THE USE AND APPLICATION OF PHYLOGEOGRAPHY FOR INVERTEBRATE CONSERVATION RESEARCH AND PLANNING

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Abstract—To conserve evolutionary processes within taxa as well as local co-evolutionary associations among taxa, habitat reservation and production forestry management needs to take account of natural genetic-geographic patterns. While vertebrates tend to have at least moderate dispersal and gene flow on a landscape-scale, there are good reasons to expect many small, flightless, ecologically specialized saproxylic invertebrates to be strongly subdivided owing to low powers of dispersal, long-lived stable microhabitats and multiple generations within a single log. Phylogeographic studies have repeatedly demonstrated that, in low vagility taxa, (1) traditional morphological taxonomy underestimates genetic diversity, (2) conservation strategies focused at and above the species-level are inadequate, and (3) it is not atypical for sedentary invertebrates to exhibit high local endemism over very fine spatial scales. Phylogeography and comparative phylogeography provide an empirical framework for maximizing the conservation benefit of reserves, and directing conservation strategies and sustainable management practices outside of protected areas.

INTRODUCTION

Sustainable forestry practices are underpinned by maintaining healthy productive forests, which in turn depend on efficient cycling of nutrients throughout the system. Rotting logs on the forest floor serve as a critical arena for nutrient cycling (Grove 2002a, 2002b, 2002c), but the biology, population structure and ecology of many members of the key invertebrate groups that aid in the decomposition of coarse woody debris are poorly studied. Many log-dependent (saproxylic) invertebrates are likely to show marked population structure over very fine spatial scales owing to their ecological specialisation and inherently poor dispersal abilities (Schiegg 2000, Warren and Key 1991). Despite this, conservation planning is often based on more mobile surrogate taxa such as mammals (Stiling 1999). Thus current forest management practices probably fail to cater adequately for the economically and ecologically important and incredibly species-rich rotting log faunal assemblages. Indeed, basic questions critical in conservation management such as how often, how large, and how far apart species habitat patches should be, remain largely unanswered (Thomas and Morris 1994).

Ecological characteristics of certain fauna tend to influence their efficiency in capturing geographical patterning in biota resulting from long-acting processes such as climatic cycles (Moritz and others 2001). Because invertebrates may have considerably smaller ranges than vertebrates, they can potentially provide fine-scale information about processes that have led to current biogeographic patterns, and given that low vagility (flightless) invertebrates often show high fidelity to their preferred habitat, they are particularly likely to be efficient indicators of historical climate change in those habitats (Yeates and others 2002). For these reasons, we propose that saproxylic invertebrates may represent an exceptional community for capturing landscape history given that these animals experience their local environment at very fine spatial scales, such that even individual creek lines and gullies may represent refuges for viable populations during cool dry glacial periods (Heatwole 1987).

Phylogeography (sensu Avise 1987) is the study of geographical distributions of closely related genealogical (genetic) lineages. It makes a critical contribution to evolutionary and population biology because it concentrates on the interface of processes acting within species (population genetics) and among species (phylogenetics) (Avise 1998, 2000). Accordingly, phylogeography can identify processes that influence speciation and illuminate population history. It has become apparent that phylogeographic analysis of unrelated, co-distributed taxa (comparative phylogeography) has unique potential to address long-standing questions about the formation of organismal communities, landscape ecology, and the sources and maintenance of biodiversity. Given that we should seek to maintain evolutionary processes, it is of paramount importance to understand how historical processes have shaped contemporary genetic and species diversity in whole communities. Although the details of such processes are likely to vary from one system to another, it should nonetheless be possible to formulate conservation strategies that protect both irreplaceable (historical) genetic diversity, as well as adaptive genetic diversity (Moritz and others 2000). Furthermore, concordant phylogeographic patterns among multiple diverse taxa generate predictions about present-day patterns of genetic variation for co-distributed taxa that have yet to be sampled, thereby potentially extending the findings of such studies to regional species assemblages (Avise 1998). Consequently, phylogeographic studies are directly relevant to conservation planning, whereby management strategies can be tailored so as to maximise the benefit of nature reserves, and the great potential for production forests to compliment within-reserve conservation can be realised through sustainable low-impact management practices that take account of the evolutionary history of biota. Unfortunately, invertebrates are poorly represented in phylogeographic studies (e.g.,

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Molecular Ecology Phylogeography Special Issue 1998, Avise 2000). Yet many invertebrates, especially sedentary terrestrial groups such as the ecologically specialised log-dependent fauna (Warren and Key 1991, Yee and others 2001), are likely to deviate from population-genetic models based on well-studied relatively large and mobile vertebrate species. For saproxylic invertebrates, management practices that maintain both spatial and temporal connectivity of dead wood are likely to be critical for retaining biodiversity (Grove 2002a, Schiegg 2000).

This review aims to inform researchers and natural resource managers of the potential benefits and applications of phylogeographic studies, with particular emphasis on invertebrates —an understudied yet exceptionally diverse group of high ecological importance (Wilson 2001). First, key considerations relating to taxon sampling are highlighted, and the array of molecular tools and analytical techniques available for answering questions about long-term population dynamics of forest invertebrate fauna and their responses to historical climate change are introduced. We then overview conservation-based applications of phylogeography, giving examples from studies of diverse invertebrate species, and illustrate the high degree of local endemism that may be typical of many saproxylic invertebrates via a case study of a log-dwelling 'giant' springtail (Collembola) from a south-east Australian temperate forest. Finally, we present some broad generalisations that can be drawn from the existing body of phylogeographic research.

TAXON SAMPLING: SPATIAL SCALE AND STRATEGY

Phylogeography usually addresses evolutionary questions at and below the level of biological species. A critical requirement is adequate sampling at an appropriate spatial scale throughout the geographic range of the populations under study (Templeton 1998, Templeton and others 1995). In the case of relatively sedentary taxa such as saproxylic invertebrates, this can be in the order of several of kilometres or less (Peterson and Denno 1998). Under a fine-scale sampling regime, precise geographic locations of contact zones among distinct genetic lineages can be identified, and the degree of population structure (i.e., genetic differentiation) can be determined with considerable accuracy. A nested sampling design (e.g., individuals within sites, sites within areas, areas within regions) allows analyses at hierarchical spatial scales, which in turn can be used to distinguish between population history and structure (Templeton and others 1995). The incorporation of independent demographic, morphological (phenotypic), and environmental data such as landscape history (e.g., geology or palaeoclimatology) and ecological information further increases the power of phylogeographic inference, and permits more sophisticated analyses that can reveal the relative influence of specific environmental and ecological components upon the present-day spatial distribution of genetic diversity (Moritz and others 2000).

MOLECULAR TOOLS IN THE 'PHYLOGEOGRAPHIC TOOLBOX'

Mitochondrial DNA

The traditional molecular marker of choice in animal phylogeographic studies has been mitochondrial DNA (mtDNA) (Avise 2000). The mitochondrial genome is usually maternally inherited (Hutchinson and others 1974), allowing interpretation of genealogical relationships that have been largely unaffected by recombination. Due to the lack of a mutation repair mechanism mtDNA sequences evolve at a much faster rate than nuclear gene sequences, making them sufficiently variable to yield information relating to evolutionary relationships at a variety of temporal scales, and across multiple taxonomic levels (Avise 2000, Harrison 1989). Further, genetic variation in mitochondrial protein-coding genes is mostly selectively neutral, such that the genetic signature of historical lineage divergence is not overwritten by natural selection (Avise 2000). Finally, the mutation rate of animal mtDNA has been widely studied, and based on calibrations using fossil and/or geological dating, coding regions in most species are believed to evolve at approximately two percent sequence divergence per million years (Brower 1994, Brown and others 1979). The application of a molecular clock permits estimates of the absolute ages of lineage splitting events, which in turn can be used to generate or test biogeographic hypotheses, and identify factors likely to have had major impacts on the evolutionary history of populations, species, and species assemblages.

However, there are several reasons why mtDNA should not be used to the exclusion of other gene regions. First, because the mitochondrial genome is inherited as a single cohesive unit, phylogeographic studies based on mtDNA alone are effectively evolutionary studies of a single molecule, not the species. Whilst mitochondrial evolution may be a good approximation of the evolutionary history of the host organism, there are well-known mechanisms by which relationships among alleles at any locus (i.e., a gene tree) will not match those of the species (Avise 2000, Ballard and Whitlock 2004). Second, some of the aforementioned beneficial characteristics of animal mtDNA do not apply in certain situations. For example, its selective neutrality has been challenged (Ballard and Whitlock 2004), and on relatively rare occasions, the presumed lack of recombination has been shown to be incorrect (Lunt and Hyman 1997). Third, in those organisms with maternally inherited mtDNA (i.e., most animal taxa), the results of any study are sex-biased: they reflect only the history of matrilines. Finally, the validity of a molecular clock is a matter of considerable debate, given that the rate of mtDNA evolution may vary among taxa, within taxa, and among the different protein-coding genes within the mitochondrial genome (Arbogast and others 2002, Ballard and Whitlock 2004). Yet despite these potential pitfalls, mtDNA makes an excellent starting point. Importantly, given the widespread use of mtDNA in phylogeographic studies, these data are connectable, and therefore permit comparisons across otherwise unrelated studies.

Nuclear DNA

The strength of phylogeographic inference is directly dependent on the number of independent lines of evidence (Templeton 2004). Accordingly, the application of multiple codominant nuclear DNA (nDNA) genetic markers can provide robust evidence that corroborates (or refutes) a phylogeographic hypothesis generated on the basis of mtDNA alone, thus better reflecting the history of the organism (Templeton 1998). In addition, because nDNA is bi-parentally inherited, phenomena such as hybridisation, sex-biased dispersal, and genetic introgression can potentially be identified (Sunnucks 2000). Furthermore, information on the relative frequency of nuclear genotypes (particular combinations of alleles at a locus), which potentially change over short (i.e., generation-to-generation) timescales, can uncover recent subdivision of a formerly panmictic population that would otherwise be undetectable. There are a variety of nuclear markers available for these studies (reviewed in Sunnucks 2000, Hare 2001), ranging from relatively inexpensive protein-based markers such as allozymes, to the DNA-based markers such as microsatellites (hypervariable repetitive DNA). Although more expensive, the latter class of molecular markers often provide greater resolution of population structure over very fine spatial scales.

In general, the use of nDNA sequence data in phylogeographic studies is not yet common practice owing to inherent difficulties with accounting for the distorting effects that recombination can have on genealogical relationships. However, when the signature of recombination is absent or negligible, much can be gained by the incorporation of nDNA sequence data, particularly since it allows a much deeper time frame (c.f. mtDNA) to be examined (Hare 2001). Several recent phylogeographic studies have demonstrated the benefits of obtaining nDNA frequency and sequence data from multiple regions of the genome in illuminating the evolutionary history of invertebrates (e.g., grasshoppers: Ibrahim and others 2002, crickets: Broughton and Harrison 2003, saproxylic Collembola: Garrick and others 2004).

Analyses

As is often the case with a new discipline, development of appropriate analytical techniques can represent a significant hurdle. Fortunately, phylogeography is open to well-established population-genetic analyses and phylogenetic techniques. In recent years, much progress has been made in the area of statistical phylogeography, which provides an array of procedures to explicitly test specific hypotheses (Knowles 2004, Knowles and Maddison 2002, Manel and others 2003). For example, Nested Clade Analysis (Templeton 1998, Templeton and others 1995) is a powerful technique enabling one to distinguish between alternative causes of geographical associations among genetic lineages (e.g., isolation-by-distance verses habitat fragmentation) and so separate pattern from process. Further, geographical information systems hold great potential for sophisticated genetic, geographic and environmental data analyses and model-building. The need to incorporate fine-scale abiotic and biotic ecological data into models of organismal history has been highlighted by Endler (1982) and Moritz and others (2000). While such studies are presently rare, it is already clear that they make a significant contribution to understanding processes that promote species diversification, historical biogeography of particular regions and community ecology (Moritz and others 2000). Continued integration of molecular phylogenetics and population genetics with analyses of phenotypic variation, reproductive isolation and independent evidence of landscape history and ecology will undoubtedly propel the field of phylogeography to the forefront of conservation research and planning, with direct applications in biodiversity indication, reserve design, identification of management units, and maintenance of species' evolutionary potential.

APPLICATIONS OF PHYLOGEOGRAPHY FOR INVERTEBRATE CONSERVATION

To date, there have been very few phylogeographic studies that explicitly focus on saproxylic invertebrates. Consequently, the following section primarily draws on literature dealing with relatively sedentary, ecologically specialised terrestrial invertebrates that are likely to exhibit patterns of population structure and local endemism akin to what we might expect to find in dead wood-dependent taxa.

Taxon-Specific Phylogeography: Uncovering Cryptic Biodiversity

Our perceptions of biodiversity are commonly based upon taxonomic divisions that rely on morphological features (Holland and Hadfield 2002). A repeated trend in phylogeographic studies is the uncovering of cryptic species (Arbogast and Kenagy 2001). This is of considerable relevance to conservation biology as it is becoming clear that in many invertebrates, genetic evolution out-paces morphological evolution, with the result that traditional morphological taxonomy may greatly underestimate the underlying genetic diversity present (Avise 1989, 2000).

Bond and Sierwald (2002) investigated patterns of genetic diversity in a morphologically conservative species of millipede (*Anadenobolus excisus*) endemic to Jamaica. This animal is associated with limestone formations, is presumed to have extremely limited dispersal abilities, and was believed to represent a single species on the basis of genitalic morphology—the features most commonly used to distinguish millipede taxa. Using mtDNA, these authors identified three highly divergent genetic lineages, two of which presently occur in sympatry. Based on these molecular data, it was concluded that *A. excisus* is actually a complex of three sibling species.

Similarly, Salomone and others (2002) applied phylogeography to investigate patterns of evolutionary diversification and speciation in soil-dwelling oribatid mites endemic to the Canary Islands. The three focal species in the genus *Steganacarus* have extremely limited powers of dispersal, and predominantly occur in dead organic matter in the surface layers of forest soil horizons. Owing to the paucity of unambiguous morphological characters, taxonomic relationships among the three species were uncertain. Indeed, even the morphological diagnosis of two of these species was contentious. Phylogenetic relationships inferred using molecular data were inconsistent with those based on morphology—this is perhaps unsurprising given that the usefulness of traditional taxonomic approaches to phylogeny in this genus is questionable. Interestingly, despite a lack of morphological variation among specimens of *S. carlosi* collected across three islands in the archipelago, genetic data identified three highly differentiated clades, each being restricted to a single island. Levels of divergence among these clades are comparable with those found between 'good' biological congeneric species in other terrestrial arthropod taxa, thus prompting the authors to suggest that each of the clades represent cryptic species. Comparable findings have been reported for other diverse invertebrate taxa (e.g., pseudoscorpions: Wilcox and others 1997, Onychophora: Trewick 1998, ladybird beetles: Kobayashi and others 2000).

Taxon-Specific Phylogeography: Identifying Management Units and Setting Conservation Priorities

Identifying appropriate units of conservation is a dynamic area of research and contention (Crandall and others 2000). One widely-accepted system is that of Moritz (1994)—an adaptation of Ryder's (1986) evolutionarily significant unit (ESU). Moritz (1994) defines an ESU as a collection of lineages with a shared evolutionary history. By first producing a gene tree, and then identifying lineages that are reciprocally monophyletic (i.e., share a single most recent common ancestor), ESUs can be determined relatively quickly and unambiguously. An advantage in using a phylogeographic approach is that one simultaneously identifies both the number, and the geographic range of ESUs.

Holland and Hadfield (2002) evaluated the phylogeographic structure within and among populations of three endemic Hawaiian tree snails in the critically endangered genus *Achatinella*, with a view to setting conservation priorities for *A. mustelina*. The focal species has limited dispersal abilities, occurs in fragmented populations occupying only upland montane habitats above 600m elevation, and is in a state of rapid decline owing to invasive species and human impacts. Despite the absence of clear morphological differentiation, six geographically isolated ESUs were identified from mtDNA sequence data. This information will guide a multi-faceted conservation action plan (e.g., delineation of areas for protection, identification of key sources of genetic diversity for captive propagation, and directing field translocations or reintroductions).

Similarly, Trewick (2001) used an ESU framework to make recommendations relating to the conservation of an endangered grasshopper (*Brachaspis robustus*) endemic to the South Island of New Zealand via a wider phylogeographic study that included two additional *Brachaspis* species. *B. robustus* is very rare and localised, flightless, and the species' range appears to have contracted since intensive field observations began. Although the molecular data identified three distinct *Brachaspis* lineages, these were not consistent with the three species recognised by current taxonomy. One of the lineages comprised both the endangered *B. robustus* and southern populations of the alpine-restricted *B. nivalis*, while northern *B. nivalis* populations formed a separate lineage that showed levels of genetic divergence comparable with that of among-species differences seen in other insects. Here, evidence to support the current classification of the endangered *B. robustus* as a distinct species was found to be weak inasmuch as it failed to satisfy the criteria of an ESU.

Comparative Phylogeography: Illuminating Processes Driving Evolutionary Diversification, and Testing Biogeographic Hypotheses

Population-genetic processes are numerous and complex, and they can be hard to separate in single-species studies (Bohonak 1999). Comparative phylogeography offers a means of assessing the relative role of historical (e.g., climate-induced) vicariance and dispersal ability in shaping the present-day distribution of taxa (Avise 2000).

Using a suite of flightless invertebrate taxa, Trewick and Wallis (2001) employed comparative phylogeography to test two competing biogeographic hypotheses proposed to explain the existence of areas possessing markedly lower levels of biodiversity and local endemicity in New Zealand—specifically, the "beech-gap" zone in the central South Island. Mitochondrial DNA-based genetic relationships were estimated both within and among taxa representing ten genera, which included log-dwelling velvet-worms (Onychophora), a mixture of geographically localised and widespread beetles (Coleoptera), as well as subalpine- and alpine-adapted cockroaches (Blattodea), grasshoppers and crickets (Orthoptera). Molecular data were not consistent with the 'Ancient Fault' hypothesis, given that the observed depths of divergences were relatively shallow, and should postdate contact of the Pacific and Australasian continental plates (c. 20-25 Million years before present, Mybp). In contrast, while phylogeographic patterning in nearly all taxa examined showed spatial patterns not inconsistent with the 'glacial extirpation' hypothesis (< 1.8 Mybp), this was undermined by the fact that most estimates of divergence times suggested that the differentiated forms predated the Pleistocene origin of vicariance. Thus the authors invoked a third scenario, Pliocene mountain building (c. 2-7 Mybp), as the most likely explanation for the observed patterns of endemism and inferred timing of speciation events.

Comparative Phylogeography: Revealing Common Genetic Patterns in Faunal Communities, and Identifying Surrogate Taxa for Biodiversity Indication

Through revealing the degree to which members of particular biotic assemblages have responded to climatic and geographic events in concert, comparative phylogeography can help identify biodiversity 'hotspots' and prioritize regions in need of protection (Avise 2000, Kuchta and Meyer 2001, Moritz and Faith 1998). Importantly, the greater the ecological and taxonomic diversity of the suite of species examined in comparative studies, the more widely applicable the findings will be (Zink 1996). As expected, it is clear that the level of regional and subregional endemism is much higher in low vagility (flightless) invertebrates, such as saproxylic taxa, than in vertebrates (Yeates and others 2002). While the distribution patterns of saproxylic invertebrates yield important insights into the pattern of endemism and effects of environmental change (Yeates and others 2002), comparative phylogeography has the special property of providing an empirical framework to explicitly assess the relative influence of various evolutionary processes in promoting and maintaining biodiversity. Individual species and whole communities are dynamic in space and time (Moritz and others 2000). Thus process-oriented conservation strategies are likely to be much more effective in a changing world than those that assume a static distribution of biodiversity (Bush 1996).

Moritz and others (2001) proposed that the efficiency of surrogate taxa in reflecting common biogeographic patterns that result from long-acting processes such as climate-induced vicariance is likely to depend on the spatial scale over which the species operate. To test this hypothesis, these authors examined the phylogeography of a suite of taxa with contrasting levels of local endemicity and dispersal abilities (including invertebrates, plants and vertebrates) from tropical rainforests in northeast Queensland, Australia. Results showed that, despite an overall congruence in phylogeographic patterning, the efficiency of surrogacy for biodiversity indication among taxa was highly asymmetric: the tremendously diverse and narrowly distributed invertebrates were strong predictors of conservation priorities for the less diverse and more broadly distributed vertebrates (and to a slightly lesser extent, plants), but not vice-versa. This asymmetry was attributed to the finer-scale distribution and greater species richness of the invertebrates, both of which serve to increase information content, and hence improve their ability to capture spatial patterns of biodiversity in other groups. Similar conclusions have been reached for ground-dwelling arthropods in temperate Australian forests (Ferrier and others 1999).

Hugall and others (2002) used the phylogeography of an Australian land snail (*Gnarosophia bellendenkerensis*), endemic to the tropical rainforests of northeast Queensland, to evaluate predictions based on palaeoclimatic modelling regarding the location and size of Pleistocene—Holocene refugia. This animal is a leaf litter / log generalist, and is expected to have low vagility. Findings from the snail mtDNA phylogeography were generally consistent with predictions from modelling using the BIOLCLIM procedure (Busby 1991), whereby potential former distributions for species are predicted by first deriving an environmental envelope from present-day distributions, then mapping this onto inferred palaeoclimatic surfaces. The presence of multiple refugia was corroborated by both molecular and palaeoclimatic data, and repeated temporal fluctuations in rainforest area and connectivity were cited as being the principal cause of deeply divergent geographically localised snail lineages. Interestingly, comparison with co-distributed herpetofauna (rainforest-restricted lizards and frogs) revealed that the snail phylogeography was essentially a composite of the patterns seen in each of the vertebrate species. The authors suggested that the snail captured the major population structure of other unrelated taxa owing to the finer geographic scale over which it operated.

CASE STUDY: PHYLOGEOGRAPHY OF A SAPROXYLIC ‘GIANT’ SPRINGTAIL FROM SOUTH-EAST AUSTRALIA

Using Tallaganda State Forest (SF) in south-east New South Wales, Australia, as a model system, we (together with collaborators) are employing comparative phylogeography to investigate the relative influence of habitat and species’ biology upon the present-day spatial distribution of genetic diversity in sedentary forest invertebrates. This research seeks to inform forestry management practices and guide conservation strategies by identifying areas that are home to evolutionarily distinct lineages of multiple log-dependent invertebrate taxa. In this program, phylogeographic patterns of paired representatives of a suite of co-distributed saproxylic taxa are being compared to each other, and to other very different members of the rotting-log community.

Recently, Garrick and others (2004) showed that an unusually large and extremely dorso-ventrally flattened saproxylic springtail (Collembola: Neanuridae) from Tallaganda SF exhibits very high local endemism over spatial scales of c. 10 kilometres or less (figs. 1A and 1B). Further, the spatial arrangement of genetically distinct populations was found to correspond with four ‘microbiogeographic’ regions identified a priori on the basis of topography and estimated landscape history. In particular, hydrological divisions of Tallaganda SF seem to capture the major phylogeographic structure of this taxon, to the extent that locations of abrupt genetic contact zones mirror those of major and/or minor catchment boundaries with considerable precision. Molecular data indicated that population divergences of the focal Collembolon at Tallaganda SF were likely to be of considerable antiquity, possibly originating in the late Pliocene—late Miocene (2.5 to 7 Mybp). Genetic data also detected at least two subsequent lineage-splitting events that occurred on different timescales (i.e., late Pliocene—early Pleistocene > 0.7 to 2 Mybp, and mid-late Pleistocene < 0.7 to 0.01 Mybp), all three of which correspond with major palaeoclimatological events that affected south-east Australia.

It has previously been proposed that areas of high diversity (e.g., hybrid zones, genetic clines, or historical refugia) should be targeted for conservation (Faith and others 2003, Mesibov 1994). Indeed, in this model system, the areas most likely to have repeatedly served as refugia for upland cool-loving saproxylic invertebrates during cold dry glacial periods are the commercially valuable tall moist eucalypt forests that occur in east-facing, topographically heterogeneous areas (fig. 1B). In order to conserve biodiversity, it is essential that evolutionarily important habitat types such as these be represented in the reserve system, and where they occur within production forests, the needs of saproxylic invertebrates must be afforded special consideration in management practices (Grove 2002c). Further, it is important to recognise the distinction between geographic areas that contain concentrations of ancient lineages versus those in which recently derived lineages occur. Although areas of both types are important reservoirs of biodiversity, the rationale for conserving them, and the optimal strategies for doing so, differ. In the former case, protection of irreplaceable phylogenetic diversity should focus on maintaining large continuous tracts of undisturbed native forest, while in the latter case, adaptive diversity is best protected by maintaining the ecological integrity and connectivity of habitats that contribute environmental gradients and ecotones across heterogeneous landscapes (Moritz and others 2000). In the case of saproxylic invertebrates, the loss of ecological integrity of dead wood habitats in production forests can be prevented by ensuring a spatially and temporally continuous (and adequate) supply of large-diameter commercially overmature trees, and by allowing dead wood to decompose in situ (Grove 2002a, 2002c).

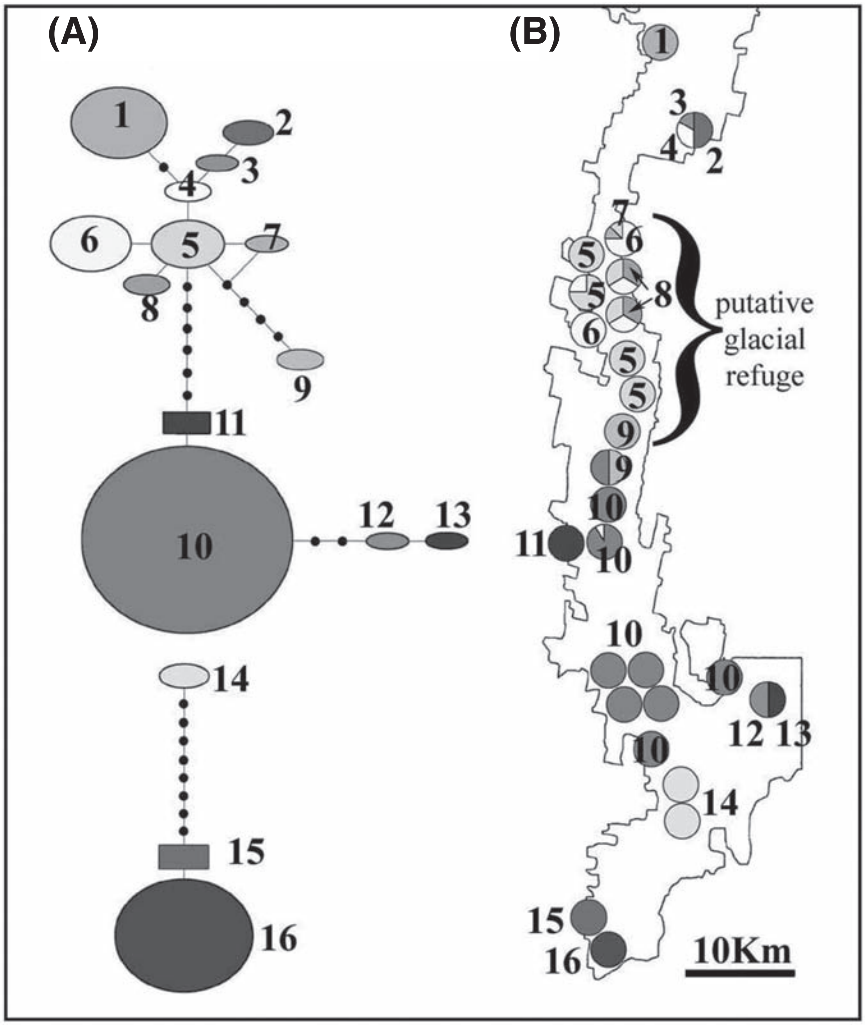

Figure 1—Phylogeography of a saproxylic springtail at Tallaganda State Forest in the Great Dividing Range of South-east Australia. (A) Statistical parsimony network depicting genealogical relationships among genetic lineages. Shaded ovals (also numbered) represent unique mtDNA sequences (where area is proportional to frequency), each single black line represents one mutational step, and solid black circles represent "missing" haplotypes, i.e., not sampled or extinct. Two disconnected networks were produced owing to the very large number of mutational steps between mtDNA lineages from the southern section of the forest (bottom network) and all other lineages (top network). (B) Map of Tallaganda State Forest showing spatial distribution of mtDNA lineages [numbered as in (A)], where each pie chart represents a single sampling site, i.e., log. This Collembolon shows very strong geographic associations among genetic lineages, and the hypothesized glacial refuge contains high evolutionary diversity.

CONCLUSIONS

Genetic diversity represents a fundamental component of biodiversity (Moritz and Faith 1998), and its conservation is critical in maintaining evolutionary processes (Frankham and others 2002). In order to achieve this, habitat reservation and forestry management needs to take account of natural genetic-geographic patterns. It is becoming clear that the predominant focus on vertebrates and vascular plants in conservation research and planning (Stiling 1999) is likely to result in management strategies that fail to cater for a large proportion of the biodiversity present in sedentary invertebrate taxa, such as the ecologically specialized saproxylic fauna. Indeed, phylogeographic studies have repeatedly demonstrated that, in these groups, (1) traditional morphological taxonomy tends to underestimate genetic diversity, (2) conservation strategies focused at and above the species-level are inadequate, and (3) it is not atypical for sedentary invertebrates to exhibit high local endemism over spatial scales in the order of several kilometers or less. Accordingly, invertebrates of low mobility have been identified as particularly effective surrogates for biodiversity indication.

Given that the proportion of total forest area that can be dedicated to the protection of biodiversity is limited, it is essential to maximize the conservation benefit of reserves and managed forest lands. There is urgent need to focus on conservation strategies and sustainable management practices outside of protected areas, as the geographic scale necessary to permit natural evolutionary and biogeographic processes to continue is often greater than can reasonably be accommodated within reserves (Moritz and others 2000). Production forestry can be tailored (if the will exists) to meet the needs of conservation. Indeed, when managed with the conservation of saproxylic fauna as a specific objective, production forests have the potential to maintain natural forest dynamics and ecological processes at the landscape-level (Grove 2002c), while still providing an economic return on timber (Grove 2002a). In contrast to organism-specific conservation strategies, the identification of areas that harbour (and more importantly, promote) the greatest proportion of biodiversity in multiple taxa offers an insight into optimal management goals that would positively impact taxonomically wide-ranging biota. Comparative phylogeography provides an empirical framework for delineating areas of congruent endemism and consequent high conservation priority, while simultaneously yielding insights into evolutionary processes driving the present-day geographic distribution of biodiversity (Avise 2000, Arbogast and Kenagy 2001, Kuchta and Meyer 2001, Moritz and Faith 1998).

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