

Deterministic assembly of land snail communities according to species size and diet

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Summary

1. We investigated whether coexisting snail species in 145 treeless fen communities in the Western Carpathian Mountains differed more in size and diet than would be expected by chance, as predicted for traits commonly associated with competition and differential resource acquisition under limiting similarity theory.

2. Contrary to expectations, coexisting snail species were no more different in body size than expected by chance under a null model. However, variation in body size played a significant role in structuring snail communities: coexisting snail species were significantly more similar with respect to body size.

3. We developed two new test statistics to expand our investigation of limiting similarity to include diet, a nominal trait. We tested whether communities of snails were characterized by a greater richness of diet, and whether different diets were represented more or less evenly within communities. Communities of snails were significantly less evenly distributed than expected by chance, with detritivores being over-represented relative to predatory strategies.

4. We also examined the effect of water pH and conductivity, herbaceous cover, and bryophyte and vascular plant richness, on these trends by examining how the effect size of our tests varied across these gradients. Convergence in species size increased with increasing habitat pH. Specifically, smaller snail species were over-represented in fen communities in general, and this effect was accentuated in increasingly calcareous fens.

5. Theory predicts that traits related strongly to environmental conditions are more likely to be convergent. Our findings support this suggestion, as small snail species have an advantage in tolerating freezing conditions over winter when refuges are limited.

6. These results add to the growing body of literature demonstrating that variation in body size and diet play a strong role in structuring communities, although frequently in ways not predicted by limiting similarity theory. Finally, our results increase our understanding of how species are assembled non-randomly into communities with respect to important traits.

Key-words: body size, coexistence community assembly, diet, environmental filtering, limiting similarity, pH, trait convergence, trait dispersion, trait divergence

Introduction

One way that species can coexist is by being sufficiently different morphologically, particularly when these differences are linked with resource requirements (i.e. limiting similarity/character divergence). Such differences can result from co-evolutionary changes in the morphology of sympatric species, or if species within the regional pool are sorted into communities non-randomly with respect to important traits (Grant 1972; Dayan & Simberloff 1998). Regardless of which

of these two mechanisms predominate, both can be expected to produce a single pattern: coexisting species will be of more varied character than expected by chance (MacArthur & Levins 1967; Abrams 1983; Szabó & Meszéna 2006), especially with respect to traits related to specialization on different resources, or on different parts of the resource spectrum. The assumption of limiting similarity is that species that are too similar in resource requirements will compete, with the less competitive species being excluded.

It is important to clarify that theory on trait-based community assembly has also predicted that coexisting species may be convergent with respect to some traits (Weiher & Keddy

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1995; Grime 2006). Weiher & Keddy (1995) suggest that traits which respond to environmental filters, and especially those related to growth in adverse environmental conditions, should be convergent. Traits related to survival in arid conditions, for example, are predicted to be convergent in habitats with consistently low levels of precipitation (e.g. deserts). However, it has also been suggested that competition between species may result in trait convergence due to the loss of species with traits conferring poor competitive ability, especially in productive, non-stressful habitats (Grime 2006). This prediction is complimented by theoretical work demonstrating that evolution under competition may lead to groups of coexisting species with similar traits (Scheffer & van Ness 2006).

Variation in body size among coexisting species has repeatedly been linked to specialization on different resources, and hence niche differentiation, for a variety of taxonomic groups (Wilson 1975). For example, differences in body size among granivorous desert rodents (Bowers & Brown 1982) and fish species (e.g. Scharf, Juanes & Rountree 2000) have been linked to diet specialization and coexistence. Also, rooting depth variation among plant species, a trait broadly related to species size, is believed to play an important role in resource specialization and species coexistence (Berendse 1979, 1981; Fargione & Tilman 2005). Furthermore, numerous important biological processes scale with body size, including metabolic rate (e.g. Enquist, Brown & West 1998), population density (e.g. White 1980), home range size (Kelt & Van Vuren 1999), prey size (e.g. Ashmole 1968; Bowers & Brown 1982; Scharf *et al.* 2000), reproductive allocation (e.g. Blueweiss *et al.* 1978; Evenson 1983) and plant species richness (Niklas, Midgley & Rand 2003). It is, therefore, not surprising that evidence suggests a role for size variation in driving deterministic patterns of community assembly (e.g. Bowers & Brown 1982; Weiher, Clarke & Keddy 1998; Gotelli & Ellison 2002; Mouillot, Šimková & Morand 2005a; Mouillot, Dumay & Tomasini 2007; Schamp & Aarssen 2009).

Evidence in support of limiting similarity theory has been identified for ant communities (e.g. Gotelli & Ellison 2002), rodent communities (Bowers & Brown 1982) and plant communities (Weiher *et al.* 1998). In contrast, Mouillot *et al.* (2005a) found evidence that coexisting gill parasites on fish tended to be significantly more similar than expected by chance for traits including size, Mouillot *et al.* (2007) found similar trait convergence in among coexisting fish species, and Stubbs & Wilson (2004) observed that coexisting plant species, at one of four scales studied, were significantly convergent with respect to size. Still other studies have observed that coexisting species are neither more nor less varied with respect to body size than expected by chance (Schamp, Chau & Aarssen 2008; Schamp & Aarssen 2009). Thus, while it is clear that variation in body size frequently contributes to the deterministic assembly of communities, continued effort is required to determine whether generality exists

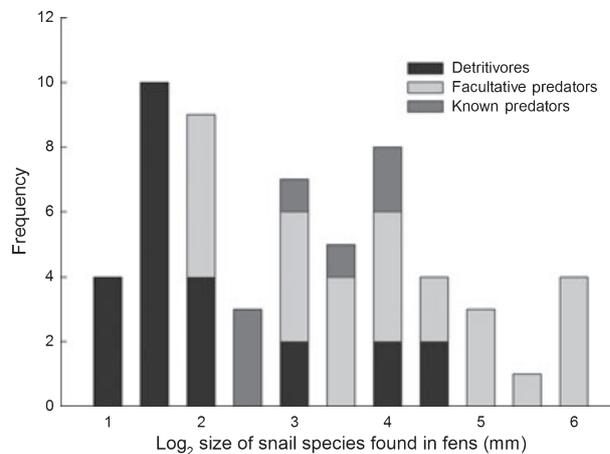


Fig. 1. A frequency histogram showing the distribution of body size for fen-dwelling snail species in the Western Carpathian Mountains. Bars are subdivided to also display species-level variation in diet: black, detritivores and herbivores; light grey, facultative predators; dark grey, known predators of snails. Body size has been log₂ transformed to more clearly visualize patterns of variation.

for the conditions under which coexisting species will be more or less similar in size than expected by chance, or neither (Schamp *et al.* 2008).

Many fen communities of the Western Carpathian Mountains are extremely diverse with respect to snail species; communities in the present study possessed an average of more than 14 species, to a maximum of 27 coexisting land snail species. These land snail species span a considerable range in body size, and vary in diet (Fig. 1), which previous studies have found important in species coexistence (e.g. Bowers & Brown 1982). Given the evidence (see references above) that variation in size and diet can contribute to deterministic community assembly and coexistence via limiting similarity, diverse land snail communities in the fens of the Western Carpathians represent an excellent opportunity to further investigate the general influence of body size and diet variation on community dynamics.

In this paper, we investigate the following hypotheses: (1) Communities of coexisting snail species in the Western Carpathian fens are structured deterministically (i.e. non-randomly) with respect to snail species size and diet; (2) Coexisting snail species are more different in size and diet than would be expected by chance, i.e. conform to the predictions of limiting similarity theory; (3) Patterns of deterministic community assembly are influenced by habitat characteristics such as water pH and conductivity, herbaceous cover and vascular plant and bryophyte species richness.

Materials and methods

STUDY SITES

Data were collected from 145 fen communities in the Western Carpathian Mountains (eastern Czech Republic, north-western Slovakia

and southern Poland). The study area is situated at 48°46'–49°32'N and 17°18'–21°57'E; covering an area of 20 578 km². Study sites spanned the existing gradient of mineral nutrients, from very mineral poor sites (Ca-concentration about 2 mg l⁻¹), to extremely mineral rich sites with Ca-concentration in water more than 300 mg l⁻¹ (Hájek *et al.* 2006; Horsák 2006). Calcium concentration in above-ground vegetation, one of the possible calcium sources for snails, increases in the same direction (Rozbrojová & Hájek 2008). Sites were small and poorly productive (in terms of vegetation) treeless fens with a median habitat area of *c.* 250 m² and only a few sites larger than 1 ha. The geological structure and climatic conditions of the studied area are described in Horsák (2006).

FIELD SAMPLING

All 145 treeless fen communities were sampled between 2000 and 2007 with each site only sampled once to increase independence of samples. Sampling consisted of collecting one 12 L sample of the upper fen-layer from a 4 × 4 m² area in the central portion of each community. Previous studies have revealed that this sample volume is sufficient for determining a community's species pool (Cernohorsky 2007). Snails were extracted from samples using the 'wet sieving technique' (Horsák 2003), in which material from each sample is gradually washed through a bowl-shaped sieve (mesh size 0.5 mm) to remove fine soil. After drying, shells were separated from the remaining material by hand-sorting under a stereo microscope and identified and counted, separating live animals and empty shells. Species nomenclature follows Juričková, Horsák & Beran (2001).

For each community sample, environmental data were collected on the same day that snail samples were taken. Water conductivity and pH were collected at the micro-sites best supplied by water in small shallow holes dug in the sample plots, using portable instruments with automatic temperature compensation (CM 101 and PH 119; Snail Instruments, Beroun, Czech Republic). Readings were standardized to 20 °C. In acid waters with pH values below 5.5, conductivity caused by H⁺ ions was subtracted (Sjörs 1952). Water conductivity is strongly correlated with the concentration of calcium ions in fens ($r = 0.9-0.95$; Sjörs & Gunnarsson 2002; Hájek *et al.* 2005) and therefore can be used as a reliable proxy of calcium concentration (Horsák 2006). Also, for each community sample, bryophyte species richness and vascular plant species richness were assessed, as well as herbaceous cover. Bryophyte and vascular plant species were recorded in the same 16 m² plot as snails. Herbaceous cover was estimated as a percentage cover of vascular plants in that plot using the nine-grade scale of Westhoff & van der Maarel (1978).

Snail species size and diet data were compiled from available literature to avoid a gradient in measurement accuracy favouring common over rare species and particularly to include species found in samples only as juveniles, potential problems that have been noted in similar studies (Bowers & Brown 1982 and Mouillot *et al.* 2007). Furthermore, body size values taken from the literature represent objective, species-level measures of potential size (e.g. Weiher *et al.* 1998; Stubbs & Wilson 2004; Schamp *et al.* 2008; Schamp & Aarssen 2009) that avoid difficulties arising from sampled snails varying in size due to age differences, and can be more clearly related to the theories being tested than can locally measured, phenotypic values that may be driven by local adaptation or competitive suppression.

As a measure of maximum body size we used length along the longest axis according to Ložek (1956) and Kerney, Cameron & Jungbluth (1983). Feeding strategies were obtained based on published data summarized in the most recent review edited by Barker & Efford (2004) by the three following types: (a) Detritivores and

herbivores, species that combine both strategies; (b) Facultative predators, species that express any tendency towards carnivory but probably do not feed directly on live snails (species with aggressive behaviour and cannibalism, feeding on snail eggs or feeding on animal tissues in general); (c) Presumptive true carnivores that may also feed directly on live snails (i.e. known facultative carnivores of snails). These diet classes indicate broad preferences; however, it is worth noting that both predatory classes of snails are known to vary in the degree to which they are omnivorous.

ANALYSIS – SNAIL SPECIES SIZE AND DIET

Snail samples subjected to analyses were based only on live snails collected from field samples. A total of 58 terrestrial snail species and 13 772 individual snails were collected in the studied fens.

We used an established null model to test for evidence of non-random organization of snail species according to size and diet; in particular, we tested for evidence of patterns expected under limiting similarity theory for both body size and diet (Stubbs & Wilson 2004; Schamp *et al.* 2008; Schamp & Aarssen 2009). This model tests whether community-scale trait distributions differ significantly from what is expected if traits are assigned to species at random. In this model, traits (i.e. body size and diet) are randomized among species without replacement, which avoids difficulties arising in some null models which randomize elements of the site by species matrix (e.g. Stone & Roberts 1990; Mouillot *et al.* 2005a). Distributions of each test statistic were generated from 3000 randomizations of the trait matrix. All null model tests are two-tailed tests, with *P*-values calculated as: $P = \text{MIN} [2S/(3001), 2L/(3001)]$ where *S* and *L* refer to the number of randomized test statistics greater than or equal to, or less than or equal to the measured test statistic, respectively (cf. Bersier & Sugihara 1997; see also Schamp *et al.* 2008; Schamp & Aarssen 2009). Null model analyses were performed in Matlab using code developed by the first author. We used analyses based on presence-absence data, but also ran tests using abundance data (i.e. trait presence in each community was weighted by abundance), as this can sometimes produce different results (Schamp *et al.* 2008).

To explore our hypotheses, we used the following test statistics: (1) Mean – This measure was used to assess whether snail communities, on average, consisted of larger or smaller species than expected by chance; this statistic is useful for identifying whether large vs. small snails are favoured within communities. (2) Range – This statistic is calculated as the maximum trait value minus the minimum trait value for a particular sample. When this test statistic is larger than expected by chance, this is evidence for limiting similarity theory. If this statistic is smaller than expected by chance, it is evidence for trait convergence. (3) Mean Nearest Trait Distance (meanNTD) – This was calculated as the mean nearest trait distance (Euclidean) between each species within a sample. The mean of plot level meanNTD among all plots was used as the measure of how spaced traits are within samples. Higher meanNTD values than expected support limiting similarity theory (Weiher & Keddy 1995), and smaller meanNTD values suggest trait convergence (Grime 2006). (4) Variance in Nearest Trait Distance (varNTD) – This is the variance in Euclidean distances between each species and its nearest species in trait space within samples; this is a measure of how regularly spaced coexisting species are with respect to the trait of interest. Values of varNTD that are lower than expected have been cited as evidence for limiting similarity (Stubbs & Wilson 2004). (5) Richness – This test statistic

Table 1. A summary of predictions demonstrating how each test statistic provides evidence in support of a specific theoretical prediction

Trait	Test statistic	Observed > Expected	Observed < Expected
Snail body size	Mean	Size-advantage	Size-disadvantage
	Range	Limiting similarity	Convergence
	MeanNTD	Limiting similarity	Convergence
	VarNTD	Not interpretive	Limiting similarity
Snail feeding types	Richness	Limiting similarity	Convergence
	Evenness	Limiting similarity	Convergence

MeanNTD, mean nearest trait distance; VarNTD, variance in nearest trait distance.

was used for categorical traits and is simply a measure of the number of categories represented within a sample. If richness is higher than expected by chance, this would suggest evidence of limiting similarity, and a lower than expected value of richness would indicate that some categories are favoured over others. (7) Evenness – This statistic was also used with categorical data and is a measure of how evenly represented different categories were within samples. This measure addresses recent suggestions that functional diversity should be measured both in terms of richness and evenness (Mason *et al.* 2005; Moullot *et al.* 2005b). High evenness is taken here as evidence in support of limiting similarity theory, while lower evenness than expected would indicate some categories are more favoured. In cases where richness and/or evenness are less than expected by chance, an additional test was done to determine which trait category was more common than expected by chance; this was counted as evidence that a particular trait category was favoured. In Table 1, we summarize the predictions associated with each of these test statistics.

COMMUNITY ASSEMBLY ALONG GRADIENTS

We tested whether these patterns changed along environmental gradients by using regressions to test for directional changes in effect-sizes (z -scores) of our tests among snail communities that span gradients in water pH and conductivity, vascular plant species richness, bryophyte species richness and herbaceous cover. Z -scores for each fen plot and each test statistic were calculated as $(O-M)/S$, where O is the observed value for each test statistic and fen plot, and M and S are the mean and standard deviation respectively for each test statistic across 3000 randomizations of the trait distribution for that snail community (Schamp & Aarssen 2009).

Table 2. Results from null model test of non-random species organization according to snail species body size and species feeding habits

Trait	Test statistic	Observed > Expected	Observed < Expected	Description
Body size	Mean		0.0007	Size-disadvantage
	Range		0.0027	Convergence
	MeanNTD		0.0213	Convergence
	VarNTD		0.5100	
Feeding habit	Richness	0.9807		
	Evenness		0.0013	Strategy advantage

This analysis uses presence-absence data as well as continuous size data (species length in mm), and nominal data (diet).

Significant results ($\alpha < 0.05$) are presented in bold. MeanNTD, mean nearest trait distance; VarNTD, variance in nearest trait distance.

Results

COMMUNITY ASSEMBLY AND SNAIL SPECIES SIZE

Fen communities are organized deterministically (i.e. non-randomly) with respect to snail species size (Table 2). Snail communities have a significantly narrower range of species size than expected by chance, and coexisting snails were more similar in size than expected by chance (Range, MeanNTD; Table 2). This is evidence of trait convergence rather than divergence, which is expected under limiting similarity theory. Furthermore, coexisting snails are smaller, on average, than expected by chance (Mean; Table 2). The results of analyses using presence-absence data did not differ from those using abundance data (not reported).

COMMUNITY ASSEMBLY AND DIET

Communities of snails nearly always consisted of species with each of the three analysed diets (detritivores, facultative carnivores and presumptive true carnivores). Consequently, it was not surprising that communities were no richer in snail diets than expected by chance. Diets were significantly less evenly represented in fen communities than expected under our null model (Evenness; Table 2). A *post hoc* randomization test was used to clarify which diets were more or less common than expected by chance. This test was similar in form to the original test, but compared the number of species with each diet in each community, to the number expected if diet were randomized (without replacement) among species. Detritivores are significantly over-represented in communities ($P = 0.002$), facultative predators are significantly under-represented ($P = 0.0013$), and the number of predator species in communities was no higher or lower than expected by chance ($P = 0.74$).

COMMUNITY ASSEMBLY ALONG GRADIENTS

The degree to which large snail species are under-represented in fen communities increases significantly with habitat pH ($R^2 = 0.114$, $P < 0.001$; Fig. 2a). Thus, small snail species are more common than expected by chance in more calcareous fens, especially in habitats where pH is higher than 7.0 (Fig. 2a). All test statistics providing evidence for commu-

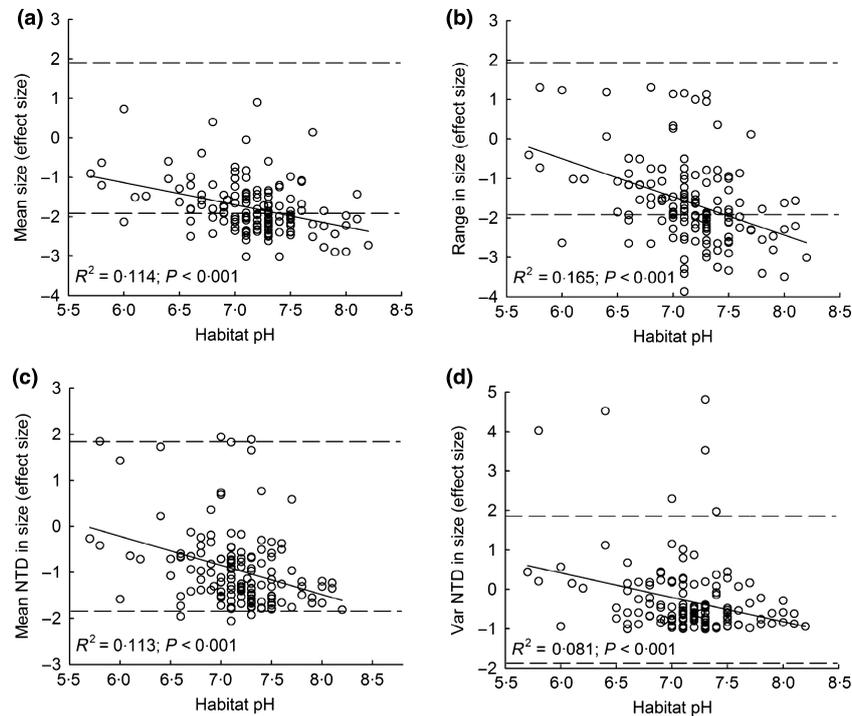


Fig. 2. Regression analyses visualizing changes in the effect-sizes of four null model test statistics across the existing gradient of habitat pH. Mean snail species size becomes increasingly significantly smaller than expected under our null model at the calcareous end of the pH gradient, indicating a size-disadvantage for snails in these habitats (a). The range in snail species size also becomes increasingly contracted at the calcareous end of the gradient, indicating that species coexisting in calcareous sites are much more similar in size than expected under our null model (b). Analysis of mean nearest trait distance demonstrates that coexisting snail species are increasingly more similar in size in more calcareous sites (c). Finally, in higher pH sites, species are more regularly spaced with respect to body size than expected by chance under our null model (d). Y-axes represent z-scores, which are a standardized measure of the degree to which the test statistic differed from what was expected by chance. As such significant trait-based assembly ($\alpha = 0.05$) is indicated when plots (each data point is a fen plot) are less than -1.96 (observed < expected), or greater than 1.96 (observed > expected). Significance boundaries are indicated by dashed horizontal lines at these values.

nity-scale convergence of snail size also decreased significantly with increasing habitat pH (Range: $R^2 = 0.165$, $P < 0.001$; Mean NTD: $R^2 = 0.113$, $P < 0.001$; VarNTD: $R^2 = 0.081$, $P < 0.001$; Fig. 2b–d). Effect-sizes did not change significantly across gradients of conductivity, plant species richness, moss species richness, or herbaceous cover ($P > 0.05$; results not shown).

Discussion

We found no evidence that snail species in fen communities coexist by being more different in body size than expected by chance (Table 2). This was true whether analyses focused on presence-absence data, or were weighted by abundance. These results contrast those of Bowers & Brown (1982), who found that body size differences among desert granivorous rodents contributed to coexistence, those of Gotelli & Ellison (2002), who observed that ant species within bogs tend to be more different in size than expected by chance, and those of Weiher *et al.* (1998) who found that wetland plant species of different size co-occur more than expected by chance. These results correspond to the findings of Stubbs & Wilson (2004), Mouillot *et al.* (2005a, 2007), Schamp *et al.* (2008), and Schamp & Aarssen (2009) that species size differences among

species did not contribute to the local coexistence as predicted by limiting similarity theory. Additionally, our results correspond to the findings of Cornwell & Ackerly (2009) who observed significant convergence in height among coexisting plant species, and those of Mouillot *et al.* (2005a, 2007), who observed significant convergence with respect to multiple traits that include body size, in gill parasites of fish and of fish assemblages, respectively. As such, these results contribute to a growing body of evidence investigating whether variation in body size, which is frequently substantial, contributes to niche differentiation, and therefore species coexistence. Taken with these other findings, accumulating evidence suggests that the role of body size in species coexistence is inconsistent across taxonomic groups.

We also found no evidence that communities of snails were more diverse, in terms of richness or evenness, in species' diets, than expected by chance (Table 2); variation in diet among snail species does not appear to contribute to niche separation, and coexistence. However, this is admittedly a course-grained test of this hypothesis, and a detailed study of diet overlap among coexisting snail species would add to this preliminary investigation. While our analysis provides no evidence of limiting similarity with respect to species diet, it is still possible that snails coexist by more fine differences in

diet. While our results provide no evidence that coexistence of snail species is driven by niche differences related to size or diet, it is certainly still possible that limiting similarity, with respect to other important species-level traits, is an important driver of land snail species coexistence in treeless fen communities.

Theoretical work by Weiher & Keddy (1995) has predicted that traits related to the competitive process should diverge, conforming to the predictions of limiting similarity theory, while traits that respond to an environmental filter, especially under adverse conditions, should be convergent, as snail size is in this study. It may then be reasonable to assume that body size variation among snail species is not important to the competitive process, or that interspecific competition is simply weak among land snails. Indeed, it has been argued that terrestrial gastropods experience at most weak levels of interspecific competition (e.g. Boycott 1934; Solem, Climo & Roscoe 1981; Solem 1984; Perry & Arthur 1991; Cameron & Cook 2001; Horsák 2006; Cook 2007). However, some clear examples of competitive exclusion among terrestrial snails exist (e.g. Frömring 1954; Mordan 1977) and several studies have found interspecific competition between pairs of species (e.g. Cameron & Carter 1979; Baur 1988; Magnin 1993). Furthermore, the existence of carnivorous species, including some malacophagous land snail species, set up clear conditions for asymmetrical competition between these and prey species (see Barker & Efford 2004). If indeed snail communities can be characterized as competitive environments, our results do not conform to the predictions of Weiher & Keddy (1995). It has also been suggested, however, that coexisting species will be more similar with respect to traits related to the competitive process (i.e. trait convergence), as the competitive process will exclude species with traits related conferring poor competitive ability, as predicted by Grime (2006). If body size variation contributes to competition, our results can be understood to support Grime's (2006) predictions. This is further supported by our result that trait convergence is to one end of the size spectrum; smaller snails are over-represented within communities relative to what is expected by chance (Table 2). However, the contrasting predictions of Weiher & Keddy (1995) and Grime (2006) make it difficult to determine, using these results, whether the observed influence of body size variation on snail community assembly is manifested by competition. Our analysis included both detritivorous and omnivorous (i.e. facultative and presumed true carnivores) snails. Therefore, interspecific interactions between snails may be characterized by competition, or by predator-prey interactions. This has the potential to introduce difficulty in distinguishing between competition and predation as mechanistic explanations of our results. However, the observed convergence in snail species size, which favours smaller, generally detritivorous snail species (Fig. 2), suggests that our results were not driven by predation.

It has also been suggested that competition among snails is greatest in more calcium-rich sites (positively correlated with water pH; Hájek *et al.* 2005), that are characterized by higher species richness and abundance of snails (e.g. Waldén

1981; Millar & Waite 1999; Hylander *et al.* 2005; Horsák & Cernohorsky 2008). Additionally, the significantly greater number of predatory snail species in more calcium-rich sites ($R^2 = 0.52$, $P < 0.001$ for water pH) suggests that competition may play a greater role in these communities. Studies of snail competition have been often conducted in relatively calcium-poor habitats characterized by low snail species richness and abundance, which may account for suggestions that interspecific competition among snails is weak (e.g. Hylander *et al.* 2005). Our results show increased convergence of snail species body size, as well as an increased over-representation of smaller snail species at this end of the pH (calcium) gradient (Fig. 2). These findings conform to the predictions of Grime (2006) that convergence of traits related to competition, favouring one end of a trait gradient, will be greatest in low-stress, increasingly productive habitats with respect to snail growth (i.e. with higher calcium availability).

For many different organisms, body size can play an important role in competition (e.g. Gaudet & Keddy 1988; Munday, Jones & Caley 2001; Reinhardt, Yamamoto & Nakano 2001; Eichenberger, Siegenthaler & Schmidt-Entling 2009). For this reason, we have examined our results in the context of predictions made regarding how communities are assembled according to traits that may be important in competition (Weiher & Keddy 1995; Grime 2006). However, it is possible that for snail species, body size plays a greater role in tolerance to adverse environmental conditions; specifically surviving under low temperatures (Ansart & Vernon 2003). For such traits, only the prediction of trait convergence has emerged (Weiher & Keddy 1995). Indeed, our results could also be interpreted as evidence that snail species size is related to survival along gradients of calcium availability and pH. Our results demonstrate that small snail species are over-represented in general (i.e. size-disadvantage), and that this is accentuated in more calcareous sites, where calcium is presumably more available (Table 2; Fig. 2a). Furthermore, more calcareous sites are characterized by coexisting snail species that are increasingly similar in body size (Fig. 2b-d). If these results can be interpreted as evidence that body size variation is linked to environmental filtering of species along calcium/pH gradients in treeless fens, there must be a cost to being large in calcareous, calcium-rich habitats. In general, land snails that are found in fens are significantly smaller than species found growing in other habitats within Europe (mean size of non-fen species = 21.9 mm, mean size of fen species = 11.9 mm) (Fig. 3). Smaller snails may be favoured in fen communities because larger species are less capable of supercooling (shell size > 20 mm; Stöver 1973; Ansart, Vernon & Daguzan 2001) and because fens, which are generally poorly productive (in terms of vegetation) compared to other plant communities, and have more consistently waterlogged soils (Hájek *et al.* 2006), provide fewer suitable winter refuges. In contrast, very small snail species are known to be freezing avoidant and can effectively cope under conditions without suitable winter shelters (e.g. Riddle 1981; Schmid 1988).

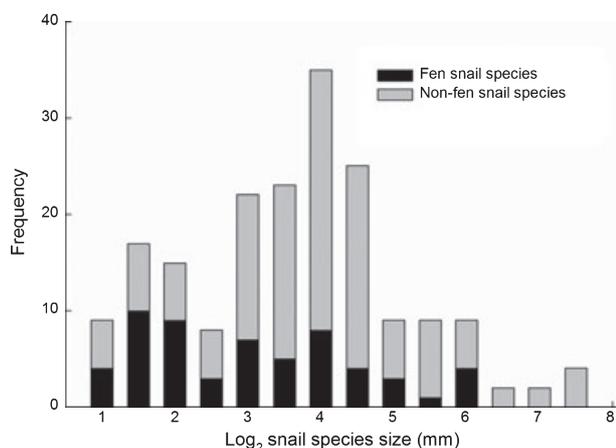


Fig. 3. A frequency histogram showing the distribution of body size for fen-dwelling snail species (black bars) in relation to non-fen dwelling snail species (grey bars) found in the Western Carpathian Mountains.

Thus, there is a clear relationship between snail size and environmental tolerance (Ansart & Vernon 2003).

There is strong evidence linking small snail species size to survival in treeless fens in general, and specifically in calcareous fens; which is concordant with our results (Table 2, Fig. 2). Additionally, in calcareous fens, the observed overrepresentation of very small species, and related convergence of species with respect to body size, is further reinforced by the fact that calcareous sites are also the most nutrient limited and consequently unproductive fens in terms of vegetation (Hájek *et al.* 2006; Rozbrojová & Hájek 2008). These sites in particular will increasingly favour small snail species over large ones, as large species are left with fewer shelters in these communities which are poorly productive with respect to vegetation, and are therefore contain only sparse vegetation. Thus, our findings related to body size variation conform to the predictions of Weiher & Keddy (1995) that coexisting species will be more similar with respect traits related to tolerance of adverse environmental conditions. These results, and their interpretations, highlight the necessity of understanding the broad evolutionary and ecological context of interspecific variation in particular traits to better assess the mechanism behind observed deterministic patterns of community assembly.

Our results contribute to a growing body of literature demonstrating a frequent but variable influence of variation in body size and diet on community assembly across taxa (Bowers & Brown 1982; Weiher *et al.* 1998; Stubbs & Wilson 2004; Schamp *et al.* 2008; Schamp & Aarssen 2009). Additionally, our findings provide support for theoretical prediction of Weiher & Keddy (1995) that traits related to environmental tolerance will be convergent (Fig. 2). Future research should be focused on exploring the generality of theoretical predictions for trait-based community assembly, and on clearly linking deterministic assembly rules to specific mechanisms. To address these goals, we recommend the use of field manipulations in conjunction with null model analyses to more clearly identify

the mechanistic basis for particular trait-based assembly rules, especially in light of the existence of conflicting theoretical predictions.

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