

Density compensation suggests interspecific competition is weak among terrestrial snails in tabonuco forest of Puerto Rico

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ABSTRACT.—In the Luquillo Experimental Forest (LEF) of Puerto Rico, composition of terrestrial gastropod assemblages exhibits little temporal variation, even in response to intense hurricanes. One might therefore expect snail assemblages to be equilibrational and structured by interspecific interactions such as competition. If competition is strong and persistent throughout an assemblage, then it should manifest as density compensation (a negative correlation in population density between competitors) and be most pronounced for species pairs that are morphologically similar, as they should compete most strongly for resources. We assessed the degree to which terrestrial snails in the LEF exhibit density compensation, from both spatial and temporal perspectives. In general, density compensation was weak, especially from a spatial perspective. Moreover, the degree of density compensation was not significantly associated with dissimilarity in body size or shell shape. These results suggest that external factors such as predation or disturbance probably maintain population densities at low enough levels that the effects of interspecific competition do not become intense or persistent enough to mold patterns of assemblage structure for terrestrial snails.

KEYWORDS.—body size, community structure, Gastropoda, interspecific competition

INTRODUCTION

A substantial literature explores the role of interspecific interactions in structuring natural communities. Of the potential types of interactions among species, competition for resources is among the most often cited as an important force shaping communities. It can do so in several ways, such as by reducing population size of competitors (Gause 1934) or exerting selective pressure to enforce a minimum degree of morphological similarity among competitors (Hutchinson 1959; Grant 1999).

The importance of competition among terrestrial gastropod species is unclear. Competitive interactions between species have been demonstrated commonly under laboratory conditions (e.g. Cameron and Carter 1979; Baur and Baur 1990) and for some pairs of large and conspicuous species (e.g. Magnin 1993). Nonetheless, pervasive effects of competition are more rarely observed throughout a gastropod assemblage (Solem 1985; Barker and Mayhill 1999).

Tropical snail assemblages, long considered depauperate (Solem 1984), are becoming increasingly well known, and are often quite species-rich (Emberton 1995; Tattersfield 1996; de Winter and Gittenberger 1998; Schilthuizen and Rutjes 2001). In such systems, snails probably are important to food web structure, filling a variety of feeding niches and providing an abundant food resource for many predators (Garrison and Willig 1996). Nevertheless, detailed studies of the ecology of most taxa are lacking, and little is known about interactions among species.

In the Luquillo Experimental Forest (LEF) of Puerto Rico, composition of terrestrial gastropod assemblages exhibits little temporal turnover, even in response to intense and large-scale disturbances such as hurricanes (Bloch 2004; Willig et al. 2007). One might therefore expect snail assemblages to be equilibrational and to display morphological patterns that are consistent with a history of competitive interactions. One

line of evidence suggests that, for one large and abundant species (*Pleurodonte* [*Caracolus*] *caracolla*), competition is unimportant, as its growth rate and maximum adult size were not affected by density of conspecifics or of other snail species over a period of 9 years (Bloch and Willig 2009). For the remainder of the assemblage, however, the importance of competition remains unexplored.

If competition is strong and persistent throughout an assemblage, it is likely to manifest as density compensation (a negative correlation in population density between competitors). Further, density compensation should be most pronounced for species pairs that are the most morphologically similar, as they should compete most strongly for resources (Hawkins and MacMahon 1989; Stevens and Willig 2000a). In gastropods, shell shape may be associated with microhabitat choice (Heller 1987; Emberton 1995) and, therefore, resource use. In addition, for some taxa, the primary axis of niche differentiation may be body size (Ritchie and Olf 1999). Therefore, we assessed the degree to which terrestrial snails in the LEF exhibit density compensation, and the extent to which it is associated with similarity in body size or shell morphology.

METHODS

Study Site and Field Methods

Long-term censuses of terrestrial snails were carried out in the Luquillo Forest Dynamics Plot (LFDP; 18°20'N, 65°49'W), a 16-ha grid in the northwest of the LEF, in the Luquillo Mountains of northeastern Puerto Rico. The LFDP lies in tabonuco forest, a subtropical wet forest type (Ewel and Whitmore 1973) found below 600 m of elevation. Although a modestly drier period typically extends from January to April (hereafter, the dry season), rainfall generally remains ≥ 20 cm in all months (Brown et al. 1983).

Within the LFDP, 40 circular plots of 3 m radius were spaced evenly in a rectilinear grid system such that 60 m separated adjacent points along a row or column (see Willig et al. 1998). Beginning in the summer

of 1995 and continuing until 2003, snail surveys were conducted twice annually, in March (dry season) and during the summer (wet season). The lone exception was the dry season of 1999, when sampling was conducted in January rather than March to assess the short-term effects of Hurricane Georges. Each plot was sampled once in the dry season of 1991, twice in each season from the wet season of 1991 to the wet season of 1993, three times per season from the dry season of 1994 to the dry season of 1995, and four times per season thereafter, except for the dry season of 2003 (two surveys).

Each time a plot was sampled for snails, 2 people surveyed it for a minimum of 15 min, during which time they searched all available surfaces (e.g., soil, litter, rock cover, vegetation) up to a height of approximately 3 m. In the wet season of 2001, we measured height and diameter of shell for each individual to the nearest 0.1 mm using dial calipers. We returned all individuals, within minutes, as closely as possible to the point of capture (and always within the plot of capture). We maintained a minimum of 2 days between sampling periods so that gastropods could recover from displacement during previous surveys and return to preferred microhabitats. All sampling was conducted at night (1930 to 0300 h) to coincide with peak snail activity (Heatwole and Heatwole 1978; Willig et al. 1998).

To minimize alteration of long-term study plots, we chose to disturb substrate as little as possible while searching for snails. This method limits our inference space, potentially ignoring small, litter-dwelling species. This can be problematic when attempting a complete taxonomic inventory of a site (Cameron and Pokryszko 2005); in many terrestrial gastropod assemblages, this approach would exclude a majority of individuals or taxa (e.g. Tattersfield 1996; Barker and Mayhill 1999; Schilthuizen and Rutjes 2001; Nekola 2005). In the LEF, however, the gastropod fauna comprises many large and arboreal taxa. In contrast, snail density in the litter community from throughout the Luquillo Experimental Forest, including tabonuco, palo colorado, and elfin

forest sites, was low (0.29 individuals per m²) based on diurnal samples (Richardson et al. 2005). Moreover, snail densities from samples that were restricted to tabonuco forest were even lower (0.17 individuals per m²), and all individuals represented a single species, *Megalomastoma croceum* (Barbara Richardson and Michael Richardson, unpublished data). Therefore, we are confident that our visual sampling method was appropriate for our focal taxa.

We estimated population density within each plot in each season as the mean number of individuals captured per night within that season. Although this measure underestimates true density, it has advantages over other measures. It does not require marking of snails for subsequent identification, imposes few assumptions, and is not biased by differences in sampling intensity among years. In addition, estimates of density using average number of captures are correlated strongly and positively with mark-recapture estimates of density for two species (*Pleurodonte caracolla* and *Nenia tridens*) on the LFDP, suggesting that average number of captures is a reasonable index to changes in density of terrestrial snails over time (Bloch, 2004).

Assessment of Density Compensation

Density compensation might be observed from either temporal (i.e., in years when density of one species is highest, densities of its competitors should be lowest) or spatial (i.e., at sites where density of a species is highest, densities of its competitors should be lowest) perspectives. We used Pearson's product-moment correlation coefficient, r (Sokal and Rohlf 1995), to assess both temporal and spatial density compensation, first estimating correlations in density from 1991-2003 between all possible pairs of species and then determining spatial correlation of densities for each species pair based on 40 plots in the summer of 2001.

If species of similar body sizes compete most strongly, then density compensation (i.e., negative correlations in density) should be strongest for species pairs that are most similar in size. For each snail spe-

cies, we used the geometric mean of shell height and shell diameter (Stanley 1986; Jablonski 1997) as a surrogate for body size (hereafter, size index). This index should correlate strongly with shell volume and the body size of the individual inhabiting the shell, as well as being non-invasive and easy to measure in the field. We obtained a single estimate of body size for each species by calculating the mean size index of individuals captured in the wet season of 2001. To assess the degree to which correlations in density among species were associated with differences in body size, we estimated the correlations between those values of r and absolute differences in size index. A strong negative correlation between size differences and temporal or spatial correlations in density would suggest that strength of competition is greatest for species that are most similar in size. For this analysis, we first examined all taxa, irrespective of diet or functional group, then repeated the test for species pairs within each of three functional groups (carnivores, arboreal grazers, and forest floor grazers/detritivores) based on diet and habitat associations.

Finally, we conducted a similar set of analyses to assess the degree to which density compensation was associated with differences in shell morphology (i.e., shape). To do so, we characterized shell shape using spire index (i.e., the ratio of shell height to shell diameter; Cain 1977). We then estimated the correlations between absolute difference in spire index and the correlation coefficients for both the spatial and temporal associations in density among species. We conducted analyses for the entire snail assemblage as well as for each of the three functional groups.

RESULTS

A total of 16 species of shelled gastropods was captured from 1991-2003, of which 14 were used in analyses. One, *Lamellaxis gracilis*, was rare and did not appear in the summer 2001 sample, so no estimate of body size was available. Finally, two species (*Oleacina interrupta* and *O. playa*) are relatively rare, morphologically similar,

and sometimes difficult to differentiate in the field. Because it is impossible subsequently to verify identities of released and unmarked individuals, we treated the two species as a single entity in analyses. This resulted in a sample of 14 species comprising 91 possible species pairs. Of these 14 species, we classified three as carnivores, seven as arboreal grazers, and four as detritivorous inhabitants of the forest-floor (Table 1).

Density compensation between snail species generally was weak (i.e., few strong negative correlations existed for densities of species pairs) from both temporal and spatial perspectives. Indeed, few significant correlations existed, positive or negative. Only three species pairs had densities that were correlated significantly and negatively over time (*Pleurodonte marginella* and *Polydontes acutangula*, $r = -0.41$, $p = 0.04$; *Megalomastoma croceum* and *Platysuccinea portoricensis*, $r = -0.40$, $p = 0.04$; *Subulina octona* and *P. portoricensis*, $r = -0.41$, $p = 0.04$; $df = 24$ in each case), whereas the densities of four species pairs exhibited significant positive correlations. None of the

negative correlations involved carnivorous species. No species pairs had densities that were correlated negatively in space during the wet season of 2001, although seven species pairs displayed significant positive correlations in density.

For all snails, regardless of functional group, degree of density compensation over time was not associated significantly with interspecific differences in body size ($r = 0.07$, $df = 89$, $p = 0.533$; Fig. 1a) or shell shape ($r = -0.07$, $df = 89$, $p = 0.537$; Fig. 1b). Similarly, for all snails captured in summer 2001, spatial correlation in density was not associated significantly with dissimilarity in body size ($r = -0.04$, $df = 89$, $p = 0.736$; Fig. 1c) or shell shape ($r = 0.06$, $df = 89$, $p = 0.576$; Fig. 1d).

For each of the three functional groups (Fig. 2), results were similar to those observed for all species pairs. Degree of density compensation was not associated with difference in body size, whether evaluated from a temporal (carnivores: $r = 0.82$, $df = 1$, $p = 0.394$; arboreal grazers: $r = 0.14$, $df = 19$, $p = 0.555$; forest floor grazers: $r = 0.60$, $df = 4$, $p = 0.213$) or spatial (carnivores: $r = 0.91$, $df = 1$, $p = 0.274$; arboreal grazers: $r = -0.19$, $df = 19$, $p = 0.410$; forest floor grazers: $r = -0.08$, $df = 4$, $p = 0.878$) perspective. Degree of density compensation also was not correlated significantly with dissimilarity in shell shape, whether density compensation was assessed from a temporal (carnivores: $r = 0.17$, $df = 1$, $p = 0.890$; arboreal grazers: $r = -0.32$, $df = 19$, $p = 0.160$; forest floor grazers: $r = 0.31$, $df = 4$, $p = 0.554$) or spatial (carnivores: $r = 0.35$, $df = 1$, $p = 0.770$; arboreal grazers: $r = -0.01$, $df = 19$, $p = 0.965$; forest floor grazers: $r = -0.19$, $df = 4$, $p = 0.719$) perspective. The nonsignificant results for forest floor grazers (6 species pairs) and especially carnivores (3 species pairs) may be a consequence of small sample size, as it would be impossible to reject the null hypothesis with a sample size of three even if two variables correlated perfectly.

DISCUSSION

Although studies of competition abound in the ecological literature, and competition is well documented for some taxa, its

TABLE 1. Terrestrial snails captured in the Luquillo Experimental Forest during the summer of 2001 and included in analyses of density compensation. Functional group assignment is based on feeding habits and most frequent location of capture.

Species	Functional group
<i>Alcadia alta</i>	Arboreal grazer
<i>Alcadia striata</i>	Arboreal grazer
<i>Austroselenites alticola</i>	Carnivore
<i>Pleurodonte caracolla</i>	Arboreal grazer
<i>Pleurodonte marginella</i>	Arboreal grazer
<i>Cepolis squamosa</i>	Arboreal grazer
<i>Megalomastoma croceum</i>	Forest floor specialist/ detritivore
<i>Nenia tridens</i>	Arboreal grazer
<i>Obeliscus terebraster</i>	Forest floor specialist/ detritivore
<i>Oleacina glabra</i>	Carnivore
<i>Oleacina playa</i> ^a	Carnivore
<i>Platysuccinea portoricensis</i>	Forest floor specialist/ detritivore
<i>Polydontes acutangula</i>	Arboreal grazer
<i>Subulina octona</i>	Forest floor specialist/ detritivore

^aIncludes *O. interrupta*

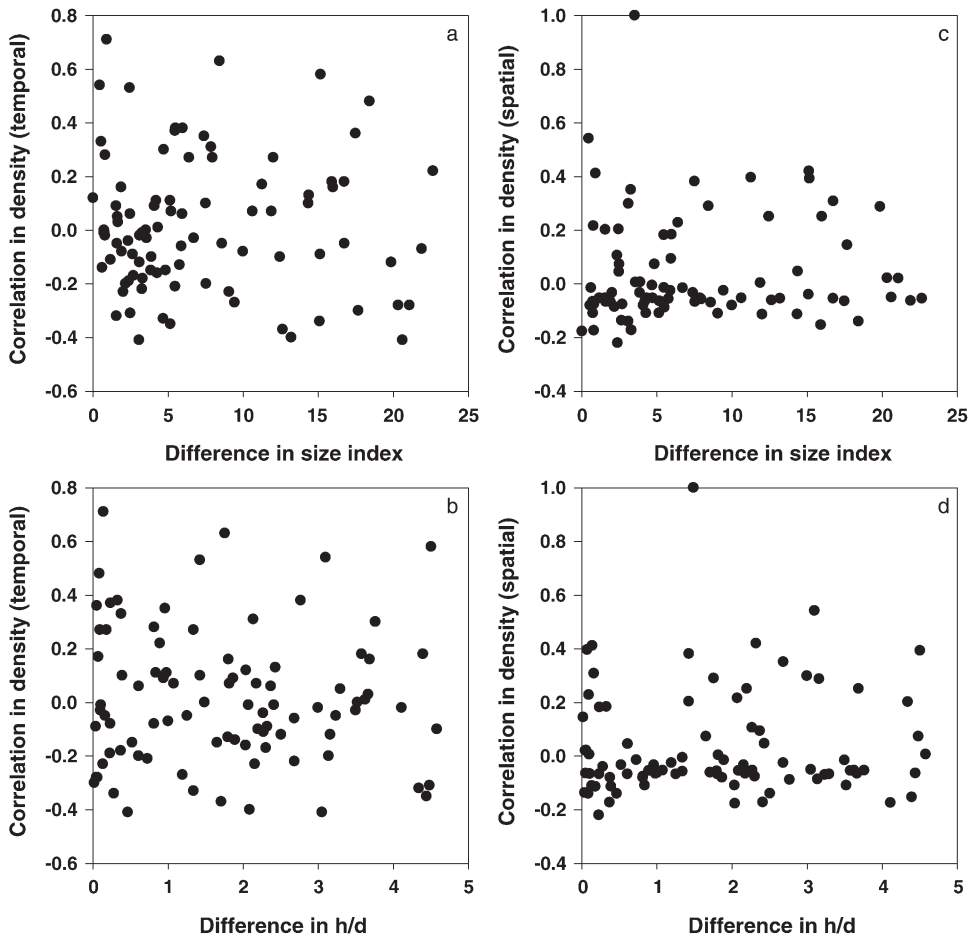


FIG. 1. Degree of density compensation (correlation in population density) for all species pairs of terrestrial snails in the Luquillo Forest Dynamics Plot, regardless of functional group membership. (a) Density compensation over time (1991-2003) as a function of difference in body size, where size index is defined as the geometric mean of shell diameter and shell height. (b) Density compensation over time as a function of difference in shell shape (spire index, h/d , where h is shell height and d is shell diameter). (c) Density compensation in space (over 40 plots) during the wet season of 2001, as a function of difference in body size. (d) Density compensation in space during the wet season of 2001, as a function of difference in shell shape.

importance has come into question for many systems. For example, many guilds or communities appear to be "unsaturated" in that not all available niche space is occupied. This is particularly true for assemblages of parasites and phytophagous insects (Lawton 1984; Rohde 2001). In addition, some recent hypotheses dispense entirely with the idea of equilibrium, suggesting instead that chance and history are more important in structuring communities than are interspecific interactions

(Bell 2001; Hubbell 2001). Nevertheless, it is difficult to demonstrate conclusively that competition is unimportant or does not occur, especially in observational (as opposed to experimental) studies. Indeed, the failure to reject a null hypothesis should not be construed as acceptance or proof of that null hypothesis (Fisher 1966). To confidently discount competition as a major structuring force in a particular assemblage requires tests of multiple hypotheses derived from competition theory (Stevens and Willig 2000b).

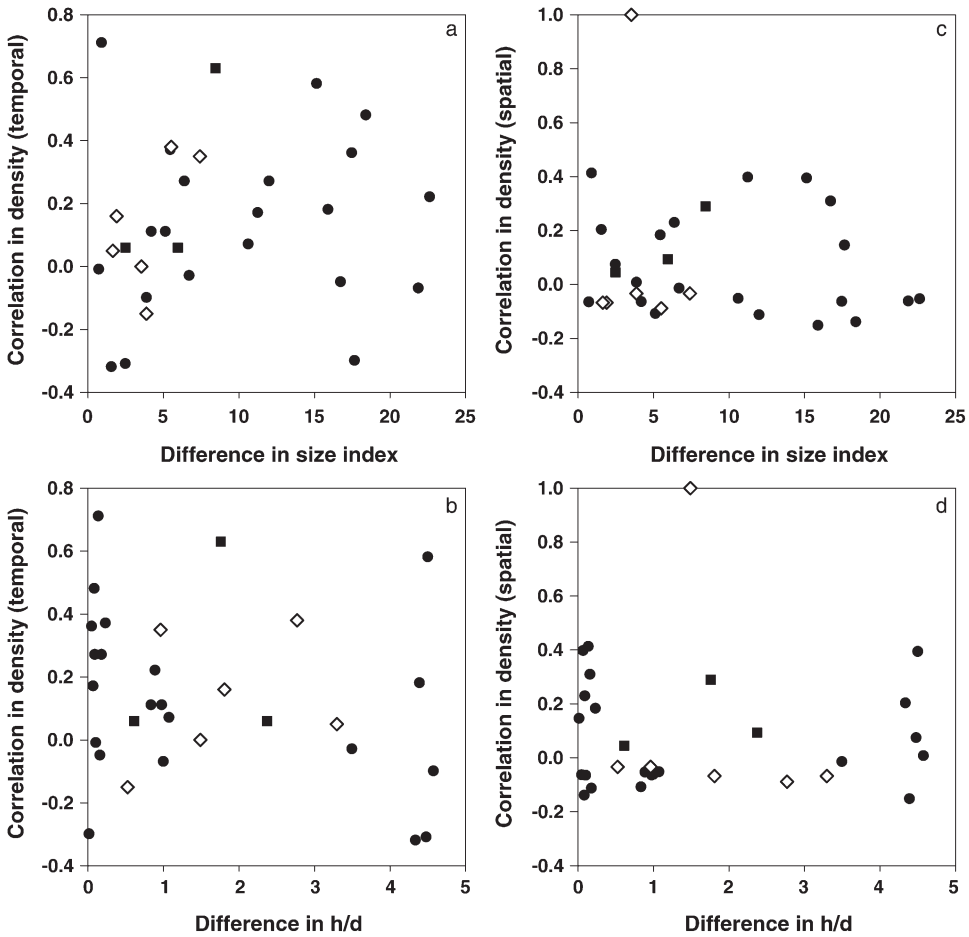


FIG. 2. Degree of density compensation for species pairs within each functional group (arboreal grazers, filled circles; carnivores, filled squares; forest floor grazers/detritivores, open diamonds). (a) Density compensation over time as a function of difference in body size, where size index is defined as the geometric mean of shell diameter and shell height. (b) Density compensation over time as a function of difference in shell shape (spire index, h/d , where h is shell height and d is shell diameter). (c) Density compensation in space during the wet season of 2001, as a function of difference in body size. (d) Density compensation in space during the wet season of 2001, as a function of difference in shell shape.

Competition can influence populations and communities in several ways. Among the most frequently documented mechanisms are the reduction of growth rates or adult size (Cameron and Carter 1979; Baur 1988), promotion of morphological hyperdispersion among competitors (Hutchinson 1959; Grant 1999), and reduction of population size (Gause 1934). The first of these has already been rejected for terrestrial snails in the LEF based on patterns of body size of *P. caracolla* (Bloch and Willig 2009), one of

the largest and most abundant snails in the LEF. Results of the current study also provide little evidence for competitive structuring based on changes in population size. Although densities of three species pairs were correlated negatively over time, density compensation was not a pervasive feature of the assemblage. Importantly, 3 significant correlations are fewer than the number that would be expected (4.55) out of 91 species pairs under the null hypothesis with a comparison-wise error rate of 5%

(i.e., $\alpha = 0.05$). Moreover, density compensation was not significantly associated with body size or morphological similarity.

For competition to be evident as an important structuring mechanism in a community, certain essential conditions must be met. First, at least one resource must be used by multiple species and limiting to the population growth of at least one (Tilman 1982). Second, densities of at least some competitors must approach carrying capacity closely enough that density-dependent processes (e.g., reduction in per capita birth rates, reduction in growth of individuals, increased per capita death rates) manifest (Stevens and Willig 2000b). Circumstances that prevent these conditions from being attained will cause communities to be structured by density-independent factors or by trophic interactions such as predation or parasitism. Several such circumstances may exist for snail assemblages in the LEF, including trophic flexibility, high productivity, and a prevalence of natural disturbances.

Dietary flexibility can preclude interspecific competition from structuring snail assemblages. Terrestrial snails generally are euryphagic (Speiser 2001). This is certainly true of *P. caracolla*, the best-known terrestrial gastropod in the LEF (Heatwole and Heatwole 1978), and probably is true of most other snail species that occur there (Garrison and Willig 1996). Although generalists often have broadly overlapping diets, they can maintain species-specific nutritional niches by consuming different amounts and ratios of particular nutrients (e.g., proteins and carbohydrates; Behmer and Joern 2008). The existence of such nutritional niches could reduce the intensity of competition for any particular resource and therefore facilitate the coexistence of competing generalists.

Productivity in the LEF is high (Wang et al. 2003). Therefore, food sources for snails (e.g., fungi and algae) probably replenish rapidly. A high rate of resource replacement relative to resource consumption should promote coexistence of competitors. Density-dependent population growth should, however, result in an equilibrium such that rates of resource replacement and resource consumption are equal (Tilman

1982). Therefore, high productivity can promote coexistence of competitors only if some additional mechanism reduces population densities.

Disturbance (*sensu* White and Pickett 1985) is one mechanism that might prevent attainment of a density-dependent equilibrium (Connell 1978). The LEF is subject to a complex disturbance regime (Willig and Walker 1999; Thompson et al. 2002) that includes intense, large-scale natural disturbances (i.e., hurricanes). Major hurricanes strike the island every 50-60 years on average (Scatena and Larsen 1991), with less intense storms occurring every 21-22 years (Scatena and Larsen 1991; Weaver 1986). Populations of some terrestrial gastropods experience catastrophic declines following the most severe hurricanes, such as Hurricane Hugo in 1989 (Willig and Camilo 1991). Such declines in response to disturbance may keep population densities sufficiently low that density-dependent reductions in population growth do not appear. In addition, historical hurricanes may have extirpated some species, opening niche space and reducing the apparent importance of competition in an assemblage. Gastropod taxa that inhabit montane forests on islands most often are endemic to a single island (Cooke 1926), suggesting that dispersal among islands or to islands from the mainland is a slow process. Therefore, it is unlikely that any snail species going extinct in the LEF would be replaced rapidly via colonization.

The interplay of disturbance and insularity provides a plausible explanation for the lack of density compensation exhibited by terrestrial snail species on the LFDP, including those that are morphologically similar. Often, species of similar shell morphology use similar microhabitats. For example, flat-shelled and tall-spined species typically forage on horizontal and vertical surfaces, respectively (reviewed in Emberton 1995), although many exceptions exist (Cain 1978; Emberton 1986; Heller 1987; Emberton 1995). Thus, species of similar shell shape could be expected to come into frequent contact, leading to the possibility (though by no means a guarantee) that they would exploit the same resources.

In an unsaturated assemblage (i.e., not all possible niche space is occupied), however, each species can exploit niche space that might, in a saturated assemblage, be occupied by another species. Thus, the deleterious effects of competition are minimized.

A final possibility for a lack of observed evidence of competition is that contemporary patterns of assemblage structure are a legacy of historical competition. Over a sufficiently long time, intense competition should lead to niche differentiation such that species minimize similarity in their use of resources (Schoener 1974). This might occur either through morphological changes that alter resource use (i.e., character displacement; Brown and Wilson 1956) or by adaptation to occupy different parts of an environmental gradient (Connell 1980). Such coevolution between competitors is difficult to demonstrate (Connell 1980; Schluter 2000), generally requiring an experimental approach (e.g., Connell 1980; Pritchard and Schluter 2001). Consequently, we cannot at this time rule out the possibility that competition in the past contributed strongly to current patterns of assemblage structure for the terrestrial snails of the LEF. Nevertheless, multiple lines of observational evidence now suggest that competition is currently rather weak.

In conclusion, interspecific competition appears unlikely to be a strong determinant of assemblage structure for terrestrial snails in the LEF. Snail populations on the LFDP generally did not display density compensation, and the degree of density compensation was unrelated to morphological similarity. This was particularly true from a spatial perspective: no two species had densities that were correlated negatively in space. In contrast, 7 species pairs exhibited positive correlations in density. This suggests that some sites provide high-quality habitat for multiple species simultaneously, including some that share guild membership (e.g., *P. caracolla* and *N. tridens*). Similarly, average adult size of *P. caracolla* is correlated positively both with density of conspecifics and with density other gastropods (Bloch and Willig 2009). In concert, these results suggest that resources are so abundant or replenished so quickly that

competition remains unimportant. Other factors such as predation or disturbance probably maintain population densities sufficiently low that the effects of interspecific competition on population growth do not become intense or persistent.

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