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Original Research Article

Positive relationship between genetic- and species diversity on limestone outcrops in the Carpathian Mountains

Anna Mária Csergő [a,*], Levente Hufnagel [b], Mária Höhn [c]

[a] Department of Botany and Biodiversity Research Centre, University of British Columbia, 2212 Main Mall, Vancouver, BC, Canada V6T 1Z4
[b] Department of Mathematics and Informatics, Corvinus University of Budapest, Villányi Str. 29-33, 1118 Budapest, Hungary
[c] Department of Botany, Corvinus University of Budapest, Ménesi Str. 44, 1118 Budapest, Hungary

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ABSTRACT

We asked if the genetic diversity of *Saponaria bellidifolia* (a habitat specialist plant) and the species diversity of its habitat are driven by parallel landscape level processes in an island-like system of limestone outcrops in the Carpathian Mountains. We tested the relationship of these two diversity levels at local and regional geographic scales. Local genetic and species diversity showed parallel patterns influenced by the number of plant communities. Likewise, at regional level there was strong evidence for parallel equilibrial dynamics of genotypes and species. However, a superimposed matrix effect enhanced the regional species diversity only. Genetic diversity of habitat specialist organisms and species diversity of these limestone outcrop islands on mainland are modulated by parallel landscape-level processes at different geographic scales, and mechanisms may be identified at very high spatial resolutions.

1. Introduction

Limestone outcrop systems represent strongly fragmented landscapes with high biological diversity (White and Miller, 1988). In such fragmented ecosystems, conservation biologists seek to identify valuable habitat patches that preserve elevated levels of both intraspecific and interspecific diversity (Taberlet et al., 2012). Several predictions on how these two levels of biodiversity might co-vary have emerged from landscape level models of biodiversity. The family of dynamic equilibrial models posits that coexistence of genotypes and species is driven by random colonization and extinction of species (MacArthur and Wilson, 1967; Hubbell and Foster, 1986; Hanski and Gilpin, 1997) and associated gene flow, genetic drift and speciation (Wright, 1940; Kimura, 1983). According to these models, habitat size and isolation affect immigration rate and population size, and are therefore key drivers of both genotypic and species diversity. The closely related "habitat diversity" hypothesis predicts that larger areas are environmentally more heterogeneous, which in turn promotes diversifying selection of both genotypes and species (Williams, 1964; Rosenzweig, 1995). If landscape level mechanisms act on both genotypes and species in a similar manner, we can then hypothesize that such mechanisms may ultimately produce similar patterns of intra- and interspecific diversity (Vellend, 2005; Vellend and Geber, 2005). In support of this hypothesis, a positive relationship of genotypic and species diversity has been detected in geographically isolated ecosystems (e.g., Johannesson and André, 2006). However, a contrary result was reported when climate-driven habitat contractions caused species loss while preserving genetic diversity (Puşcaş et al., 2008), and high habitat heterogeneity favored increased abundance and genetic diversity of particular species while lowering species diversity (Odat et al., 2010) (see Vellend and Geber, 2005 for effects of habitat heterogeneity on the relationship of genetic to species diversity).

Extended models of island biogeography have incorporated a larger variety of ecological, geographical and historical factors to explain diversity patterns of isolated habitats (Lomolino, 2000; Whittaker, 2000; Heaney, 2007), thereby refocusing the research of parallel genotypic and species diversity patterns to a broader context. For example, it has been shown that diversity patterns may vary substantially across different geographic scales (Whittaker, 2000). Extinctions and drift of "sink" populations can deplete local diversity (Shmida and Wilson, 1985), but increase regional diversity of genes and species (Pulliam, 1988). Likewise, disturbance can lower local genetic and species diversity by differential survival of genes and species, but increase regional diversity (Evanno et al., 2009).

* Corresponding author.
E-mail addresses: csergo@mail.ubc.ca, csergo.anna.maria@gmail.com (A.M. Csergő), leventehufnagel@gmail.com (L. Hufnagel), maria.hohn@uni-corvinus.hu (M. Höhn).

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Evidence for parallel patterns of intra- and interspecific diversity has often been expected from oceanic islands, where a sharp ecological contrast with the landscape matrix provides an ideal environment for dynamic equilibrial processes. Yet, it is not clear whether we can anticipate identical patterns in island-like habitats of mainland. While in oceanic island systems area/heterogeneity and isolation may be prime drivers of diversity, in mainland islands additional factors such as the matrix effect (Cook et al., 2002) and climate-driven habitat contractions and expansions (Puşcaş et al., 2008) further complicate the interpretation of biological patterns. Although there is accumulating theoretical and empirical support for similarity between oceanic and mainland island systems (Vellend, 2003; Vellend and Geber, 2005; Wehenkel et al., 2006; Sei et al., 2009; Lamy et al., 2013), nonsignificant (Puşcaş et al., 2008; Taberlet et al., 2012) and negative (Silvertown et al., 2009; Fady and Conord, 2010) correlations have also been reported. An important source of these contradictory results is the lack of a clear outline of the history of fragmentation and extent of habitat isolation, despite readily available frameworks (Watson, 2002). The older the fragmentation and the more pronounced the ecological contrast with the landscape matrix, the more likely the mainland habitat patches are to follow biogeographical processes typical of isolated oceanic island systems. Yet, few studies have investigated the mechanisms of coexistence of genotypes and species in such well-defined mainland island systems, despite an evident need for generalizations (Watson, 2002; Taberlet et al., 2012).

A small island-like system of limestone outcrops that represent the only localities of the rare habitat specialist plant *Saponaria bellidifolia* in the Apuseni Mountains (Southeastern Carpathian Mountains, Romania) is an ideal environment in which to test whether mainland islands produce parallel patterns of intra- and interspecific diversity. The outcrops consist of Triassic crystalline limestone and dolomite rocks uplifted from marine deposits during the Alpine orogeny and subsequently eroded to their current shape (Cocean, 2000). These old geological formations differ substantially from the surrounding landscape of valleys, forests and flat areas in age, geomorphology, geology, soil types and vegetation history, and therefore classify for mainland islands rather than habitat fragments. An earlier study in this system has shown a positive response of genetic diversity of *S. bellidifolia* to outcrop area/heterogeneity and isolation (Csergő et al., 2009b). The primary aim of the research reported here is to test the hypothesis that patterns of both the intraspecific- and interspecific diversity are shaped by similar landscape level mechanisms. Specifically, we tested if outcrop area, heterogeneity and isolation produced parallel patterns of genetic diversity of *S. bellidifolia* and species diversity of its habitat. In addition, to account for scale-dependency of coexistence processes, we examined if patterns were similar at local and regional geographic scales.

2. Materials and methods

2.1. Study system

The eight South-facing limestone and dolomite outcrops studied here represent the entire area of distribution of *S. bellidifolia* in the Apuseni Mountains (Southeastern Carpathian Mountains, Romania). The outcrops are scattered on an area of less than 200 km^2, ranging between 729–1382 m above sea level and 180–730 m above the landscape matrix; pairwise geographic distances between them are 1–13 km. Three outcrops (Dealul Vidolm (VID), Piatra Urdaşului (URD) and Vârful Cornului (COR)) are smaller and peripheral relative to the other five central, clustered outcrops (Scăriţa-Belioara (SC-BEL), Cheile Runcului (RUN), Cheile Pociovaliştei (POC), Pinet (PIN), Cheile Poşegii (POS)) and are spatially closer to the border between the Apuseni Mountains and the Transylvanian Plain (Fig. 1, Supporting material 1). *S. bellidifolia* is a very long-lived,

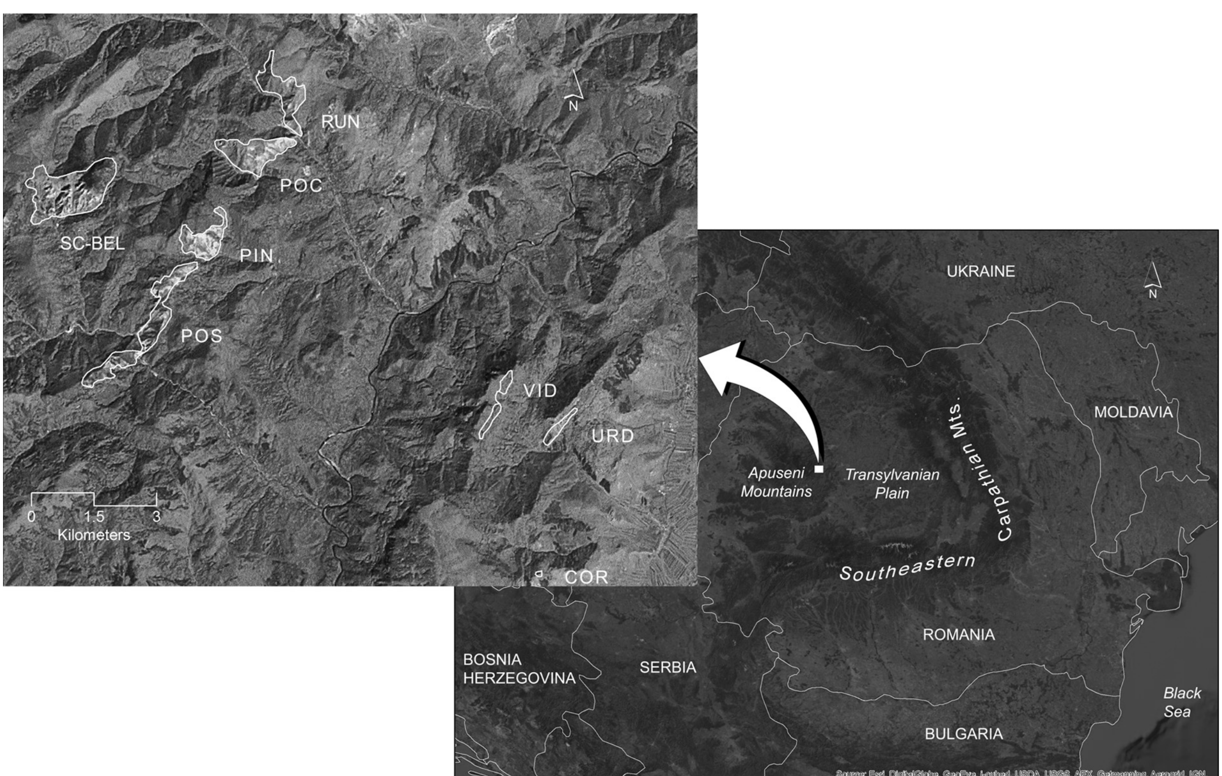

Fig. 1. The island-like system of outcrops inhabited by *Saponaria bellidifolia* in the Apuseni Mountains (Carpathian Mountains, Romania), and the location of the study area in Europe.