Niche-based mechanisms operating within extreme habitats: a case study of subterranean amphipod communities

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It has been suggested that both niche-based and neutral mechanisms are important for biological communities to evolve and persist. For communities in extreme and isolated environments such as caves, theoretical and empirical considerations (low species turnover, high stress, strong convergence owing to strong directional selection) predict neutral mechanisms and functional equivalence of species. We tested this prediction using subterranean amphipod communities from caves and interstitial groundwater. Contrary to expectations, functional morphological diversity within communities in both habitats turned out to be significantly higher than the null model of randomly assembled communities. This suggests that even the most extreme, energy-poor environments still maintain the potential for diversification via differentiation of niches.

Keywords: subterranean communities; neutral theory; ecological niches; Niphargus

1. INTRODUCTION

The puzzling question of how species-rich communities are assembled and sustained has recently been addressed through models that combine niche-based and neutral mechanisms [1–7]. Classical, niche-based models assume that differences in resource use among species facilitate coexistence as they tend to increase negative intraspecific interactions relative to negative interspecific interactions [8]. In contrast, neutral models assume that species are functionally equivalent and the species composition of communities depends on stochasticity in demographic rates [9,10].

Communities in extreme environments, where one or more environmental parameters exhibit extreme values, present intriguing test cases. On a global scale, such environments have only narrow ecological niches. Their inhabitants are expected to be highly filtered subsamples of regional species pools [11,12], and natural selection is likely to accumulate convergent adaptations [13]. The role of competition in community structure within extreme habitats is controversial. Although stressful environments may lower competition, it has been shown theoretically that harshness alone does not lessen the importance of species interactions in community structure [14]. Also, because these habitats are infrequently invaded and act as cul-de-sacs for species that do invade them, they are characterized by low dispersal and low recruitment. These, in turn, are conditions favouring the evolution of functional equivalence according to mathematical models [10]. The overall prediction from the above considerations is that communities in extreme habitats will consist of morphologically similar, convergently evolved and ecologically equivalent species.

In this study, we looked at communities in the subterranean realm. In this high-stress environment, extremes are imposed by permanent complete darkness and food scarcity [16]. Food webs are truncated at the bottom (no primary producers) and at the top (few obligate predators) [11,17]. Local communities may have up to 100 species [17]. Subterranean communities are presumably old [11], leaving enough time for ecological functions of species to converge according to Hubbell’s model [10]. Convergent evolution is well documented for morphological [18], physiological and behavioural traits [19]. Furthermore, migration is constrained in subterranean habitats, high endemism and small ranges being the rule [20]. Finally, the inability to monopolize food resources might promote the coexistence of species [21].

Our aim was to test the prediction that subterranean communities consist of functionally equivalent species, the diversity of which is shaped by neutral, rather than niche-based processes. The underlying assumptions are that morphological traits of a species reflect its ecological role, and that lack of similarity among coexisting species is a sign of interspecific competition [22]. We undertook a morphometric analysis of a species-rich group of subterranean amphipod crustaceans (genus Niphargus) and compared convex hull trait volumes [23] of coexisting assemblages with those of randomly derived assemblages.

2. MATERIAL AND METHODS

The amphipod genus Niphargus is an appropriate model taxon for ecology research in cave biology. It is a species rich, ubiquitous and widespread across European subterranean waters, monophyletic at low taxonomic rank, but morphologically more diverse than most other amphipod genera [24,25]. Local communities comprise up to nine species.

We analysed two basic types of subterranean aquatic habitats: caves and interstitial groundwater. Caves are physically much more diverse; the size of available spaces varies between less than a millimetre in tiny crevices and hundreds of metres in large cave lakes. The interstitial is a homogeneous system of small voids between grains of sand and other unconsolidated sediments. We analysed nine cave communities that count between three and nine species, and seven interstitial communities of three to six species. Details can be found in the electronic supplementary material.

To explore the range of assumed ecological roles of species, we analysed their functional morphological traits in two-dimensional morphospace. A multivariate treatment is needed because traits do not act independently of one another, and species may differentiate via a combination of several traits [26]. We focused on traits known to evolve repeatedly and convergently in subterranean habitats, as these are the traits most probably involved in functional equivalence. The most widespread morphological changes of subterranean species include loss of pigmentation and eyes [18], but these are invariant in Niphargus as all species are eyeless and depigmented [25]. Other presumably adaptive morphological traits evolve differently in cave and interstitial amphipods. In caves, amphipods evolve a larger body size and longer appendages [27]. Interstitial amphipods, by contrast, need to cope with narrow spaces and are...
miniaturized, more slender, with reduced pleopods and remarkably elongated pereopod VII [28]. Consequently, we measured antenna and body lengths in cave amphipods, and the relative pereopod VII length and the relative shape of coxal plate III in interstitial amphipods. Because in the latter group all species are small, we eliminated size as a variable. The width–depth ratio of coxal plate III served as a surrogate for the body shape, i.e. slender versus stout: slender species have shallow and wide coxal plates, stout species narrow and deep ones (figure 1).

We used convex hull volume (CHV) as a measure of morphological disparity [23]. CHV quantifies the volume of the trait space occupied by species in a community. In a two-trait case, it reduces to a convex polygon area. It is insensitive to trait distribution and can be extended from one to n traits, keeping in mind that the number of species in a community must exceed the number of traits [29]. The measure proved useful in detecting similarity within communities as in habitat filtering and functional similarity [30]. Morphological disparity of a community depends on the number of species in the community. To eliminate the impact of species number, we generated disparity null models for each community size class by drawing 1000 random communities from a regional pool of 94 species (details can be found in the electronic supplementary material). CHV of real communities were then compared with null model expectations using the two-tailed Wilcoxon-signed rank test. We used scripts in R-project, and the program PASW STATISTICS v. 18.

3. RESULTS AND DISCUSSION

Results for both types of subterranean habitats indicate that most local communities consist of species that are morphologically more disparate than expected if communities were assembled at random (figure 2). CHV of actual communities were significantly larger compared with null models both in caves ($Z = -2.09, p = 0.037$) and in interstitial groundwater ($Z = -2.37, p = 0.018$).
Thus, we reject the hypotheses of functional equivalence among species in subterranean communities. Instead, higher than expected disparity in functional traits suggests that niche-based mechanisms operate even within narrow niches of extreme environments.

The finding that extreme, energy-poor environments still maintain the potential for diversification via differentiation of niches is somewhat surprising, but not entirely unexpected [14]. The subterranean realm itself is heterogeneous [17], and functional diversity might be correlated to differences among microhabitats. However, it is difficult to exactly establish microhabitat associations for subterranean species. Frequent floods and other events can perturb species and obfuscate their place of origin [31]. A recent study of functional morphological diversity in North American subterranean amphipods found no conclusive connection between morphology of species and their habitat [27]. However, the study did not discriminate between sympatric and allopatric occurrence of species, and did not use null models. The different results obtained in our study may be due to the fact that we circumvent the problem of a priori ecological assumptions, and explicitly test observed species associations against null hypotheses.

Functionally, variation in body size makes sense in caves where all size classes of aquatic habitats are available, while the homogeneous pore size of the interstitial restricts it. In the interstitial, on the other hand, niche-differentiation seemingly requires differentiation of body shape, related to the aeration capacity and to feeding mode [28]. These findings are in line with the high-dimensionality hypothesis, which states that co-existence of similar species is aided by hidden additional niche dimensions [32]. The high-dimensionality hypothesis is a purely niche-based explanation that yet remains to be tested for subterranean environments. For now, we cannot exclude that neutral mechanisms, too, operate within the studied communities. Morphological trait values do not seem to be evenly spaced, and clumps of similar species may exist in some communities.

We thank Dolph Schluter for valuable comments. The study was supported by the Slovenian Research Agency Programme P1-0184.