *Phanaeus* at the intersection of the Amazonian and Cerrado biotas.

### Applying the Biogeographic Crossroad Strategy

Targeting biogeographic crossroads as conservation priorities should be seen as complementary to both larger- and smaller-scale strategies for setting conservation priorities. One possible approach would be to first focus on global hotspots and then on the important biogeographic crossroads within the hotspots. Similarly, existing ecoregional analyses could be used to identify regions of high complexity within an ecoregion (Dinerstein et al. 1995; Ricketts et al. 1999). Where the spatial configuration of ecoregions brings multiple ecoregions into contact, biogeographic crossroad parks can be established to straddle the transitions. PNNKM is such a region, and many others easily can be found. Alternatively, when reserve-optimization algorithms are used at the local or regional scale, zones of high beta diversity could be targeted; contiguous grid squares across the intersection zones could be given greater weight to ensure prioritization of all sides of the intersection zone.

In some cases, biogeographic crossroad parks may be aimed at conserving areas of outstanding richness, such as the Madidi park envisioned by Remsen and Parker (1995) that would have protected over 1200 bird species. In other situations, biogeographic crossroad parks could be configured to overcome the difficulties of protecting species-poor areas of high conservation priority. By pooling biotas in a single reserve, biogeographic crossroad parks could raise the overall richness of the proposed reserve to politically viable levels (for example, species-poor but critical areas around the confluence of the Argentine pampas, the Paraná flooded savannas, and the Uruguayan savannas).

### Caveats

There are questions about this strategy that will bear further investigation. Foremost, perhaps, are the implications for species’ persistence in parks situated at the edges of their ranges. Conventional wisdom holds that the edges of species’ ranges tend to harbor more variable, more fragmented, and ultimately more extinction-prone populations (Brown 1984; Brown 1995). If this is the case, then conserving many species at the edges of their ranges may focus efforts on peripheral or perhaps even sink populations whose persistence is uncertain.

Although the macroecological pattern of lower and more variable population densities at range peripheries may be valid, a series of recent studies suggests that “conservation biologists . . . should reevaluate the assumption that populations inhabiting small, peripheral, or otherwise isolated ecosystems are doomed to extinction” (Lomolino & Channell 1995). Instead, Lomolino and Channell (1995) and Channell and Lomolino (1998; 2000) have demonstrated that many endangered species are persisting on the peripheries of their ranges, not in the cores. Rather than precarious demographic sinks, Lomolino and Channell assert, peripheral populations are more numerous and pre-adapted to a wider variety of ecological conditions, making it more likely that some of those peripheral populations will be among the survivors of environmental change. Alternatively, peripheral populations may simply be the last to face extinction forces that spread like a contagion across the landscape. Regardless of which explanation is correct, this new understanding of the importance of conserving species at the peripheries of their ranges implies that biogeographic crossroads are not necessarily a recipe for conserving the “living dead.”

Importantly, in many of the world’s hotspots, remaining habitat lies in scattered patches at the edges of historical ranges (Brooks 2000). In these cases, the theoretical implications of abundance, population growth, and range position become secondary, and peripheral areas take on higher priority as the last opportunities to conserve representatives of vanishing ecosystems. Biogeographic crossroad parks may fit well with this scenario by protecting the edges of ranges where species and communities are persisting in the face of habitat loss in the cores of ranges.

Another question that will require consideration is how large biogeographic crossroad parks must be to function; the answer will likely be “it depends.” Ulti-
mately, it will depend on the size of the ecological gradients occurring at the biogeographic crossroad and the processes that maintain the habitats of each ecoregion. In PNNKM, for example, maintenance of the current fire regime within the park will be critical to sustaining savannas and other relatively open habitats in PNNKM, and the park must be large enough to contain the dynamic movement of boundaries between forest and savanna which fire creates. The scale at which these key processes occur will dictate the scale at which biogeographic crossroad parks must be designed.

Conclusion

Biogeographic intersections are dominant landscape features in all regions of the world. In South America, for example, major intersection zones occur where the Amazon Basin meets savannas and shrublands on its southern and northern edges, semideciduous forests on its southwestern edge, Guiana shield forests on its northeastern edge, and montane forests where the basin meets the Andes. The Andes in turn meet Caribbean and Pacific coastal forests, coastal deserts, pampas, and temperate rainforests as they run from Colombia to Tierra del Fuego. In short, the opportunities for conserving these regions exist in all corners of South America and, presumably, the globe. Perhaps the commonness of biogeographic crossroads on the landscape makes their identification and protection an easily understood and politically workable strategy.

Biogeographic crossroads appear to provide conservation strategists with opportunities to simultaneously conserve high species richness, zones of high beta diversity and complementarity, and evolutionary processes. Magueles and Pressey (2000) state that reserves should be judged on their success in achieving representativeness and long-term persistence. If this is true, then increased attention to the opportunities offered by conserving biogeographic crossroads will contribute to the process of setting conservation priorities and designing reserves.

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