

Montane refuges and topographic complexity generate and maintain invertebrate biodiversity: recurring themes across space and time

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Abstract If a common set of landscape characteristics seem to predict spatial patterns of biodiversity in several regions with different biogeographic histories and community compositions, these could inform conservation. Two papers recently published in *Journal of Insect Conservation* provided evidence that topographic heterogeneity can play a major role in harbouring invertebrate community biodiversity, and that upland areas potentially function as refugia from infrequent but severe climatic conditions that occur over ecological timescales. Similar findings are being echoed in the growing body of phylogeographic literature on terrestrial invertebrates from montane landscape settings. The purpose of this short communication is to place the two recently published papers into a broader context. Phylogeographic studies usually focus on genetic diversity within and among populations, and at relatively deep evolutionary timescales. The parallels that appear to be emerging across different levels of biological organisation and temporal spectra suggest that (1) microevolutionary processes operating at the level of populations may ‘scale-up’ to macroevolutionary processes operating at the level of species or higher, and (2) certain landscape features—particularly topography—may be particularly important when formulating strategies to protect terrestrial invertebrate biodiversity.

Keywords Conservation biogeography · Genetic diversity · Landscape history · Management units · Phylogeography · Population structure

Introduction

With limited conservation resources, an alternative to species-specific conservation is the identification of centres of biodiversity in distantly-related, co-distributed members of the same ecological community (Moritz 2002). This approach lends itself to management strategies that are likely to have taxonomically far-reaching benefits. Indeed, conservation biogeography can make important and novel contributions to protected area prioritisation (Whittaker et al. 2005). Phylogeography is a sub-discipline of biogeography that focuses on population-level responses to past climate change operating over long-term evolutionary timescales, and the way these responses have been shaped by landscape context (Avice 2000). Outcomes of phylogeographic studies that consider multiple co-distributed species have ranged from strong congruence of spatial-genetic patterns and underlying microevolutionary process, to largely idiosyncratic histories. In those cases where the interaction between historical climatic cycles and landscape setting seems to yield predictable spatial patterns of biodiversity, this information could be used to tentatively identify a priori management units to be re-assessed (and modified) using new empirical data. In addition, the long-term perspective offered by phylogeography permits consideration of the dynamic nature of biodiversity throughout the Pleistocene. This is important because a single snapshot from the present-day can be inadequate for formulating effective management plans (Samways et al. 2006). Furthermore, understanding species’ responses to past climate change provides critical baseline data for predicting future impacts (Norgate et al. 2009).

In a recent study of terrestrial arthropod species diversity at Table Mountain in the Cape Floristic Region, South Africa, Pryke and Samways (2010) sought to identify

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general principles to guide conservation management both at that site, and at other similar mountains. The authors found high species richness and beta diversity with many ecologically-specialized local endemics present only in upland forest habitats, and elevation was an important determinant of community composition. In the same issue of *Journal of Insect Conservation*, Hardy et al. (2010) focused on a related issue—the potential for upland habitats to *repeatedly* serve as refuges. These authors hypothesized that because climatic extremes with detrimental impacts on lowland populations are cyclic over ecological timescales, montane refuges should facilitate species' persistence and act as important sources of recolonization when ameliorating conditions return. This hypothesis was largely supported by emergence and development data for the butterfly *Anthocharis cardamines* (and the reverse situation, where lowlands support upland populations, was also true).

The significance of findings from the two aforementioned studies become more apparent when considered in the broader context of emerging phylogeographic research. Population-level molecular data now exist for suites of co-distributed terrestrial invertebrates from several topographically complex montane landscapes across the globe. Given that these taxon sets are usually composed of distantly-related species that play different ecological roles, a preliminary assessment of some general unifying principals is now possible. Here I provide a brief overview of the role of upland refuges, topographic heterogeneity and habitat stability in generating and maintaining terrestrial invertebrate biodiversity. The primary focus of this paper is on landscapes that remained mostly free of ice sheet advances throughout the Pleistocene, because local faunal assemblages are less likely to have had more ancient phylogeographic patterns completely overwritten by Quaternary climatic oscillations (e.g., Soltis et al. 2006, cf. Hewitt 2000). Examples are drawn from four landscape settings, and together with the conclusions of Pryke and Samways (2010) and Hardy et al. (2010), I highlight some recurring patterns that may have applications to invertebrate biodiversity conservation.

As a preface to the following discussion, brief descriptions of the four exemplar landscape settings (Table 1) are given here.

Wet Tropics, Australia

This remnant of Gondwanan-derived rainforest in northeast Queensland (<10,000 km²) is semi-continuous along a ~400 km north–south axis. The Wet Tropics is comprised of a series of mid-elevation peaks and plateaus surrounded drier coastal lowlands, and the cool upland rainforest blocks are centres of endemism that have been divided onto

13 biodiversity subregions (Moritz et al. 2001). Multiple rainforest-dependent taxa show evidence for long-term persistence in refugia either side of a prominent biogeographic break, the Black Mountain Corridor (Hugall et al. 2002). Pleistocene glacial-interglacial cycles that occurred on ~100 thousand-year rotations, particularly the high-amplitude cycles that dominated the past 0.4 million years (MY; Bowler 1982), caused severe forest contractions followed by re-expansions. These recurrent historical gaps in rainforest distribution are likely to have heavily impacted spatial structuring of inter- and intraspecific invertebrate biodiversity (Bell et al. 2007 and references therein).

Tallaganda, Australia

This moderate-elevation, isolated section of the Great Dividing Range in southeast New South Wales, is flanked by valleys to the north, east and west. Tallaganda has a linear configuration (~100 km long by 3–15 km wide) and its ridgeline is north–south oriented. Tall and moist temperate *Eucalyptus* forests occur on the east-facing slopes that receive orographic rainfall. The mountain range has been geologically stable for ≥90 MY, and based on ancient drainage systems together with estimated palaeoclimatic impacts on forest distributions, five microbiogeographic regions for low-mobility forest invertebrates were identified a priori (Garrick et al. 2004). One of these was predicted to have served as a particularly important refuge during the cool and dry Pleistocene periglacial periods when the tree line receded down slope into sheltered gullies (Garrick et al. 2008 and references therein). Nonetheless, multiple local refugia are typical for species from heterogeneous environments in southern Australia (Byrne 2008).

South Island, New Zealand

This area has been geologically active since the late Miocene, when extensive uplift occurred along the Alpine Fault. Mountain-building intensified in the early Pliocene creating the Southern Alps which later extended northward and became a significant physiogeographic barrier separating eastern and western biota (Leschen et al. 2008; O'Neill et al. 2009). The central mountains were repeatedly covered by glaciers throughout the Pleistocene, and so this region was affected by glacial outwash. Forest distributions were most severely restricted during the Last Glacial Maximum, when glaciers extended 700 km along the Alps (Marske et al. 2009). Glacial outwash has been proposed as a cause for the disjunct distribution of *Nothofagus* forest (beech-gap) in the region (Trewick and Wallis 2001). This hypothesis implicates two major forest refuges to the north and south of the beech-gap, but multiple microrefugia

Table 1 Summary of findings from terrestrial invertebrate phylogeographic studies conducted in four exemplar landscape settings

Region/taxonomic group	Ecology	Intraspecific differentiation			Habitat refugia		Reference(s)
		No. of groups	Sequence divergence ^a	Supporting data ^b	Characteristics	Antiquity	
Wet Tropics, Australia							
Coleoptera							
<i>Tennoplectron aeneopiceum</i>	Dung-feeder; rainforest specialist	3	6.7% (COI)	E	Upland tropical rainforest	Early–Mid Pleistocene	Bell et al. (2007)
<i>T. subvolutans</i>	Dung-feeder; rainforest specialist	4	9.7% (COI)	E	Upland tropical rainforest	Late Pliocene–Early Pleistocene	Bell et al. (2007)
<i>T. politulum</i>	Dung-feeder; rainforest and wet sclerophyll	1	2.3% (COI)	E	Upland wet sclerophyll forest	Last Glacial Maximum	Bell et al. (2007)
<i>T. reyi</i>	Dung-feeder; rainforest and wet sclerophyll	1	2.4% (COI)	E	Upland wet sclerophyll forest	Last Glacial Maximum	Bell et al. (2007)
Diptera							
<i>Drosophila serrata</i>	Yeast-feeder; ecological generalist	2	7.2% (ND5)	N, M, B	?	?	Kelemen and Moritz (1999); Schiffer et al. (2004)
<i>D. birchii</i>	Yeast-feeder; rainforest specialist	1	0.3% (ND5)	N	Lowland riparian rainforest	Last Glacial Maximum	Kelemen and Moritz (1999); Schiffer et al. (2007)
Gastropoda							
<i>Gnarosophia bellendenkerensis</i>	Herbivore; leaf litter/rotting log generalist	6	15.0% (COII)	E	Upland tropical rainforest	Late Pleistocene	Hugall et al. (2002)
Tallaganda, Australia							
Arachnida							
<i>Atrax</i> sp. nov.	Predator; forest floor generalist	6	8.8% (COI)	N, B	Upland wet sclerophyll forest	Pleistocene	Beavis and Rowell (2006); Beavis (2008)
<i>Hadronyche</i> sp. nov.	Predator; rotting-log specialist	1	1.4% (COI)	N	Ex situ	?	Beavis and Rowell (2006); Beavis (2008)
Collembola							
<i>Acanthamura</i> sp. nov.	Slime mold grazer; rotting-log specialist	4–6	8.1% (COI)	N	Upland wet sclerophyll forest	Mid Pliocene–Early Pleistocene	Garrick et al. (2007, 2008); Garrick and Sunnucks (2006)
<i>Pseudachorutinae</i> gen. nov. sp. nov.	Slime mold grazer; rotting-log specialist	4	6.6% (COI)	N	Upland wet sclerophyll forest	Late Pliocene	Garrick et al. (2004, 2008); Garrick and Sunnucks (2006)
Onychophora							
<i>Exuperipatoides rowelli</i>	Predator; rotting-log specialist	4	20.0% (COI)	N, M	Upland wet sclerophyll forest	Early Pliocene	Sunnucks and Wilson (1999); Sunnucks et al. (2000); Sunnucks and Tait (2001)

Table 1 continued

Region/taxonomic group	Ecology	Intraspecific differentiation			Habitat refugia		Reference(s)
		No. of genetic groups	Sequence divergence ^a	Supporting data ^b	Characteristics	Antiquity	
Platyhelminthes							
<i>Artioposthia lucasi</i>	Predator; rotting-log specialist	4–5	4.9% (COI)	–	Upland wet sclerophyll forest	Late Pliocene	Sunnucks et al. (2006)
<i>Caenoplana coerulea</i>	Predator; rotting-log specialist	4–5	2.5% (COI)	–	Upland wet sclerophyll forest	Early–Mid Pleistocene	Sunnucks et al. (2006)
South Island, New Zealand							
Coleoptera							
<i>Brachynopus scutellaris</i>	Fungus-feeder; rotting-log specialist	10	? (COI)	–	Beech-podocarp-broadleaf forest	Pleistocene	Leschen et al. (2008)
<i>Hispanonia hystrix</i>	Fungus-feeder; tree and shrub specialist	4–5	? (COI)	–	Beech-podocarp-broadleaf forest	Late Pleistocene	Leschen et al. (2008)
<i>Agyrtodes labralis</i>	Fungus-feeder; forest edge specialist	7	? (COI)	E	Beech-podocarp-broadleaf forest	Late Pliocene–Early Pleistocene	Marske et al. (2009)
Hemiptera							
<i>Maoricicada campbelli</i>	Sap-sucker; ecological generalist	2	5.4% (COI + ATP6,8)	S	Exposed subalpine surfaces	Last Glacial Maximum	Buckley et al. (2001); Hill et al. (2009)
<i>Kikihia subalpina</i>	Sap-sucker; forest/forest-edge specialist	3	1.7% (COI + COII)	–	Lowland shrubland-grassland	Late Pleistocene	Marshall et al. (2009)
Orthoptera							
<i>Deinacrida connectens</i>	Herbivore; alpine scree specialist	7	13.0% (COI)	–	High-elevation scree slopes	Late Pliocene	Trewick et al. (2000)
Phasmatodea							
<i>Niveaphasma annulata</i>	Herbivore; ecological generalist	3	4.3% (COI)	N	Southern coastal and inland areas	Early Pleistocene	O'Neill et al. (2009)
Southern Appalachians, USA							
Arachnida							
<i>Hypocheilus thorelli</i>	Predator; mesic rocky uplands specialist	3	11.0% (COI)	M	?	?	Hedin and Wood (2002)
<i>Fumontana deprehendor</i>	Predator; rotting-log specialist	5	6.6% (COI)	N, M	Upland hemlock-dominated forest	Mid Pliocene–Early Pleistocene	Thomas and Hedin (2008)
Blattaria							
<i>Cryptocercus punctulatus</i>	Wood-feeder; rotting log specialist	5	? (16S + COII)	K, H	Low-mid elevation forest/Piedmont	Pleistocene	Nalepa et al. (2002); Nalepa (2003); Everaerts et al. (2008)

Table 1 continued

Region/taxonomic group	Ecology	Intraspecific differentiation		Habitat refugia		Reference(s)	
		No. of genetic groups	Sequence divergence ^a	Supporting data ^b	Characteristics		Antiquity
Coleoptera							
<i>Anillinus langdoni</i> complex	Predator; forest litter specialist	4	6.8% (COI)	M	Mid-elevation deciduous forest	Pleistocene	Sokolov et al. (2007)
Diplopoda							
<i>Narceus</i> spp.	Detritivore; leaf litter/rotting log generalist	5	14.6% (12S + 16S)	E	Mixed mesophytic deciduous forest	Pleistocene	Walker et al. (2009)

^a Maximum corrected or uncorrected pairwise sequence divergences between groups (or within, if only one group); ? = not reported; mitochondrial DNA gene region(s) given in parentheses

^b Supporting data categories abbreviated as follows: E, ecological niche modelling; N, nuclear DNA loci; M, morphology; B, behaviour; K, karyotype; S, song; H, cuticular hydrocarbons

and/or transient *ex situ* refugia on previously exposed parts of the continental shelf are also plausible.

Southern Appalachians, USA

This ancient and topographically complex region is comprised of distinct physiographic subregions. The Blue Ridge Province has many high-elevation mountains, and the rocky escarpments of the Cumberland Plateau represent some of the oldest uplands in North America. Other important subregions include the Valley and Ridge Provinces to the west, and the lower elevation forests of the Piedmont to the south and east (Hedin and Wood 2002; Thomas and Hedin 2008). Several plants and animals show a marked east–west phylogeographic break—a pattern that is usually attributed to persistence in refugia on opposite sides of the north–south running mountain chain (Soltis et al. 2006 and references therein). However, emerging evidence suggests multiple stable refugia within the southern Appalachians. During the numerous late Pleistocene glacial cycles, periglacial conditions forced tree lines to recede. This left discontinuous mid-elevation pockets of spruce forest in ravines and along slopes adjacent to river valleys, and these habitat mosaics could have harboured invertebrate biodiversity (Nalepa et al. 2002).

Montane invertebrates often show considerable population-level genetic differentiation

Pryke and Samways (2010) reported that species richness at Table Mountain was very high and that many specialists and local endemics were found only in mature forest. This led the authors to conclude that because these habitats are important reservoirs of biodiversity, they are irreplaceable. Similarly, phylogeographic studies have frequently detected high levels of *intraspecific* genetic diversity in montane terrestrial invertebrates. For example, for the mitochondrial DNA (mtDNA) *cytochrome oxidase I* gene, within-species differences are usually on the order of $\leq 2\%$ (Hebert et al. 2003; but see Cognato 2006 for limitations associated with using percent nucleotide differences as a metric for species boundaries). However, Table 1 shows that mtDNA sequence divergences among individuals or populations of montane invertebrates that are currently recognised as a single species can exceed this considerably. Indeed, phylogeographic studies have repeatedly demonstrated that low-mobility forest invertebrates can be strongly differentiated into multiple geographically localized allopatric or parapatric genetic lineages, over very fine spatial scales (e.g., on the order of tens of kilometres or less; reviewed by Garrick et al. 2006). From a conservation perspective, these

distinct genetic lineages represent unique evolutionary histories, and in some cases they have been evolving as essentially independent units for considerable lengths of time. Under most criteria, the within-species lineages reported in Table 1 qualify as separate management units (Fraser and Bernatchez 2001). Furthermore, most of the studies summarized here are not based on mtDNA alone, which is important because single-locus datasets have inherent limitations with respect to invertebrate conservation (Forister et al. 2008). In the examples given in Table 1, supporting evidence comes from biparentally-inherited genetic markers, morphology, behaviour, song, cuticular hydrocarbon profiles, karyotypes (chromosome counts), and/or ecological niche modelling. Of the 26 recognized species included in Table 1, as many as eight were considered to at least potentially consist of two or more ‘cryptic species’ by the authors. Subsequent work showed that two of these taxa include lineages that would qualify as separate species under the biological species concept (i.e., *Drosophila serrata*, Schiffer et al. 2004; *Euperipatoides rowelli*, Sunnucks and Tait 2001). However, the latter detailed assessments are possible only when divergent lineages meet at contact zones.

It is important to note that previously unrecognised intraspecific diversity will not necessarily directly relate to conservation priority. For example, only a subset of the catchment-based regions at Tallaganda that reflect the locations of evolutionarily distinct lineages in multiple forest invertebrates are currently subject to the potentially detrimental impacts of commercial forestry operations (Table 1 and references therein). By extension, there is no reason why invertebrates from topographically complex montane regions should be automatically be afforded higher conservation priority than lowland taxa—the nature and magnitude of landscape- or species-specific threatening processes remains an important consideration.

Upland refuges repeatedly served as reservoirs of biodiversity throughout the Pleistocene

Hardy et al. (2010) drew attention to the *potential* role of upland habitats as refuges for species impacted by projected climate warming, and from contemporary habitat reduction or destruction or extreme weather events that occur in lowlands. The idea that refugia are centres for generation and retention of biodiversity in fluctuating environments has been proposed previously (e.g., Heatwole 1987), but recent evidence suggests that one factor—Pleistocene habitat stability—is a particularly strong predictor of spatial patterns of biodiversity in low-dispersal taxa, and this applies both below and above the species-level (Carnaval et al. 2009; Graham et al. 2006,

respectively). Indeed, there are numerous parallels between findings of intra- and interspecific studies, raising the possibility the microevolutionary processes scale-up to the macroevolutionary level. If so, conservation recommendations drawn from research that is focused on different levels of biological organization (e.g., populations, species, functional groups etc.) could be mutually complementary (Moritz and Faith 1998). For example, topographically heterogeneous montane landscapes that retained moist forest refuges during Pleistocene glacial cycles are known to harbour many wet-adapted, short-range endemic *species* (Harvey 2002). At the same time, phylogeographic studies have provided compelling evidence that terrestrial invertebrate *populations* also persisted in montane refuges throughout the Pleistocene and earlier (Table 1). In the latter cases, these refuges are recognizable because they are geographic centres of genetic diversity (i.e., contain the largest number of alleles, and/or the most ancient lineages). Upland refuges are also usually identified as the likely origin of range expansion into neighbouring lowland areas, as revealed by molecular signatures of rapid population growth or source-sink migration dynamics (Table 1). Although these late Pleistocene to early Holocene-aged range expansion events inferred in phylogeographic studies are older than the generation-to-generation ecological timescale considered by Hardy et al. (2010), the notion that upland refuges serve as sources of recolonization into neighbouring areas still holds.

In landscape settings that were largely free of historical ice sheet advances, contemporary population processes may reinforce (rather than overwrite) patterns of genetic diversity that arose during the Pleistocene. Accordingly, there will not necessarily be a strong discord between the present-day locations of high quality habitat compared to their locations in the past. For example at Tallaganda, the same general locations that served as long-term refugia for several distantly-related rotting-log-dependent invertebrates (i.e., areas of deeply dissected topography containing tall, moist eucalypt forest in sheltered, east-facing gullies that receive orographic rainfall; Garrick et al. 2004, 2007, 2008; Sunnucks et al. 2006) should also offer protection from infrequent but high-intensity wildfires that occur on ecological timescales. Similarly, the ridgelines separating major water catchments at Tallaganda are long-standing physiogeographic features that seem to have exerted strong influences on population-genetic structuring of some saproxylic forest invertebrates, presumably because these high-elevation peaks were treeless during Pleistocene periglacial cycles (Garrick et al. 2008, and references therein). Today, these ridgelines have relatively sparse canopy cover with the dominant tree (*Eucalyptus pauciflora*) generating only small-diameter coarse woody debris. Compared to large logs, small-diameter logs

support a lower diversity of insect species (Grove 2002) and have reduced thermal buffering from daily and seasonal extremes in ambient temperature (C. Schmuki et al., unpublished data). Accordingly, it is possible that ridgelines inhibit effective migration of desiccation-susceptible forest invertebrates across catchment boundaries during both glacial and interglacial cycles. Similar ecological constraints may also be operating in the Southern Appalachians, where high-elevation fir-spruce forest communities are thought to limit connectivity among lineages of the *Anillinus langdoni* species group, both today and in the past (Sokolov et al. 2007). Indeed, the potential utility of catchment-based management units for terrestrial invertebrate conservation seems to extend beyond Tallaganda (e.g., South African cicadas *Platypleura plumosa* and *P. stridula*, Price et al. 2007, 2010), but a formal meta-analysis is needed to determine if this is broadly applicable.

While the present paper has focused on areas that remained largely ice-free during the Pleistocene, species-level work on butterflies from the heavily glaciated European Alps provided some of the first evidence that montane areas acted as refuges for biodiversity and facilitate species' persistence (e.g., Dennis et al. 1991, 1995). A novel contribution of phylogeography over the past decade has been the considerable body of evidence showing that the fine-grained habitat heterogeneity characteristic of upland areas can have strong and lasting impacts on spatial structuring of biodiversity and the population-level. Numerous phylogeographic studies have been conducted in areas that were previously impacted by extensive ice sheets, and so consideration of those findings is warranted here. Based on early comparative studies, it appeared that central and northern Europe were recently recolonised from three major southern refuges (the Balkans, south of the Pyrenees, and south of the Alps; Taberlet et al. 1998; Hewitt 2000). Consistent with this scenario, population-level genetic data from a Central European grassland butterfly (*Erebia medusa*) indicated a short evolutionary history (i.e., < 30 KY since population splitting) characterized by shallow genetic structure and a signature of rapid population growth (Hammouti et al. 2010). However, in contrast to the general paradigm of post-Pleistocene recolonization of glaciated areas from unglaciated refugia, Pfenninger and Posada (2002) showed that the land snail *Candidula unifasciata* persisted in multiple refugia in the south of France, much closer to the Alps than expected. These authors also found that distinct genetic lineages were of considerable antiquity (c. 300 KY). Similarly, Schmitt and Haubrich (2008) reported that important refuge areas for a butterfly species characteristic of the mountain coniferous forest biome (*Erebia euryale*) also existed at the southeastern edge of the Alps. Inferences of survival along the margins of glaciated high mountain ranges also extend

to several other butterfly species (e.g., Schmitt et al. 2006; Schmitt and Besold 2010). Ultimately, these findings highlight that there is no fundamental requirement for landscapes to have remained completely ice free in order for them to have served as important reservoirs of invertebrate biodiversity.

Elevation can impact population-level biodiversity, but its effects are understudied

It has now been reasonably well-established that in montane areas, species beta diversity (measured along an elevation gradient) can be high, with different topographic strata occupied by distinct sets of invertebrate fauna (Pryke and Samways 2010 and references therein). However, generalizations about whether this phenomenon also operates at the intraspecific level cannot be made because isolation-by-elevation is not usually tested in phylogeographic studies. For example, of the 26 species listed in Table 1, the impact of elevation on rates and directionality of gene flow or on spatial-genetic structuring was assessed in only two cases (*Drosophila birchii* from the Wet Tropics, Schiffer et al. 2007; *Cryptocercus punctulatus* in the Southern Appalachians, Nalepa 2003). Although no significant effects were detected, other landscape systems provide at least some anecdotal evidence that the same principals discussed by Pryke and Samways (2010) can sometimes apply at the population-level. For example, in a phylogeographic study of the endemic Galápagos moth *Galagete darwini*, Schmitz et al. (2008) detected marked population-genetic differentiation correlated with elevation zones, a pattern that was repeated on several volcanoes in the western (younger) islands of the archipelago. In Europe, population-level studies of functional genetic variation have provided evidence for adaptation of insect populations to different elevations, and sometimes a single gene can have a large effect (e.g., alleles at the *phosphoglucosomerase* locus in alpine versus lowland populations of the butterfly *Lycaena tityrus*, Karl et al. 2009; the *malate dehydrogenase* locus in the dung fly *Sepsis cynipsea*, Kraushaar et al. 2002). The latter studies focusing on functional genes support Crandall et al.'s (2000) argument that if the long-term survival of distinct populations is a key management goal, criteria for delineating evolutionarily significant units for conservation below the species-level should explicitly consider adaptive variation. Accordingly, in addition to the need for more frequent assessment of isolation-by-elevation in population-genetic studies, the identification of conservation units will be most powerful when phylogeographic inferences (i.e., those based on selectively neutral genetic markers) are integrated

with complementary data (e.g., ecology, physiology, behaviour, or genetic markers of adaptive significance).

Conclusions

Recurring patterns are emerging from phylogeographic studies focusing on terrestrial invertebrates from topographically complex landscape settings that were not subject to extensive ice sheet advances during past glacial cycles. Two major outcomes have been the realisation that montane invertebrates often show considerable population-level genetic differentiation, and upland refuges repeatedly served as reservoirs of biodiversity throughout the Pleistocene. Whether these microevolutionary process scale-up to the macroevolutionary level remains poorly understood, but some insights emerge when considering these ideas in light of existing work. The studies by Hardy et al. (2010) and Pryke and Samways (2010) represent a nice contrast (i.e., single species versus community-level focus), but at the same time, they arrived at overlapping conclusions about the sorts of landscape features that can play an important role in generating and maintaining invertebrate biodiversity. Here I have attempted to illustrate some of the same general themes by drawing on findings from phylogeographic studies of a diverse set of taxa and landscape settings (i.e., 5–7 co-distributed species from each of four montane regions across the globe, including temperate and tropical latitudes). Low-mobility is conducive to historical inference (Cruzan and Templeton 2000), and flight-limited or flightless invertebrates have been particularly informative about the number and locations of ancient upland refugia (Table 1). Many low-mobility terrestrial invertebrate species persisted in areas too small to support more vagile taxa during Pleistocene glacial cycles, and the fine-scale patterns of population differentiation revealed by phylogeographic studies may predict local biodiversity hotspots in co-distributed vertebrates (Hugall et al. 2002; Hodges et al. 2007). Indeed, similar predictive power based on invertebrate biodiversity has been reported at and above species-level (Moritz et al. 2001). In this context, there is considerable scope for the use of metrics such as ‘phylogenetic diversity’ (Faith 1992), applied at both the inter- and intra-specific levels of biological organisation, to identify geographic areas of considerable importance for conservation (e.g., Moritz and Faith 1998; also see Rosauer et al. 2009).

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