RESPONSE

Frontiers in identifying conservation units: from neutral markers to adaptive genetic variation

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Conserving endangered species is always a complex task. Our recent study on the endangered walia ibex *Capra walie* outlined that using multiple approaches, including molecular phylogeny, population genetics and ecological data, can considerably help to identify conservation units and management strategies (Gebremedhin *et al.*, 2009). Crandall (2009), Festa-Bianchet (2009) and Schwartz (2009) all highlighted a central point: the importance of adaptive genetic variation in the identification of conservation units. In the near future, we believe that adaptive genetic variation will become an increasingly important topic of conservation genetics.

Neutral genetic markers (or markers assumed to be neutral) are currently the most common tools to reconstruct phylogenies, assess gene flow and spatial structure and to identify conservation units (Hoffmann & Willi, 2008). This is because adaptive genetic markers have not been generally available, and because neutral loci can provide unbiased estimates of time since reproductive isolation, and the amount of genetic drift (Luikart *et al.*, 2003; Storz & Nachman, 2003) (Fig. 1a). However, adaptive gene markers are becoming available, can provide better estimates of evolutionary differentiation caused by ecological gradients (Fig. 1b) and could provide additional information useful for identifying conservation units (e.g. Bonin *et al.*, 2007; Crandall, 2009; Schwartz, 2009).

Ecological data, and the recently available tools of ecological niche modelling, can provide important insights and help incorporate information on ecological traits when identifying conservation units (Guisan & Thuiller, 2005).

However, the ecological distinctiveness among taxa, as revealed by ecological niche models, cannot be considered conclusive. Indeed, models are calibrated on the observed distributions of species, which reflect the physiological response of species to abiotic factors, but also historical contingency, human influence and biotic interactions, the so-called realized niche by Grinnell (1917) and Hutchinson (1957). A truly ecological distinctiveness between taxa should be based on the fundamental requirement of species (i.e. the fundamental niche, *sensu* Hutchinson). Only translocation or controlled experiments, which are not feasible for both practical and ethical reasons (but see Vetaas, 2002), would allow us to test differences in the fundamental ecological niche of the two taxa. However, given the very sharp difference we observed in the realized ecological niche between *C. walie* and *Capra nubiana*, we are relatively confident that, in this case, the species have different requirements. The combination of neutral genetics with ecological modelling can reveal patterns that would be impossible to perceive with the use of only a single approach (Gebremedhin *et al.*, 2009), but we believe that an additional step will be possible in the near future: the use of adaptive gene markers.

Local adaptation is a key point of evolutionary diversification, and should be a focus of conservation efforts (Waples, 1995; Crandall, 2009; Festa-Bianchet, 2009; Schwartz, 2009). Variation at adaptive loci might have profound effects on population dynamics, heavily impacting the response to environmental changes, stress, diseases and, finally population persistence (Reusch & Wood, 2007;
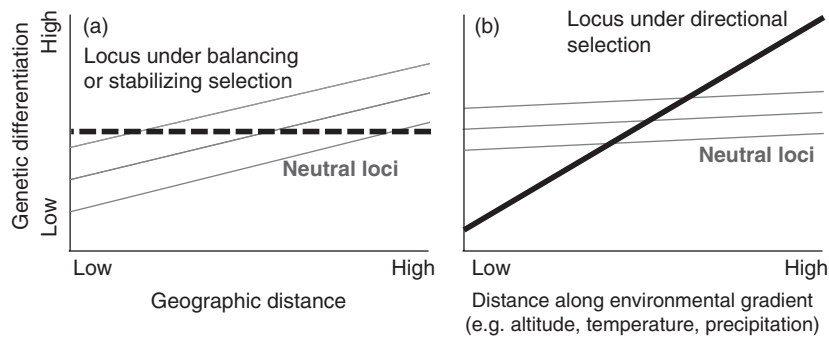
Figure 1 Models of genetic differentiation on specific loci, determined by geographic distance and ecological gradients. (a) Geographic isolation causes differentiation at neutral loci (grey lines), but not at loci under stabilizing or balancing selection (dashed line); (b) environmental gradients cause stronger differentiation at loci under directional selection (black line) than at neutral loci (grey lines). Note that in the case of *Capra walie* and *Capra nubiana*, geographical and ecological gradients are partially overlapping. Redrawn after Schmidt *et al.* (2008).

Hoffmann & Willi, 2008). Rapid adaptive evolution is possible when species colonize a new environment (Stockwell, Hendry & Kinnison, 2003), and genes associated with environmental responses can evolve more quickly than other sections of the genome (Hoffmann & Willi, 2008). Therefore, differences at adaptive genes could help describe the differentiation between closely related taxa, such as *C. walie* and *C. nubiana*. On the other hand, we observed very low variation and heterozygosity at neutral microsatellites, and this reduced genetic diversity raises a strong conservation concern. Nevertheless, using microsatellites alone, we do not know the full extent to which this loss of genetic diversity will actually reduce population persistence and adaptive potential. For example, selection to maintain heterozygosity might maintain polymorphism at certain loci under selection, such as the MHC (see e.g. Aguilar *et al.*, 2004; Bensch *et al.*, 2006).

Considering adaptive loci, in addition to supposedly neutral ones, can provide additional important information (Hoffmann & Willi, 2008). Until now, adaptive variation has had a limited role in conservation genetics because its study has been mostly limited to model organisms. The growing availability of large sets of markers at a reduced price can allow performing genome scans, revealing potential adaptive differences among populations (Bonin *et al.*, 2007). Tracking adaptive genes to really understand what makes the walia ibex a unique entity represents a challenge at the moment, but will probably be feasible in the very near future. First, conservation genetics can take strong advantage of the availability of genomic data from closely related species (Kohn *et al.*, 2006): the genome of the domestic goat will probably be available in a couple of years, and will clearly benefit our knowledge of the walia ibex, and of other threatened wild goats. Furthermore, recent technologies promise that sequencing entire genomes will soon be much cheaper and faster (e.g. Eid *et al.*, 2009).

Despite the undoubtedly great potential of adaptive genetic markers, there are certainly some pit-falls regarding whether one should use these markers to delineate or prioritize conservation units. First, it can be difficult to reliably sample or characterize adaptive variation genome-wide from populations. What proportion of adaptive genetic variation is really detectable? Second, even if we can reliably characterize adaptive genes (genome-wide), these might reflect past/historical adaptations that are unimpor-

tant today, and perhaps unlikely to be adaptive in future changing environments. However, if some of the adaptive loci are functionally related to the most important bioclimatic variables identified in niche modelling, it should be reasonable to take into account these loci when identifying conservation units.

The walia ibex has features that can make it a useful model species for conservation genetics: it is endangered, with a severely depleted genetic diversity, and is closely related to a domestic species. Studying the genetics of the walia ibex will have an important impact on conservation strategies, but may also contribute to more basic scientific questions. For example, the comparison of the genomes of *C. walie* and *C. nubiana* might shed light on the genes responsible for adaptations to extremely contrasted environments. It might also help to understand how a population can persist despite a very low neutral variation.

Finally, when studying endangered species we should always keep in mind the conservation issues. Resources for improving our knowledge of species' genetics will have a huge impact on the future of conservation, but should not be taken from the already scarce resources for management. For the walia ibex, future management strategies should prioritize the establishment of a new population in a protected area, to avoid the extinction of the single current population following a catastrophic event, while facing the issues of poaching, competition with livestock and growing human impact on these high-altitude areas. Indeed, appropriate actions require considerable resources; strategies to increase the ecotourism towards this charismatic ibex might help to gather the money needed to secure the future of the unique biota of the Simen mountains.

Acknowledgements

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