

Strategies to Protect Biological Diversity and the Evolutionary Processes That Sustain It

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Abstract.—Conservation planning has tended to focus more on pattern (representation) than process (persistence) and, for the former, has emphasized species and ecosystem or community diversity over genetic diversity. Here I consider how best to incorporate knowledge of evolutionary processes and the distribution of genetic diversity into conservation planning and priority setting for populations within species and for biogeographic areas within regions. Separation of genetic diversity into two dimensions, one concerned with adaptive variation and the other with neutral divergence caused by isolation, highlights different evolutionary processes and suggests alternative strategies for conservation. Planning for both species and areas should emphasize protection of historically isolated lineages (Evolutionarily Significant Units) because these cannot be recovered. By contrast, adaptive features may best be protected by maintaining the context for selection, heterogeneous landscapes, and viable populations, rather than protecting specific phenotypes. A useful strategy may be to (1) identify areas that are important to represent species and (vicariant) genetic diversity and (2) maximize within these areas the protection of contiguous environmental gradients across which selection and migration can interact to maintain population viability and (adaptive) genetic diversity. These concepts are illustrated with recent results from analysis of a rainforest fauna from northeast Australia. [Biodiversity; conservation genetics; ESUs; phylogeography; prioritization.]

CHALLENGES AND GOALS FOR CONSERVATION

The overarching aim of conservation biology is to protect biological diversity and the processes that sustain it in the face of perturbations caused by human activity. Stating this aim is simple. The challenge is to devise practical strategies for achieving it, recognizing that (1) our knowledge of both pattern and process is incomplete, (2) both natural and anthropogenic change to natural systems is inevitable, and (3) conflicts between the needs of biological diversity and human societies are common and must be reconciled through trade-offs and setting priorities. In this context, it is essential that conservation biologists are able to articulate clearly a common goal and agree on strategies to prioritize conservation effort and resources across the spectrum of biological diversity. This will require us to reconcile perspectives derived from ecology, systematics, and evolutionary biology (Bowen, 1999).

In prioritizing taxa and habitats for conservation effort, we seek to maximize both representation and persistence of diversity (Balmford et al., 1998; Cowling et al., 1999; Desmet et al., 2002). Both aspects need to be assured across the full hierarchy of biodiversity, spanning ecosystems, communities,

species, and genetic diversity (Noss, 1990; Purvis and Hector, 2000). Substantial progress has been made toward efficient algorithms that maximize *representation* of diversity, that is, which efficiently sample the spatial *pattern* of diversity, based on mapped vegetation communities, species distributions, or environmental surrogates thereof (Margules and Pressey, 2000; Ferrier, 2002; Funk and Richardson, 2002). Overall genetic diversity can be captured via phylogenetic weighting of species or areas (Vane-Wright et al., 1991; Faith, 1992; Crozier, 1997), but how best to represent genetic diversity below the level of taxonomic species remains contentious (see below). In this context, those searching for ways to represent genetic diversity at or about the species level can learn much from techniques developed for assessing higher-level diversity, a theme to which I return below.

Less progress has been made on how to prioritize habitats, species, or populations in relation to *persistence*, that is, ensuring that the *processes* that sustain current and future diversity are protected (Cowling and Pressey, 2001). This is despite the increasing recognition that in a changing environment both the ecological (ecosystem and demographic) and evolutionary processes (Frankel, 1974; Smith et al., 1993; Balmford et al., 1998) that

will sustain diversity must be maintained. To paraphrase from Frankel (1974), the general goal for conservation can be stated as follows:

To maintain evolutionary processes and the viability of species and functional landscapes necessary to achieve this.

This statement acknowledges explicitly the need to retain the ecological integrity of populations and the habitats that sustain them, while also stressing that natural change, mediated via processes of evolution and succession, is vital and must be accommodated.

The purpose of this paper is to explore strategies for recognizing and protecting genetic diversity that are consistent with the above goal and with our understanding of evolutionary process. I first consider the nature of genetic diversity and then give attention to recent debates over how to delineate and prioritize conservation units below the level of taxonomically recognized species. I then shift attention from individual species to biological communities and geographic areas. Specifically, I ask how our understanding of evolution and measures of diversity within species can contribute to planning at this higher level of organization, this level being where much of the attention and effective conservation action by governments is focused.

GENETIC DIVERSITY AND EVOLUTIONARY PROCESSES

The major concerns of conservation genetics have revolved around the maintenance of fitness and the capacity for evolutionary response to environmental change (Franklin, 1980; Frankel and Soule, 1981; Hedrick, 1996; Lynch, 1996). In parallel, and with increasing emphasis as the concepts and tools of phylogeography have improved, has been the protection of major historical lineages within species (Avice, 1992; Moritz, 1994a). This development of two strands of conservation genetics has been mirrored by debate about the relative significance and contribution of molecular versus quantitative genetic and phenotypic approaches to conservation (e.g., Milligan et al., 1994; Moritz, 1994b; Hard, 1995; Lynch, 1996).

Greater clarity can be achieved by partitioning genetic diversity into two components: that arising from adaptive evolution

and that resulting from long-term historical isolation such as can arise through "vicariance" (Fig. 1). The former is measured by analyzing phenotypic variation, preferably using appropriate quantitative genetic and experimental methods to demonstrate heritability and differences in fitness (Endler, 1986; Lynch and Walsh, 1998; Ritland, 2000). Only rarely will molecular analyses of specific genes predict variation in total fitness, although statistical associations may well exist between fitness components and specific genotypes. Conversely, the vicariance axis is readily assayed through molecular phylogeography (Avice, 2000a). Thus, both approaches have their place, but for measuring different components of intraspecific diversity.

The two axes of diversity relate to distinct evolutionary processes, conservation issues, and potentially, complementary strategies for management and monitoring (Sherwin and Moritz, 2000). On one hand, differential adaptation arises primarily through divergent selection pressures and is facilitated by, but does not require, genetic isolation (Endler, 1977). Historical isolation, on the other hand, can proceed independently of divergent selection and consequent phenotypic divergence (e.g., Schneider and Moritz, 1999). Where both long-term isolation and differential adaptation are operative, leading to congruence of molecular phylogeographic and phenotypic divergence, different populations would be regarded as distinct species by the majority of practicing taxonomists. Both evidence and theory demonstrate that speciation can occur with either process alone—that is, strong divergent selection in the presence of (limited) gene flow (Endler, 1977; Rice and Hostert, 1993) and long-term isolation without divergent adaptation (Mayr, 1963; Avice et al., 1998)—or more commonly, the two together (Mayr, 1963; Dobzhansky, 1970; Orr, 1997).

In relation to conservation issues and strategies, the adaptive axis relates most directly to persistence, specifically the retention of individual fitness and population viability in current and future environments. The vicariance axis, in contrast, is typically considered in relation to representation, in particular to ensure that major evolutionary lineages within recognized species are protected. In the following sections I suggest strategies for conserving each aspect

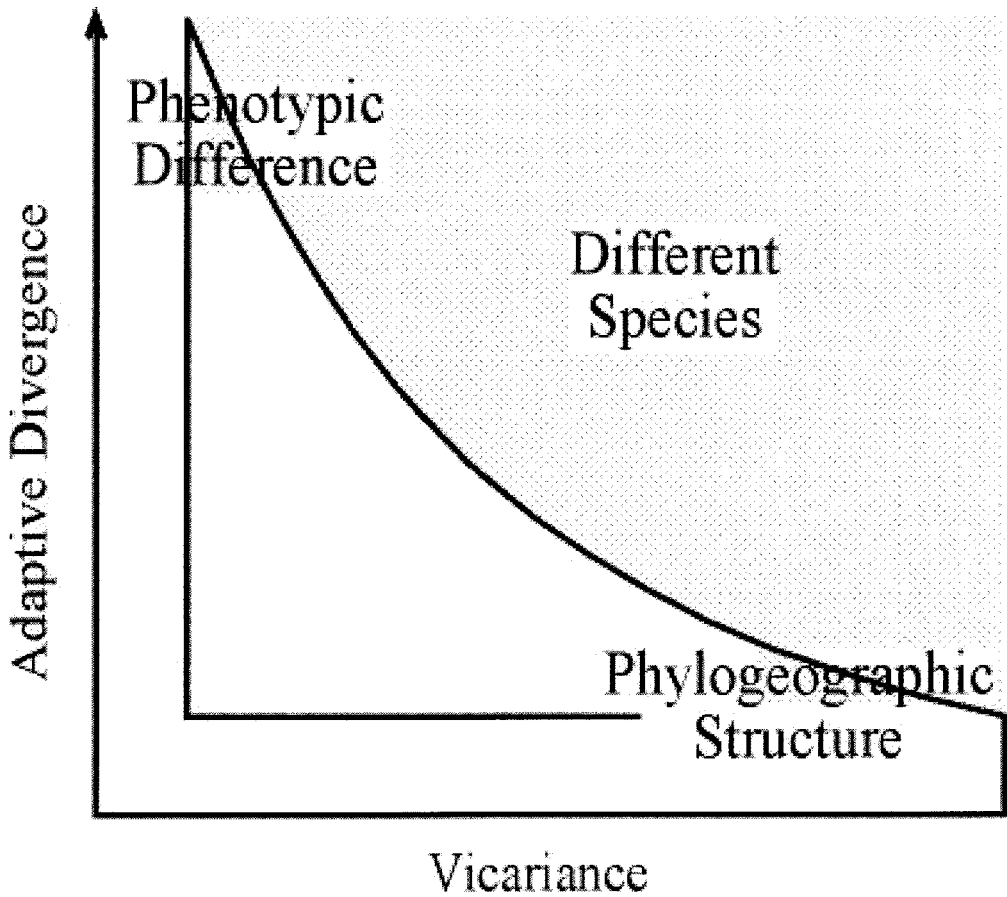


FIGURE 1. Separation of genetic diversity into two components: adaptive variation that arises through natural selection, and neutral divergence due to vicariant evolution. The former is typically assayed through analysis of phenotypes and the latter through molecular phylogeography. The stippled area above the curve signifies conditions where populations are likely to be considered as separate species under most concepts.

of diversity in the context of the potential to recover lost variation. Once lost, major historical lineages cannot be recovered, other than by repetition of long-term isolation, which is beyond the scale of realistic time-frames for management. Hence, representation of these entities is crucial. In contrast, functional diversity (adaptive phenotypes) can potentially be recovered through recurrent selection, subject to the viability of the populations under selection and to maintenance of the appropriate environmental context (see below). Thus, for the adaptive component of diversity, a conservation strategy could be directed towards protection of the process, that is, the context for selection, rather than the products themselves. The challenge is to find effective indicators or spatial surrogates for such processes

(Sherwin and Moritz, 2000; Cowling and Pressey, 2001).

CONCEPTS AND CRITERIA FOR IDENTIFYING CONSERVATION UNITS WITHIN SPECIES

Identification of intraspecific units for conservation and management was originally based on taxonomically recognized subspecies, a practice that continues to the present. However, over the past two decades several deficiencies of this approach have been noted, including uneven application of the subspecies category across taxa, inadequate or confused criteria, and frequent misalignment between historical subdivisions as revealed by molecular assays and current boundaries of subspecies (Avice and Ball,

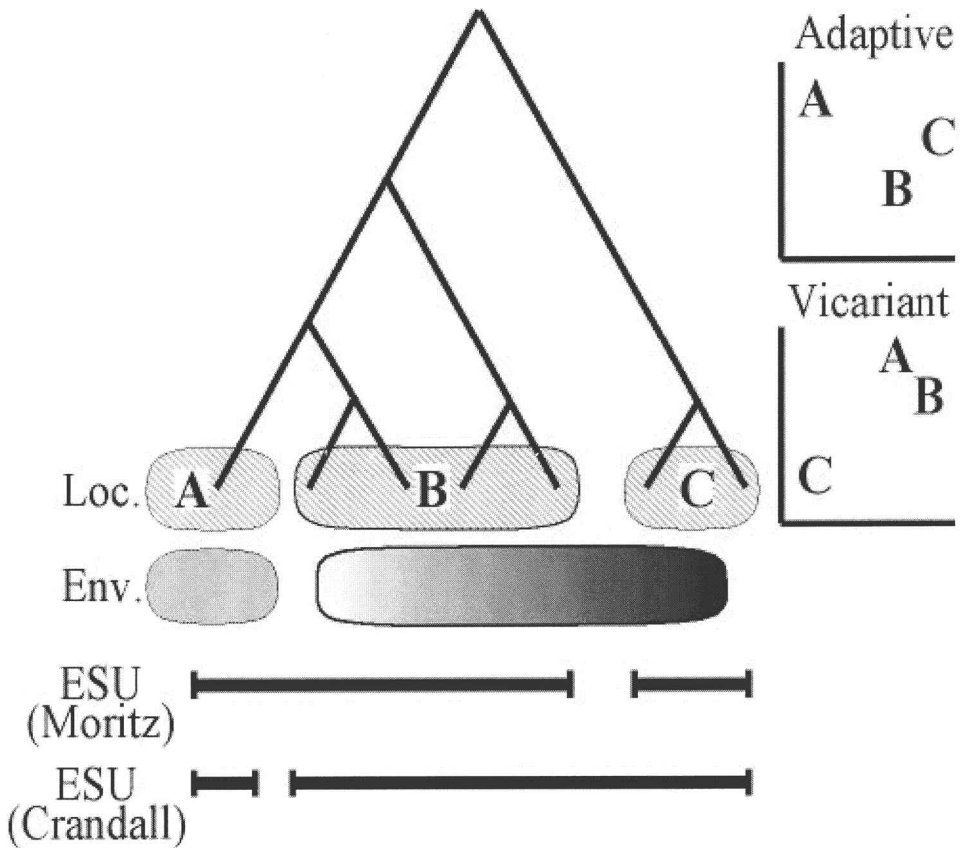


FIGURE 2. Schematic illustration of continua for genealogy (vicariance) and environmental conditions (adaptive diversity) that accompany divergence of populations. These sets of populations can be represented as dichotomies (ESUs) with emphasis on vicariant (e.g., Moritz, 1994b) or adaptive (e.g., Crandall et al., 2000) components of diversity or can be displayed in continuous space (e.g., as ordination plots). In this simple example, if only two sites could be selected, A + C would maximize representation of both vicariant and adaptive diversity. Loc. = location, Env. = environment.

1990; O'Brien and Mayr, 1991). The concept of the "evolutionarily significant unit" (ESU) was introduced to guide prioritization of intraspecific units for captive management (Ryder, 1986) and then adopted as a more general term for "distinct population segments" (of salmonid species), which qualify, for protection under the US Endangered Species Act (Waples, 1991, 1995). For the latter purpose, an ESU was proposed to have as basic properties some level of reproductive isolation and adaptive distinctiveness.

The continuing debate over principles and criteria for recognizing ESUs mirrors the longer standing issue of how to best to define species (e.g., Endler, 1989; Howard and Berlocher, 1998). Both areas of contention reflect the underlying genealogical continuum

from more or less distinctive populations to reproductively isolated species and the variety of processes and time-scales involved in arriving at the latter (Avice and Wollenberg, 1997; deQueiroz, 1998) (Fig. 2). This gray zone of divergence preceding full speciation creates a dilemma. As evolutionary biologists, we recognize this continuum and try to understand how various processes interact to shape it. As biologists seeking to inform policy and conservation managers, we need to reduce the complexity and provide practical information relevant to assessment and prioritization of biodiversity. One option is to abandon our efforts to delineate units below the level of fully isolated species. Instead, we could represent measurable phenotypic and molecular diversity in multivariate

space (Fig. 2) and use appropriate algorithms (e.g., Faith and Walker, 1996) to prioritize populations that collectively represent the maximum adaptive and historical diversity according to some specified target (see also Ferrier, 2002). The second option is to persist with delineating intraspecific units (ESUs) on the basis of a clearly defined strategy that is consistent with both our conservation goal and our understanding of the evolutionary and ecological processes pertinent to the species in question. Although the first option is sound conceptually and warrants further consideration, in the following I persist with the second option, delineating subspecific units (ESUs) in recognition of their immediate practical value.

Since the need to prioritize intraspecific units for conservation was first identified, both the concepts and criteria for recognizing ESUs have been debated actively, and a consensus is yet to emerge. The term ESU itself is value-laden; concepts are clouded by differences over the relative importance of adaptive difference (primarily indicated by phenotypic or quantitative genetic information, or both) versus historical isolation (primarily indicated by molecular data) and how ESUs might relate to species under various concepts about the latter. Debate is ongoing over how stringent criteria should be, with concerns about both over- and undersplitting the intraspecific units. To complicate matters further, there is also disagreement about essentially parochial issues such as interpretation of how criteria for ESUs reflect the intent of local legislation and regulations (Pennock and Dimmick, 1997; Waples, 1998). It is important to resolve these issues, or at least identify where the differences of opinion lie, and why, if the ESU concept is to be applied by conservation biologists and the results implemented by managers.

In a recent critique, Paetkau (1999) noted that several commentators have confused the underlying goals with the criteria by which we might identify such units. In the following I discuss these in turn, using as a reference point the concepts and criteria I put forward earlier (Moritz, 1994a; see also Moritz et al., 1995; Moritz, 1999), recognizing that these have been widely used (often with considerable latitude; see Crandall et al., 2000) and have proved to be something of a lightning rod for debate. In brief, in Moritz (1994a) I proposed the following:

- The goal is to ensure that major historical lineages with recognized species are protected and that the evolutionary potential inherent across the set of ESUs is maintained. Emphasis was placed on delineating sets of populations that are historically isolated from others, rather than on current adaptive diversity (see below). A second category, management units (MU), was suggested to recognize demographically distinct populations that should be managed to ensure the viability of the larger ESU.
- The criteria for recognition of these conservation units were that (1) ESUs should be reciprocally monophyletic for mitochondrial (mt) DNA alleles and show significant divergence of allele frequencies at nuclear loci, and (2) MUs should have a significant divergence of allele frequencies at nuclear or mitochondrial loci, regardless of the phylogenetic distinctiveness of the alleles (for useful critiques of the use of genetic data to define MUs, see also Taylor and Dizon, 1999; Taylor et al., 2000).
- As conservation units, ESUs complement recognized species; thus, recently diverged (or introgressed) recognized species should be protected regardless of whether or not they satisfy the criteria for an ESU.

Debate About Goals and Concepts

ESUs are equivalent to, and should be replaced by, species.—Several authors have argued that, as historically isolated and diagnosable sets of populations, ESUs are equivalent to species, as defined under the Phylogenetic Species Concept, and should be formally recognized in order to maximize effectiveness of systematics as the foundation for conservation assessments (Cracraft, 1997; Cracraft et al., 1998). In accordance with the philosophy of cladistic systematics, the Phylogenetic Species Concept seeks to identify the boundary between reticulation and divergence and uses as a criterion fixed character states (of any sort) that distinguish populations (e.g., Goldstein et al., 2000). This is one among many views of species and is by no means universally accepted by practicing taxonomists or evolutionary biologists because it has the potential to trivialize the spatial and temporal

complexity of the speciation process and to identify as “species” groupings that are inherently ephemeral (Templeton, 1989; Avise, 2000b). In a thoughtful review of species as evolutionary lineages, deQueiroz (1998; see also Mayden and Wood, 1995) points out that each of the plethora of definitions of species emphasizes a particular stage of divergence, evolutionary process, or criterion/methodology and that multiple criteria should be used to delineate species. In this context, the assertion that the description of biological diversity should be solely within the realm of systematics and exclusive of population genetic and evolutionary theory (Goldstein et al., 2000) is misplaced. We need to draw on both evolutionary theory and systematics to document diversity and understand the evolutionary processes that sustain it (Bowen, 1999).

ESUs should emphasize adaptive variation.—The majority of authors have argued that ESUs should be identified to protect both (presumed adaptive) phenotypic variation and historically isolated segments within species, that is, both axes of genetic diversity (Fig. 1). Particular concern has been expressed about overemphasis on presumed neutral molecular variation when phenotypic and quantitative genetic variation is what underlies fitness in current and future environments (Hard, 1995; Lynch, 1996; Pamilo and Savolainen, 1999; compare with Dimmick et al., 1999). This debate is exemplified by differences between views expressed in Moritz (1994a, 1999) and Crandall et al. (2000); whereas I argued that explicit preservation of current adaptive phenotypes not only is difficult but could retard evolutionary responses, the latter gave priority to presumed adaptive variation over evidence for historical (or current) isolation (Fig. 2). Given that historically isolated units cannot be recovered, the suggestion that historically isolated but phenotypically similar (“ecologically exchangeable”) populations should be considered as components of a single ESU (cases 4 and 7 in Fig. 1 of Crandall et al., 2000) seems inappropriate.

Remarkably, both views are based on a common goal: to maintain evolutionary processes. Furthermore, both seek to retain viable populations of species across the maximum diversity of habitats. The fundamental difference of opinion relates to perceptions about recoverability of adaptive phenotypes,

that is, whether populations can remain viable under selection to restore an optimal phenotypic distribution. For some groups of organisms, notably plants and fish, extensive evidence from both comparative studies and field experiments indicates that specific phenotypes can be regenerated under recurrent selection (reviewed in Moritz, 1999; Moritz et al., 2001a). Recognizing the high frequency of convergent evolution of life histories and ecomorphs within fish, Bernatchez (1995) suggested that rare phenotypes should be accorded more weight in establishing conservation priorities. Clearly, in certain circumstances a combination of extrinsic threatening processes, life history attributes, and intensity of selection will reduce population viability (Pease et al., 1989; Lande and Shannon, 1996). Yet the challenge is to identify such situations and respond accordingly, rather than to give blanket priority to protection of phenotypic variants at the expense of historical lineages.

A second limitation of the argument that phenotypic difference should be paramount is the assumption that this variation reflects heritable and adaptive divergence (Phillips and Ehlinger, 1995). Even demonstrating that the traits in question are heritable within a population is insufficient evidence because phenotypic differences among populations can arise through genotype by environment interaction (Lynch and Walsh, 1998). Often, there is no evidence to indicate that differences in geographic differences in phenotype are either truly genetic or adaptive. I conclude that the most effective means to protect the adaptive component of diversity is to focus on maintaining the context for selection—that is, viable populations across heterogeneous environments—rather than protecting specific phenotypes (other than when these are essential to retain population viability).

Debates About Criteria

The criterion for an ESU suggested earlier, reciprocal monophyly of mtDNA alleles and significant divergence of allele frequencies at nuclear genes (Moritz, 1994a; see also Dizon et al., 1992; Vogler and DeSalle, 1994), has the advantage of being qualitative, but it can be criticized on several grounds. One valid concern is that this criterion imposes an arbitrary threshold on a continuum of divergence (Crandall et al., 2000). At the cost of

increased ambiguity, this could be overcome by weighting sets of populations according to their phylogenetic or nucleotide divergence (see Moritz and Faith [1998] for caveats).

Several have argued that, as an absolute criterion, requiring reciprocal monophyly could be either too stringent or too sensitive (Legge et al., 1996; Angers and Bernatchez, 1998; Paetkau, 1999; Crandall et al., 2000; Goldstein et al., 2000) and is also prone to sampling error. On the assumption that the mtDNA variants are selectively neutral, the time taken to achieve reciprocal monophyly depends on the prior population structure and on subsequent effective population sizes (N_e), and is $\sim 4 N_e$ generations, in cases where a single panmictic population has been sundered into two equal size units (Neigel and Avise, 1986). The reciprocal monophyly criterion has also been deemed too stringent because distinct species that have arisen from recent and rapid adaptive divergence do not qualify as ESUs (Paetkau, 1999; Crandall et al., 2000; Goldstein et al., 2000). However, these criticisms overlook the fact that ESUs are intended to complement recognized species, not replace them (Moritz, 1994a). Thus, recognized but recently derived species of cave spider (Crandall et al., 2000) or bears (Paetkau, 1999) should be protected even though they appear as monophyletic lineages within larger paraphyletic sister taxa.

A broader and valid concern raised by Crandall et al. (2000) is that, because researchers are concerned about the fate of the populations they have studied, they sometimes apply the criteria of Moritz (1994a) with a lack of rigor. Obviously, once a strategy and criterion have been selected, the available evidence should be interpreted within the expected norms of phylogenetic or statistical rigor, bearing in mind the need to consider power and the consequences of

their conclusions (Taylor and Dizon, 1999). Debate about strategies, criteria, and methods of inference for ESUs is important and undoubtedly there is room for improvement; e.g., use of Nested Clade Analysis (Crandall et al., 2000) to establish historical isolation or maximum likelihood methods to estimate divergence time from gene trees (Edwards and Beerli, 2000). More generally conservation biologists should consider the evolutionary processes operating within the taxon in question and then develop a strategy and criteria relevant to protecting evolutionary processes and diversity in that taxon.

EXTENSION TO AREAS: COMBINING SPECIES AND GENETIC LAYERS OF DIVERSITY

Driven by international and national agendas to conserve global biodiversity, and also by regional issues, intensive efforts have been made to develop methods for describing and prioritizing areas for protection or rehabilitation (Margules and Pressey, 2000). These methods typically apply principles of complementarity, endemism, or irreplaceability to prior knowledge of vegetation or species diversity (or environmental surrogates for these) to capture the maximum diversity at these hierarchical scales. For conservation geneticists, the question is how, within this process, to represent the major elements of intraspecific diversity and the processes that generate them. A second question is whether protection of genetic diversity can be accommodated by approaches focused on species and community diversity or whether complementary strategies are needed.

Progress towards answering these questions can be made by seeking parallels between measures of local and regional diversity for species and measures of genetic diversity within species (Table 1). According to Cody (1996), species diversity can be

TABLE 1. Parallels between geographic pattern of species and genetic diversity and possible predictors or surrogates for these.

Distribution	Species diversity	Genetic diversity	Predictors or surrogates
Within habitat and region	α diversity	Heterozygosity, additive variance	Habitat area and suitability ($\rightarrow N_e$)
Between habitats	β diversity	Phenotypic divergence (Q_{st})	Habitat heterogeneity
Between regions within habitats	γ diversity	Phylogeographic divergence (D_a , PD)	Geographic distance; paleoclimatic modeling

partitioned into local richness (α diversity), turnover among habitats (β diversity), and turnover between biogeographic regions within habitats (γ diversity). The corresponding measures for genetic diversity within species are heterozygosity (or additive variance for polygenic traits), geographic phenotypic diversity (Qst; Lynch et al., 1999), and phylogeographic diversity (PD; Moritz and Faith, 1998; or net nucleotide divergence D_a ; Nei, 1987). In broad terms, the first two measures relate to the adaptive component of diversity whereas the last is a measure of the vicariance axis.

To illustrate a possible condition for congruence between species and intraspecific diversity, consider a hypothetical set of communities distributed across a set of areas separated by substantial temporal isolation and within which multiple habitats exist. Some species are habitat specialists or have diverged across biogeographic units or adjacent habitats; others are widespread but with substantial phenotypic variation among habitats and phylogeographic structure across biogeographic units (Fig. 2). Simplistically, and assuming community and evolutionary equilibrium, habitats of maximum area will contain maximum α species diversity and local genetic diversity (through a large N_e). Combinations of the most environmentally divergent habitats will maximize β species diversity and adaptive genetic diversity for widespread species. Combinations of biogeographic units that have sustained the longest periods of isolation will represent the maximum γ species diversity and phylogeographic (vicariant) diversity. Given this scenario, use of algorithms to maximize species diversity could also represent intraspecific genetic diversity efficiently.

Of course, this idealized situation will rarely apply in nature: Communities or species will depart from equilibrium in response to recent fluctuations, whether driven by natural or anthropogenic disturbance or because of idiosyncratic effects on community structure or species diversity. Thus, it is necessary to test, rather than assume, the efficiency with which species-based algorithms can represent adaptive and historical diversity within species that are widely distributed across the same area. A further consideration is that the extent of congruence is likely to vary according to the geographic

scale of the area in question, vagility of the organisms concerned, and the degree to which historical climatic or geological factors have caused long-term vicariance among biogeographic units. For example, Ferrier et al. (1999) observed substantial γ diversity for low-vagility invertebrates, but not vertebrates, across forested habitats in northeast New South Wales. For this same area, analyses of phylogeographic diversity in wet-forest herpetofauna (Moritz, C. Hoskin, and B. Phillips, unpubl. data) revealed either low or geographically discordant structure, suggesting an absence of major vicariance events for vertebrates.

The above discussion concerns mostly representation of species and genetic diversity. We also need to consider persistence of both species and the evolutionary processes that sustain genetic diversity (Cowling et al., 1999; Cowling and Pressey, 2001). In general, the principles for sustaining diversity of species and genetic diversity within habitats are well established: maximize area and habitat quality. To maintain the process of isolation, translocations of species or of individuals from widely distributed species among biogeographic units should be actively prevented (Rieseberg and Wendel, 1993; Rhymer and Simberloff, 1996; Moritz, 1999). Yet areas that represent natural admixtures between historically isolated biogeographic units, identifiable through zones of secondary contact for multiple species (e.g., Hewitt, 2000), warrant protection so as to maintain this evolutionary process, even though they will often be ranked low according to complementarity measures (e.g., the Australian Wet Tropics example below).

What is stressed less often is the need to also protect the connectivity across a mosaic of habitats, e.g., across environmental gradients, within biogeographic units. Ensuring connectivity of distinct habitats allows for migratory responses to seasonal and longer term variation in the spatial distribution of habitats, and thus β diversity of species (Huntley, 1998; Stoltz, 1998). Further, as this is establishing conditions for clinal variation, it also maximizes the range of genetically based phenotypic variation available for future selection (Endler, 1977), that is, the adaptive component of genetic diversity. Both issues are very pertinent to planning for viability under rapid climate change

(Kareiva et al., 1993). Protecting connectivity of habitats across environmental gradients is consistent with the calls to protect ecotones as areas of active diversification (Smith et al., 1997) and to maintain environmentally peripheral populations as sources of genetically determined stress-resistance (Lesica and Allendorf, 1995; Hoffman and Parsons, 1997). However, this approach differs starkly from that based on the perception that species-rich communities can be protected by protection of optimal habitats alone, often as patches within a sea of heavily modified landscapes.

From the discussions above, we can derive a general strategy for conservation planning:

1. *Keep the pieces.* Identify combinations of areas that maximize representation of species or historically isolated segments of widely distributed species (or both).
2. *Maintain evolutionary processes.* Add areas that represent specific evolutionary processes such as adaptive diversification or an admixture of historically isolated populations.
3. *Ensure persistence.* Within the areas identified in 1 and 2, ensure that contiguous habitats of sufficient area are protected across major environmental gradients.

Of course, the robustness of the outcomes will rest on the extent and quality of the data on distributions of community, species, and genetic (phenotypic and molecular) diversity. In many cases, species groups for which data are adequate (e.g., trees, birds, butterflies) may not be good surrogates for other groups, even where there is an underlying biogeographic correlation of species diversity and complementarity (Moritz et al., 2001b). Further, evidence on historical biogeography from molecular data, paleoecology/geology, or both is frequently lacking. Whether or not environmental data or mapped vegetation distributions can serve as adequate surrogates of species diversity is debatable (Faith and Walker, 1996; Ferrier, 2002) and is likely to be context-dependent. In general, congruence among taxa and between geographic patterns of species and (vicariant) genetic diversity will be greatest across systems with a long-term history of vicariance and persistence within Quaternary refugia. Evidence from one such system, the Wet Tropics rainforests of northeast

Australia, is reviewed in the following case study.

CASE STUDY: THE FAUNA OF THE
AUSTRALIAN WET TROPICS RAINFORESTS
*Historical Biogeography and Evolutionary
Processes*

The Wet Tropics rainforests of northeast Australia (Fig. 3) represent the largest area, with the highest endemism and greatest richness of species, within a chain of upland, cool, rainforested environments surrounded by a relatively xeric and warm environment along the east coast of Queensland (Nix, 1991; Moritz et al., 1997). Within the Wet Tropics, endemic species of vertebrates and low vagility insects (excluding ants) are concentrated in the mid- to high (>400 to 1600 m) elevations (Monteith, 1996; Williams et al., 1996) across a series of massifs along the geologically old Great Dividing Range. Because the area is small (~750,000 ha of rainforest) and intensively studied, unusually good information is available on both taxonomy and distributions of species. Not surprisingly, overall richness of endemic species and of local endemism is greater in low-vagility invertebrates than in vertebrates (number of endemic species/percent restricted to single subregions: snails, 190/46%; insects, 330/43%; vertebrates, 64/11% [Moritz et al., 2001b]).

Both paleoecological (Nix, 1991; Hopkins et al., 1993; Kershaw, 1994) and molecular phylogeographic (Schneider et al., 1998; Hugall et al., in press) evidence indicates that the mesothermal rainforests and their specialist fauna have undergone substantial contraction for much of the Quaternary (and possibly much earlier; Kershaw, 1994) (Fig. 3), with the current distribution representing an early to mid-Holocene (8,000 years ago) expansion. Relative to the current distribution (Fig. 3A), paleoclimatological modeling (Fig. 3B; Nix, 1991) predicts a very different potential distribution of rainforests, with a major vicariance around the present Black Mountain Corridor (BMC) and virtual or complete loss of currently rainforested areas to the south and west (e.g., HU, SU, LE, WU) under the cooler, drier conditions that prevailed for much of the Quaternary. Conversely, modeling of cooler, wetter conditions during the mid-Holocene (7,500–5,000 years ago) predicts greater connectivity

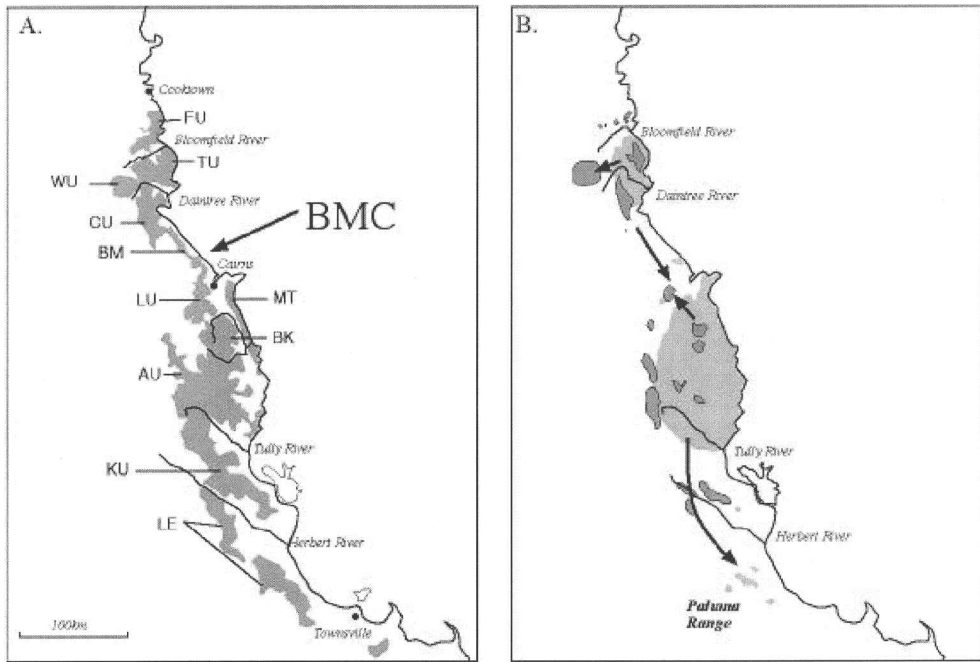


FIGURE 3. Maps of the Wet Tropics region of northeastern Australia showing (A) the current distribution of upland (300–1,600 m above sea level) rainforest and (B) the predicted distribution of refugia during the last glacial maximum according to paleobioclimatological modeling (light stippling; Nix, 1991) and plant phylogeography (modified from Schneider et al., 1998). Key areas mentioned in the text are labeled in A. In B, the heavy arrows indicate probable routes for early Holocene range expansion (see Schneider et al., 1998, for details).

of mesothermal climates than at present (Nix, 1991), suggesting the opportunity for colonization of newly expanded forests and the admixture of historically isolated faunas.

This evidence for long-term vicariance and potential retention of multiple geographically disjunct refugia is expected to dominate regional patterns of richness and complementarity for endemic species and also to dominate phylogeography within species. For endemic terrestrial vertebrates, richness within biogeographic subregions correlates positively with area and habitat diversity and negatively with convolution of shape (Williams and Pearson, 1997). Further, both richness and complementarity (primarily γ diversity) of endemic species of vertebrates, insects, and to a lesser extent, snails are correlated among areas (Moritz et al., 2001b). Inspection of ordination plots (Figs. 4A–C) suggests common patterns of species turnover (γ diversity) across the BMC and, to a lesser extent, a grouping of sites from the central regions (AU, BK, KU, LU). Two geographically intermediate areas (BM, MT) have more idiosyncratic distributions in these ordinations.

Intraspecific phylogeography of mtDNA has been examined for several species of vertebrate endemic to, and widespread across, the Wet Tropics: four species each of frogs and lizards (Schneider et al., 1998, 1999; M. Cunningham, pers. comm.) and five of birds (Joseph et al., 1995). In addition, data from one species of snail endemic to upland rainforests have been examined (Hugall et al., in press). In all but two species (birds), the phylogeographies are dominated by splits across the BMC, and supplementary phylogeographic breaks—indicative of additional Quaternary refugia—are present in some species (e.g., the torrent frog *Litoria nannotis* and the gecko *Carphodactylus laevis* in Schneider et al., 1998). Further, several species have clear signals of recent range expansion in their mtDNA gene trees (e.g., Schneider and Moritz, 1999), and populations from the southern subregions tend to have subsets of alleles found in populations to the north (Joseph et al., 1995; Schneider et al., 1998), consistent with the hypothesis that these communities were recently established from major refugia (e.g., AU). Finally, evidence now points to zones of secondary

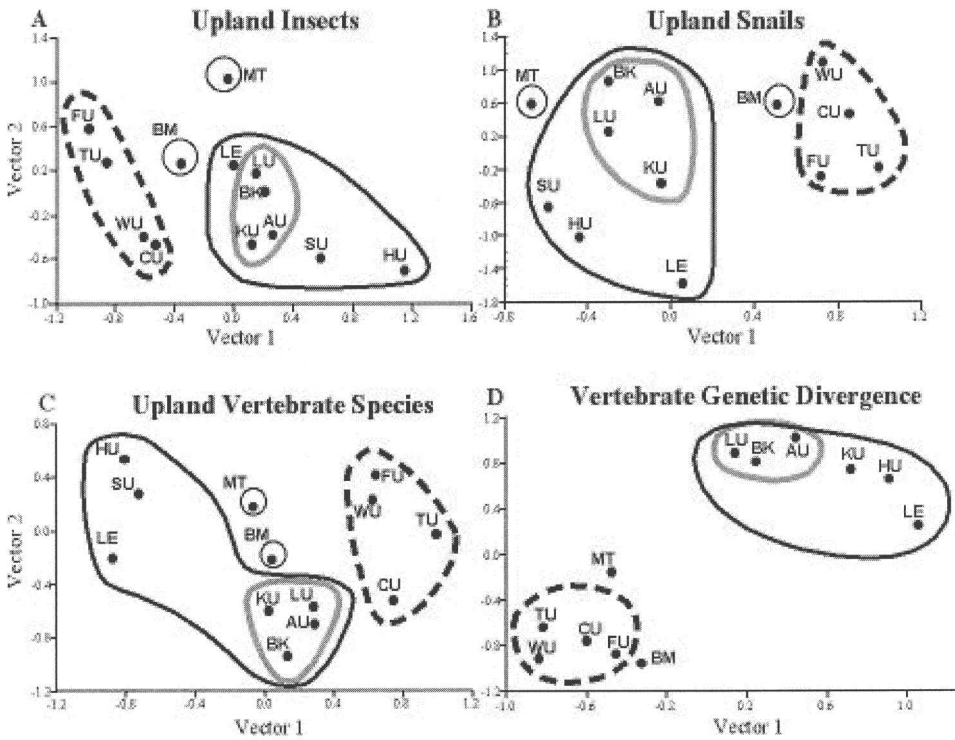


FIGURE 4. Ordination (MDS) plots illustrating general similarity of patterns of geographic turnover for endemic species (γ diversity) and genetic divergence among subregions of the Wet Tropics rainforests. These plots were generated from matrices of pairwise dissimilarity for species presence—(A) low-vagility insects; (B) snails; (C) vertebrates (see Moritz et al., 2001b, for details), and (D) averaged mtDNA net sequence divergence across 12 species of vertebrates. In all cases, areas to the north of the BMC grouped separately from those to the south and, within the latter, central sites (AU, LU, BK) were also associated.

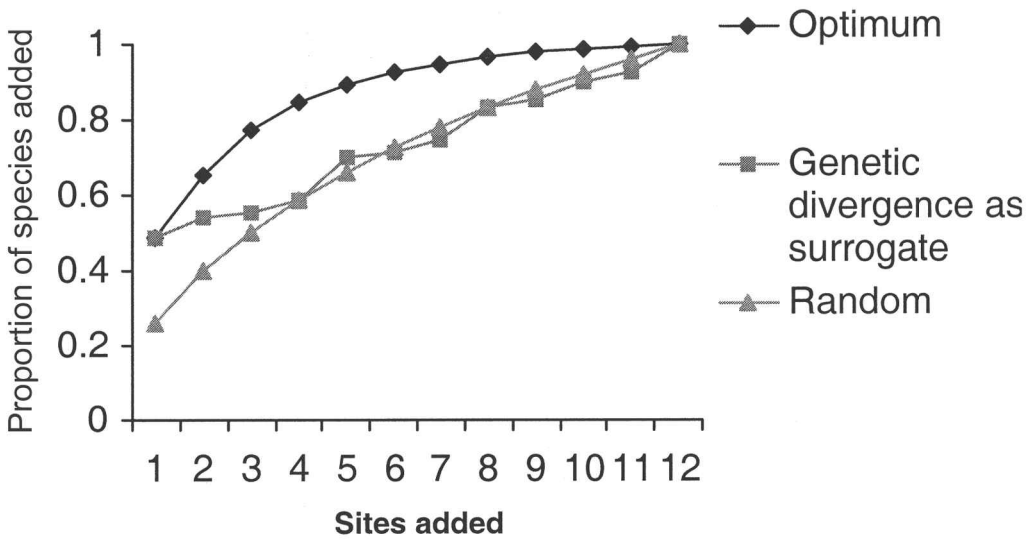
contact between historical isolates in several species, particularly at the boundary of LU and AU, where lineages formerly isolated across the BMC now meet and are hybridizing (Fig. 3B) (Pope et al., 2000; Phillips et al., unpubl.).

The combined evidence from paleoecology and phylogeography suggests the scenario for historical biogeography illustrated in Figure 3B. Remarkably, comparison of morphology between populations to the north and south of the BMC has revealed only subtle, if any divergence, even for species with 8% or greater net divergence in mtDNA sequences across this break (Schneider and Moritz, 1998; Schneider et al., 1999). In contrast, in the skink *Carlia rubigularis*, comparison of morphology across adjacent environments reveals marked changes in body size and shape, possibly reflecting differences in predation rates (Schneider et al., 1999). These observations reinforce the notion that evolution across the adaptive and

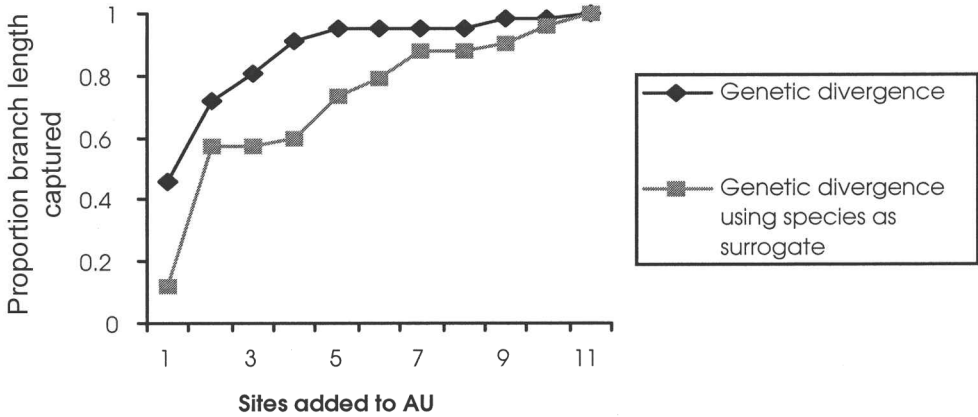
historical axes of diversity can proceed independently.

Conservation Priorities for Areas: Species Versus Genetic Diversity

These observations and inferences about the biogeographic and evolutionary processes operating in Wet Tropics fauna provide the basis for illustrating steps 1 and 2 of the conservation strategy outlined above. Analysis of conservation priorities for endemic species of insects, snails, vertebrates, and one family of plants (Moritz et al., 2001b), using irreplaceability (Ferrier et al., 2000) and a target of representing each species in at least one area, identified five upland areas (AU, CU, BK, TU, and FU) that collectively represented >80% of overall species diversity. Each of these areas was predicted by paleomodelling to contain mesothermal rainforest refugia (Fig. 3B). In contrast, the five lowest ranked upland subregions (HU, WU,



(A)



(B)

FIGURE 5. Efficiency of species diversity as a surrogate for representing genetic divergence and vice versa. (A) Proportional accumulation of faunal species in the Wet Tropics with addition of sites in the sequence determined by irreplaceability analysis on the species data (optimum), the genetic divergence (Da) matrix (genetic divergence surrogate), or random addition of sites (see Moritz et al., 2001b, for methods). (B) Proportional accumulation of total genetic divergence (branch length normalized to the total) for vertebrates from the Wet Tropics as based on the genetic data themselves to prioritize sites (genetic divergence) compared with the sequence determined for species data.

LE, SU, and BM) all represent regions for which paleomodels predict little if any retention of rainforests under a full glacial climate (see Fig. 3B). Interestingly, subregions for which the comparative phylogeography indicates secondary contacts (LU)—or a mixture of northern lineages in some species, southern in others, and phylogeographically distinct in yet others (MT)—have intermediate priority in the analysis of species irreplaceability.

For the vertebrate genetic data, matrices of pairwise net nucleotide divergence among areas (Da ; Nei, 1987) were averaged across species to estimate relative “community” divergence time (assuming that each species represented a sample of a common historical process). The averaged matrix was then represented hierarchically (as a neighbor-joining tree) and nonhierarchically by way of multidimensional scaling (Fig. 4D). Areas were selected iteratively to capture the

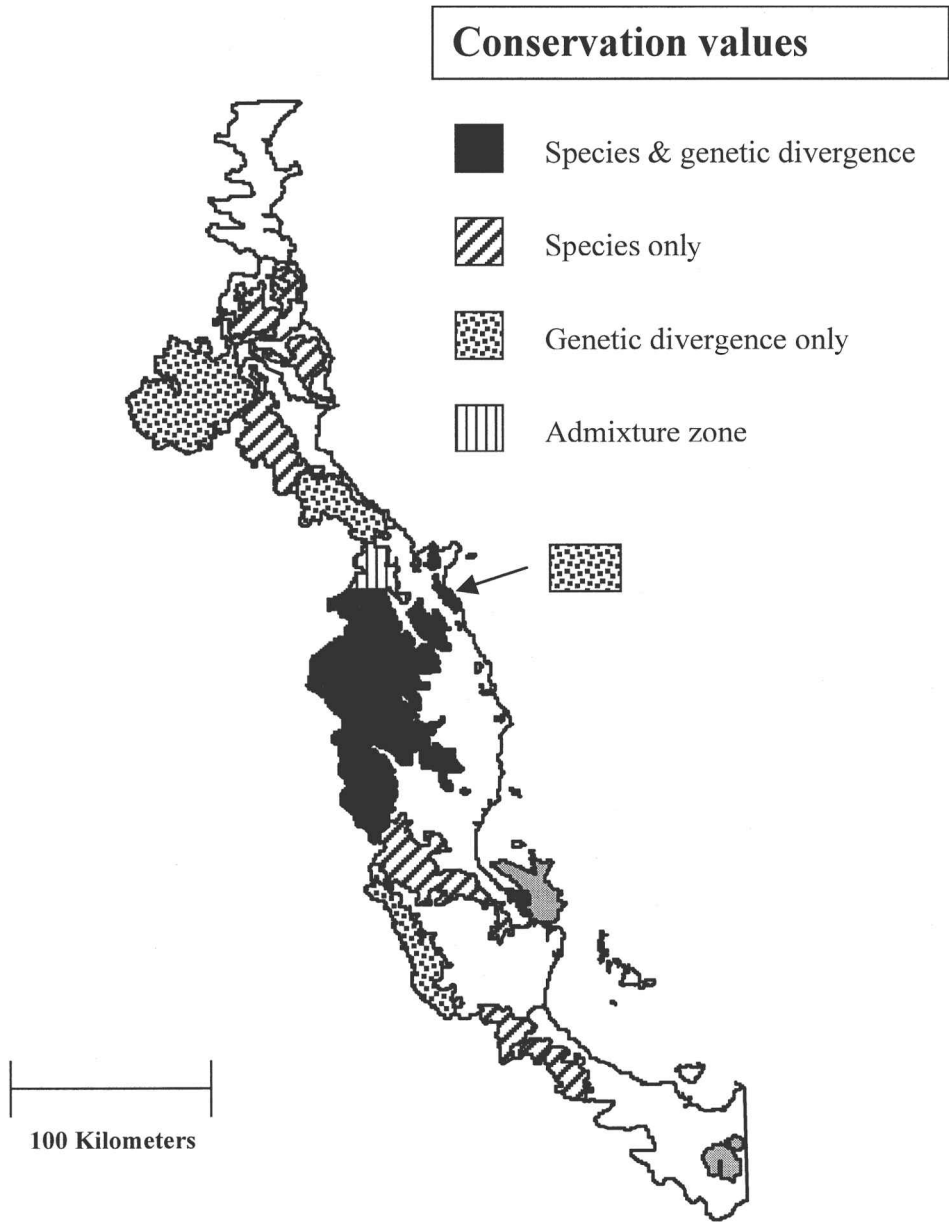


FIGURE 6. Visual summary of faunal conservation values recognized for different subregions of the Wet Tropics rainforests. Note that some areas have not been ranked here. The two areas shaded in gray were not included in the present analysis (but see Moritz et al., 2001b) because no data for vertebrate genetic divergence were available there.

maximum genetic divergence (D_a) in multidimensional space by using the ED algorithm described by Faith and Walker (1996). Starting with AU, sites were added in the order WU, LE, MT, BK, BM, KU, TU, LU, FU, HU, and CU; 95% of the total branch length on the neighbor-joining tree was captured across the top six sites (Fig. 5A). Not

surprisingly, successive sites were added from opposite sides of the BMC.

The priority accorded to sites differs markedly between the analyses based on faunal species distributions versus those for genetic divergence of vertebrates. Excluding AU and BK, four of the top six sites for genetic diversity were in the bottom five of sites

for species diversity (in order of decreasing importance for species diversity: AU, BK, CU, TU, FU, KU, HU, MT, LU, WU, LE, BM). Considering just the 12 sites for which (faunal) species and (vertebrate) genetic data are available, the sequence of sites optimized by using genetic data performed significantly worse at accumulating species than did that using the species data; in fact, optimization of the genetic data did no better than random addition of sites (Fig. 5A). Conversely, the order of sites optimized for species performed poorly for accumulating vertebrate genetic divergence in comparison with using the genetic data themselves (11 vs. 6 sites required to achieve 95% of total branch length, respectively) (Fig. 5B).

The main message from this analysis is that we cannot assume, at least for this system, that conservation priorities set to maximize representation of species will adequately protect the (vicariant) genetic divergence present among populations with species. This is despite the observation that, for both species (γ) and genetic (Da) diversity, the geographic pattern is dominated by the same biogeographic feature, the BMC (Figs. 4A–D). For the species analysis, greatest priority was accorded to sites predicted to have retained discrete refugia during the cool/dry periods of the Pleistocene (compare Figs. 3B and 6). For vertebrate genetic divergence, the addition sequence was dominated by the BMC, and several of the presumed areas of refugia added little genetic divergence, possibly because they acted as sources for recent recolonization to other areas. Whatever the reason for the discrepancy, conservation planning should recognize that some areas will be important for representing both genetic and species diversity (AU, BK), some primarily for species diversity (CU, TU, FU, KU, HU), and still others primarily for genetic diversity (WU, LE, MT, BM) (Fig. 6).

Interestingly, neither approach to prioritization identified LU, the region with multiple admixture zones, as being of high significance (relative to other areas). This area was not predicted to have populations that are refugia (Fig. 3B); phylogeographic analysis, however, shows LU to be an area with multiple zones of secondary contact following recolonization from both north (presumably CU) and south (AU or BK). Given the significance of this area for protection of a significant evolutionary process (hybridization), it

should also be included in the set of priority areas for conservation effort (Fig. 6). The outcome, then, is that of the regions for which both genetic and species data exist, 12 are perceived as being important to represent diversity, but the reasons for doing so vary, as may management strategies.

CONCLUSIONS

This paper follows the theme set by Frankel (1974) in emphasizing the importance of protecting evolutionary processes. Four general themes emerge:

1. Conservation strategies for species may be improved, and made more flexible, by considering separately the genetic diversity that arises from adaptive rather than vicariant processes.
2. Conservation geneticists must find ways to incorporate the geographic tools and concepts developed for prioritizing areas according to other levels of diversity (species, ecosystems, environmental surrogates).
3. Phylogeographic and species diversity data can be usefully combined for integrated conservation planning at the level of communities and biogeographic subregions.
4. Whether working at the level of single species or biogeographic regions, no single prescription best predicts how to protect the evolutionary and ecological viability of the biota. Rather, the underlying evolutionary and ecological process should be considered for each species/system and a strategy devised accordingly.

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