Preserving genetic connectivity in the European Alps protected area network

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ABSTRACT

Due to their static nature, protected areas (PAs) are vulnerable to global change, and resident species will likely need to colonize new sites and exchange migrants to sustain viable local populations. Alpine habitats often have a high level of protection, yet extensive environmental heterogeneity and the limited dispersal ability of many endemic species makes it unclear whether PA networks provide sufficient connectivity to protect vulnerable species. We assess landscape connectivity in the European alpine PA network by combining measures of habitat and genetic connectivity using community landscape genetics approaches. Examining 27 plant species, we compare levels of genetic diversity in PA and non-PA sites, and rank non-PA sites for their potential value in facilitating genetic and habitat connectivity, as well as preserving species richness in 893 alpine plants. Non-PA sites do not significantly enhance overall levels of genetic variability across species. However, spatial genetic turnover (allele frequency variation across space) is influenced by geographical and environmental distance, suggesting that genetic connectivity, and by extension landscape connectivity, is impacted by gaps in the PA network. A subset of non-PA sites, when measured for habitat connectivity, genetic connectivity and species richness using spatial graphs, substantially increase landscape connectivity for alpine plants, although there are discrepancies among metrics in ranking sites. We provide the first example of the evaluation and prediction of new PAs including levels of intraspecific genetic diversity for a whole community. This has significance for the management and extension of the European alpine network, especially in identifying valuable unprotected sites.

1. Introduction

Networks of protected areas (PAs) play an integral role in preserving biodiversity and mitigating land-use changes that threaten species conservation in the wild (Ferraro and Pressey, 2015; Margules and Pressey, 2000). They are considered the most widespread and effective means to conserve biodiversity (Jenkins and Joppa, 2009) and globally comprise nearly 14% of all terrestrial habitat (Chape et al., 2003; Orlikowska et al., 2016). However, in many regions, PAs provide insufficient coverage across the distribution of rare or highly endemic species (Rodrigues et al., 2004; Venter et al., 2014), and they are also highly vulnerable to global change due to their static nature (Gaston et al., 2006; Hole et al., 2009).

The coverage of habitat types in PAs varies, but is well developed in montane regions (Brooks et al.,2004) and surpasses the '10% target of area to set aside' that is often set in conservation recommendations (McNeely, 1993). This high level of coverage is important, because mountains make up half of the world's biodiversity hotspots while only comprising about one quarter of the total land surface (Kollmair et al., 2005; Rodríguez-Rodríguez et al., 2011). Montane habitats support approximately one third of terrestrial biodiversity (Spehn et al., 2011), have a high percentage of endemic species (~9% of vascular plants in the European Alps; Mörschel, 2004), and provide numerous ecosystem services to human communities, including clean water, carbon storage, and a wealth of natural resources (Spehn and Körner, 2005). Unfortunately, PAs are highly susceptible to habitat fragmentation, disturbance, and climate change (Rodríguez-Rodríguez et al., 2011), and montane sites in particular are understudied when compared to other

Table 1

Analytical framework employed to test how landscape connectivity is maintained in the alpine protected area (PA) network.

Study question	Statistical analysis	Expected results
(1) Do levels of genetic diversity differ within and outside protected areas?	Compare the mean allelic diversity and DW (AFLP marker rarity) estimated among PA and non-PA sites.	If non-PA sites harbor more or less genetically diverse populations, or rarer markers, there will be statistically significant differences in measurements of diversity.
(2) Does geographical or environmental distance explain genetic turnover among sites?	Calculate the correlation of genetic distance with geographical distance and environmental resistance across all sites.	If either space or environmental heterogeneity is important in landscape connectivity, genetic distance will be significantly correlated with geographical or environmental distance.
(3) Do sites outside of the protected area network influence levels of isolation by distance or by resistance among PA sites?	Compare isolation by distance, or resistance, among PA and non-PA sites.	If non-PA sites are important to maintain genetic structure among reserve sites, there will be statistically significant differences in measurements of diversity or distance.
(4) Does genetic connectivity decline if non-PA sites are removed from population networks?	Compare the degree and strength of genetic connectivity among plant populations in a spatial graph when non-PA sites are removed.	If non-PA sites are important in maintaining landscape connectivity in the network, the number and strength of connected nodes in the spatial graph of PA sites will decline as they are removed.
(5) Which non-PA sites are critical to maintaining landscape connectivity in the Alps?	Calculate and compare the mean contribution of non-PA sites to overall alpine plant species richness, as well as habitat connectivity and genetic connectivity across 27 alpine plant species.	If particular non-PA sites are important, there will be a significant association in the mean contribution to alpine plant species richness, habitat and genetic connectivity across plant species.

protected habitats (Orlikowska et al., 2016).

In order to sustain biodiversity, networks of PAs must be robust to climatic perturbation (Baron et al., 2009). The stability of communities that inhabit ecological networks depends to a large degree on connectivity, which allows for dispersal to sustain local populations in each PA and increases species persistence (Andrello et al., 2015). Recent studies have highlighted how connectivity is fundamental to the effectiveness of marine and terrestrial ecosystems (e.g. Baguette et al., 2013; Magris et al., 2014; Santini et al., 2016), and now, most rankings of PAs consider whether they function as integral parts of ecological connectivity networks (Fenberg et al., 2012). A highly connected network is more efficient to manage, as natural ecological processes have a higher functionality and require less human intervention (Gaines et al., 2010; Groves et al., 2012; Pardini et al., 2010). The importance of connectivity among PAs is likely to be higher in montane habitats, because dispersal is limited by strong environmental heterogeneity in topographically complex landscapes (Keyghobadi et al., 2005; Savage et al., 2010). Paralleling our knowledge of the role of connectivity in ecosystem function, we also have a good understanding of how connectivity affects genetic diversity within populations (e.g. Aguilar et al., 2008; Gómez-Fernández et al., 2016; Sork and Smouse, 2006), where it mitigates inbreeding and sustains evolutionary potential (Eizaguirre and Baltazar-Soares, 2014; Woodruff, 2001).

The European Alps are considered one of the most important regions for the preservation of biodiversity in Europe. However, most climate change models indicate above-average temperature increase and significant impending reductions in biodiversity, due to dispersal limitations and changing suitability of habitats across the alpine range (Dullinger et al., 2012). Possibly exacerbating this threat, climate change models do not account for land-use change and the isolation of PAs, which could further limit connectivity. The question of whether PAs provide a sufficient level of connectivity now ranks among the most important issues related to the maintenance of the European Alps ecological network (Walzer et al., 2013). Both international governmental groups (Convention on Biological Diversity, or CBD) and non-governmental organizations (Pro Natura Switzerland and the IUCN World Commission on Protected Areas) have called for better connectivity between PAs, which is not always implemented by national governments. Under the 2020 Aichi Biodiversity Targets, the CBD calls for an increase in the amount of protected area globally. The main goal of the Alpine Network of Protected Areas (ALPARC) has been to pursue nature conservation and landscape management to address the Alpine Convention, across 600 small and 400 large (> 100 ha) PAs (http://www.alparc.org/the-protected-areas/). Currently, empirical evaluations of connectivity are missing for the Alps region, with the only assessments focusing at the continental scale of the entire European

Union for the Natura 2000 PA network (Maiorano et al., 2015; Opermanis et al., 2012). As Maiorano et al. (2015) showed, PAs typically enclose only a fraction of the habitat of endemic species in Europe and provide limited connectivity for range-restricted and poorly dispersing species.

The alpine plant community provides a good model to assess connectivity across the existing PA network due to their limited dispersal capacity and high sensitivity to environmental change (Joppa et al., 2013; Pauli et al., 1996), as well as the availability of comprehensive data on species richness and intraspecific genetic variation from the IntraBioDiv project (EU Framework Programme 6, GOCE-CT-2003-505,376; Gugerli et al., 2008). The goals of this project were to assess the contribution of intraspecific genetic variation to species richness patterns, to identify environmental drivers of plant biodiversity, and to integrate intraspecific genetic diversity in the design of PAs. Previous publications have shown high concordance of genetic structure among species with similar bedrock preferences (Alvarez et al., 2009) and in the location of within and among-species genetic 'break-zones' in areas with large elevation changes (Thiel-Egenter et al., 2011). Despite the concordance in intraspecific genetic diversity patterns among species, genetic diversity hotspots are not congruent with alpine plant species richness hotspots (Taberlet et al., 2012a). More recently, the published genetic database has been used to show that environmental and geographical data can be used as a proxy of genetic diversity in conservation planning (Hanson et al., 2017).

Several important questions remain, including whether the existing PA network maintains high landscape connectivity across the European Alps, and how genetic diversity is preserved in the current design? Furthermore, how would the extension of protected status to non-PAs improve the existing network, and how do we evaluate whether each new site adds value to the national (or international) system (Davey, 1998; SANBI and UNEP-WCMC, 2016)? Here we assess landscape connectivity to test fundamental questions about whether PAs maintain genetic connectivity, as well as species diversity (see Table 1 for an overview of the questions, methods and predictions in our study). First, do levels of genetic diversity differ within and outside PAs? Second, does geographical distance or environmental heterogeneity influence spatial genetic turnover (the spatial change in allelic diversity or frequency) among PA sites, and are PA sites more genetically isolated when non-PAs are removed? Third, which non-PA sites are most important to preserve alpine plant species richness, habitat and genetic connectivity across the alpine region? We apply spatial graph theory to estimate the stability of the existing PA network and identify critical unprotected areas among alpine plant populations in the Alps (Rozenfeld et al., 2008; Watson et al., 2011), as this provides a quantitative framework to relate genetic and habitat variation to spatial