Elevation-driven ecological isolation promotes diversification on Mediterranean islands

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\textbf{A B S T R A C T}

The percentage of single island neo-endemic species (an indicator for evolutionary diversification) was found to be independent of geographic distance to the continent in the case of the Aegean archipelago. It was concluded that speciation is independent of geographic isolation, while evolutionary processes are rather enhanced by habitat heterogeneity. An island’s maximum elevation was used as an indicator for habitat heterogeneity. In contrast, we argue that habitat heterogeneity (i.e. the richness in different habitats) may be positively related to biotic richness, but a positive effect on speciation is yet to be proven. For any other type of heterogeneity, we propose a precise wording, especially when assessing its effect on speciation processes.

Alternatively, we propose that \textit{elevation-driven ecological isolation} causes the pattern of endemic species on high-elevation islands. Environmental filtering along an elevational gradient differentiates ecosystems, leading to an increase of isolation with elevation. The reason is that comparable ecosystems are much farther apart than is the case for lowland ecosystems. In addition, ecosystems on neighboring islands or on the continent that may be source regions for colonizing species are small in area in high elevations in comparison with lower elevation ecosystems. Consequently, an increased speciation rate resulting in a larger percentage of single island endemic species can be expected for higher elevations on islands and high mountains. Support for this \textit{elevation-driven ecological isolation} hypothesis comes from other islands in the Mediterranean region (e.g. Crete and Corsica), where an increase of the percentage of endemic species with elevation has been observed. Thus, the assessment of (genetic-) isolation should incorporate the distance to similar habitats instead of simple land-to-land connections.

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\textbf{1. Increasing isolation and speciation with elevation}

Recently, it was claimed that speciation on continental islands is not directly driven by isolation because no relationship between geographical distance to the mainland and the percentage of neo-endemic species was found (Kallimanis et al., 2011). Instead, it was proposed that \textit{habitat heterogeneity} expressed by an island’s maximum elevation drives speciation. A positive effect of \textit{habitat heterogeneity} on speciation has been assumed by several studies (Halas et al., 2005; Stuessy et al., 2006). However, we alternatively suggest that elevation controls speciation rather via the effect of \textit{elevation-driven ecological isolation} (sensu Steinbauer et al., 2012a).

Genetic isolation, as especially provided by islands, is reported to support speciation processes (Heaney, 2000). The degree of genetic isolation is, above all, affected by the number of individuals or propagules that are exchanged among populations. Isolation, however, varies between ecosystems depending on the location on the island (Steinbauer et al., 2012a). The geographical distance between landmasses, as applied by Kallimanis et al. (2011), is only reasonable for coastal habitats. Especially high-elevation ecosystems (e.g. Mount Psiloritis [2456 m a.s.l.] on Crete or Monte Cinto [2706 m a.s.l.] on Corsica both reaching far into the alpine zone) differ considerably in their environmental setting from the low-elevation regions on the neighboring continent. Here, the distance to comparable continental ecosystems is a better indicator for the degree of isolation (Steinbauer et al., 2012a). This distance increases with elevation, as comparable mainland ecosystems are likely to be located distant from the coast (Fig. 1). In addition, not only focal island ecosystems but also the related continental ecosystems tend to become smaller in area with elevation. A smaller source region is likewise linked to a decline in the number...
of arriving colonists (i.e. propagule pressure) (MacArthur and Wilson, 1967), leading to an additional increase of isolation – and thus speciation processes – with elevation on islands. This hypothesis of an elevation-driven ecological isolation (sensu Steinbauer et al., 2012a) results in an increase of the percentage of single island endemic species (pSIE) with elevation. pSIE is used as an indicator for diversification processes (Emerson and Kolm, 2005) and its increase with elevation was recently proven for oceanic islands (Steinbauer et al., 2012a).

2. The situation on Crete and other continental islands

While oceanic islands generally consist of volcanic bedrock, continental islands may have a more diverse geological history. They often integrate bedrock from the continental plate that is less susceptible to erosion than bedrock of volcanic origin. Continental islands are often geologically older than oceanic ones.

Elevation-specific datasets for islands in general and for continental islands (i.e. true geographical islands surrounded by water but geologically part of the continental plate) in particular are rare. For continental islands the postulated elevation-driven ecological isolation hypothesis can be assessed using data for Crete, the highest of the 19 Aegean Islands that actually contain single island endemic species (pSIE) with elevation. pSIE is used as an indicator for diversification processes (Emerson and Kolm, 2005) and its increase with elevation was recently proven for oceanic islands (Steinbauer et al., 2012a).

The observed increase in the percentage of endemic species with elevation is associated with an overall decrease in species richness of high elevation floras, both on Corsica (Thompson, 2005) and Crete (Greuter, 1972). Their relatively low species richness and the associated unoccupied niches are additional evidence for ecological isolation. Indeed, species diversity of island mountain floras was presumably never as high as that of comparable continental high mountains.

The combination of species-poor ecosystems with “empty niche space” and genetic isolation likely drives increased speciation rates at high elevations on islands. Whittaker and Fernández-Palacios (2007) indicated that ancient continental islands host a higher percentage of endemic species than oceanic islands. Values reaching 40–50% of endemic species in high-elevation ecosystems on Mediterranean islands are comparable to the high-elevation ecosystems of oceanic islands like the Canary Islands (Steinbauer et al., 2012a) or La Réunion (Strasberg et al., 2005).
3. Human influence

An increase of the ratio of endemic species with elevation can be associated with decreasing impact of humans. Endemic species might have gone extinct in low elevations due to the tremendous human pressure on lowland habitats, while endemics could survive in more pristine high-elevation ecosystems (Sarnat and MoreauX, 2010). Losses of endemic species were presumably induced by human overexploitation (Panitsa and Tzanoudakis, 2001). Nevertheless, human influence can hardly explain the increase of pSIE with elevation. The number of endemic species driven to extinction that would be needed in low elevation ecosystems to reach the extraordinary high ratios of high-elevation ecosystems is immense. These hypothetically missing species would need to be new (now unknown) species as community composition differs considerably along elevation due to very strong ecological filters. In fact, the endemic plant species of Greece show narrow geographical and altitudinal distribution ranges (Georgiou and Delipetrou, 2010). Recent studies have emphasized the general tendency to overestimate the magnitude of anthropogenic influence on vegetation composition in the Mediterranean (Collins et al., 2012). Nonetheless, the reported increase of Balkan floral elements on Crete in congruence with a decline in Euro-Mediterranean species along the elevational gradient (Kazakis et al., 2007) can be interpreted in favor for both hypotheses: human influence or elevation-driven ecological isolation. The higher ratio of Mediterranean species in low elevations on Crete may result from an above-average rate of introduction of Euro-Mediterranean species to low-elevation ecosystems, or from environmental filtering along the elevational gradient favoring mountain species in higher elevations.

4. Isolation via environmental filtering along elevational gradients

Evidence suggests that isolation of continental islands (i.e. located on the shelf close to the continent and consisting of continental parent material) is less effective for inducing speciation than is the case for oceanic islands (volcanic islands on the oceanic crust) (Cody, 2006). This seems to be especially true for the Aegean Islands (Parmakelis et al., 2006; Poulaakakis et al., 2008). Yet islands that are located on the shelf of continents are often older than oceanic islands. In addition, the probability for an island to be part of a dense agglomeration of neighboring islands of comparable age is rather high on the shelf. Furthermore, Kallimanis et al. (2011) propose that speciation processes on the Aegean Islands are rather associated to random than to adaptive differentiation (Bittkau and Comes, 2005; Edh et al., 2007; Georgiou and Delipetrou, 2010). Random differentiation is usually induced by very efficient genetic isolation. The distances between coastlines alone can hardly be related to isolation of high-mountain habitats and populations (Fig. 1), owing to the fact that it was likely to be much lower during times of reduced sea level. The strong correlation between maximum island elevation and pSIE on the Aegean Islands identified for neo-endemic species (i.e. in-situ evolution) by Kallimanis et al. (2011) can therefore also hint at elevation-driven ecological isolation (sensu Steinbauer et al., 2012a) on the archipelago.

However, the phenomenon of elevation-driven isolation is not restricted to island systems. The increase of pSIE with elevation is also reported for continental mountain systems (Kessler, 2002; Mallet-Rodrigues et al., 2010) that exhibit strong spatial isolation and genetic distinctness of biota (Mota et al., 2002). Overall, the highest proportions of endemism in the whole Mediterranean region can be found in high mountains (Médail and Quézel, 1997; Verlaque et al., 1997).

5. The role of heterogeneity for speciation

The understanding and definition of the term habitat differs among researchers. Partly it is given a species-specific meaning indicating the living conditions of a species’ population (e.g. Tscharntke et al., 2012). However, it is also common to apply habitat in a comprehensive way at the community scale. Then, habitat diversity is used synonymously to habitat heterogeneity and often quantifies the number of vegetation units (see e.g. Tews et al., 2004; Stuessy et al., 2006; Kallimanis et al., 2011; Triantis et al., 2012) or as the sum of land cover classes (Kisel et al., 2011), which are often correlates of the elevational range. In this case, there is strong evidence that on islands habitat diversity (i.e. sum of vegetation units) contributes to both species richness and endemic richness (e.g. Hortal et al., 2009; Kallimanis et al., 2010; Panitsa et al., 2010; Steinbauer and Beierkuhnlein, 2010). Via direct relation high numbers of species are expected to result in a large number of endemic species, if assuming an equal speciation rate for all species.

Here, however, we are interested in how different environmental variables contribute to an increase in speciation rate per species, which would be reflected in an increase in the percentage of endemic species per given area. Stuessy et al. (2006) found the proportion of species evolved through adaptive radiation to be positively related to habitat diversity (i.e. sum of vegetation units) on islands. Assuming that speciation through adaptive radiation is much faster than random drift, this can be interpreted as an increase of speciation rate per species with increasing habitat diversity. In consequence there is some evidence that island elevation as a proxy for habitat diversity supports diversification processes within islands (Stuessy et al., 2006). Stuessy et al. (2006) identified a strong collinearity between habitat diversity and elevation with the latter being the better predictor for the percentage of species evolved through adaptive radiation. Thus we argue that other processes such as the elevation-driven ecological isolation are driving adaptive radiation on islands rather than habitat diversity per se.

However, the heterogeneity of habitats reflected by differences of environmental properties between and within habitat types may also enhance speciation (Svenning, 2001; Halas et al., 2005). This fact is not covered by the common understanding of habitat diversity (i.e. the mere number of habitat types). Environmental micro-heterogeneity may result in genetic differentiation in plants even in very small scales (in some cases even on scales smaller than 1 m; Linhart and Grant, 1996; Leimu and Fischer, 2008). The edaphic heterogeneity found within temperate meadows is for instance reported to stimulate within-species differentiation of herbs (Silvertown et al., 1999). Resulting small-scale genetic differentiation facilitates local adaptation by natural selection (Eguiarte et al., 1992). Accordingly, in situ speciation should be promoted in “environmentally diverse localities” (Panitsa et al., 2010). Thus we claim that the heterogeneity of the environment is likely to support speciation processes even on very small scales. Approaches towards the quantification of ecological heterogeneity and complexity could address, beside others, microclimatic settings (e.g. Scherrer and Körner, 2011), surface roughness (e.g. Leutner et al., 2012; Steinbauer et al., 2012b), soil types and disturbance regimes (e.g. Buhk et al., 2007). However, detailed investigations and especially a coherent concept and terminology are still missing (see Palmer, 1994). While “heterogeneity” as a vague term is already included in ecological theory (Whittaker et al., 2008) it is neither precisely defined nor measured in standardized ways. In fact it is likely that pronounced scale effects (grain and extent; in case of topography in three dimensions), methodological problems and a missing general concept have hindered a profound examination of heterogeneity effects.
6. Conclusion

Assessing the role of isolation for speciation is not trivial and should at least focus on the distance to environmentally similar habitats rather than to terrestrial surfaces or land-to-land connections. In addition, large islands between the focal one and the coast ecosystems might act as both source systems (Fernández-Palacios et al., 2011) and stepping stones. Climatic fluctuations and the associated elevational shift of vegetation will additionally affect the occurrence of endemic species on islands. Climatic changes are also connected to temporal trends in propagule pressure from the past. In the past, the probabilities of dispersal and gene flow in the Mediterranean have been substantially different from the present (Thompson, 2005). Thus, distance and/or connectivity to refugia, where species could survive long-term climatic fluctuations, can be another good indication for isolation depending on the timeframe associated with the process under focus (Médail and Diadema, 2009).

While habitat diversity is directly linked to the size of regional species pools, local environmental heterogeneity is likely to be positively related to speciation processes. However, this assumption is yet to be proven. An appropriate quantification of spatial heterogeneity and of its reflection in ecological complexity is required. Last but not least, a precise wording for spatial and ecological settings is needed in order to identify generality.

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