

EFFECTS OF COMPETITION ON SIZE AND GROWTH RATES OF *CARACOLUS CARACOLLA* (L.) IN PUERTO RICO

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ABSTRACT

Although interspecific competition has been demonstrated between some pairs of terrestrial gastropod species, little work addresses its importance in tropical assemblages, which are often characterized by high species richness or population densities. A 9-year data set was used to assess growth rates and median shell size of a common Puerto Rican snail, *Caracolus caracolla*, as a function of density of conspecifics and potential interspecific competitors. Neither the rate nor the magnitude of growth of *C. caracolla* were inhibited at high densities. No association existed over time between density and size or growth rate. In contrast, *C. caracolla* generally was largest at sites with high densities of conspecifics. Several factors may be responsible for the apparent unimportance of competition, including the broad, flexible diet of *C. caracolla*, high productivity of the study site or periodic changes in microclimate or resource availability associated with hurricane-induced disturbance and recovery.

INTRODUCTION

Competition has long been considered an important mechanism structuring ecological communities (Chase & Leibold, 2003; Tilman, 1982). However, its importance for terrestrial gastropods is debatable. Many studies document interspecific competition between pairs of large or conspicuous species (e.g. Cameron & Carter, 1979; Baur, 1988; Baur & Baur, 1990; Magnin, 1993). Documentation of pervasive effects of competition throughout an assemblage, however, is quite rare (Solem, 1985; Barker & Mayhill, 1999). Generally, evidence for the importance of interspecific competition in structuring snail assemblages is weak or non-existent (Boycott, 1934; Solem, Climo & Roscoe, 1981; Waldén, 1981; Solem, 1984; Perry & Arthur, 1991; Cameron & Cook, 2001; Cook, 2007). Few studies have evaluated the role of interspecific interactions such as competition in structuring tropical assemblages of terrestrial gastropods, although recent evidence suggests that such assemblages are considerably more species-rich (Emberton, 1995; Tattersfield, 1996; De Winter & Gittenberger, 1998; Schilthuizen & Rutjes, 2001) than traditionally believed (Solem, 1984).

In the Luquillo Experimental Forest (LEF) of Puerto Rico, the assemblage structure of terrestrial gastropods is compositionally stable, exhibiting little temporal turnover in species composition, even in the face of intense and large-scale disturbances (i.e. hurricanes; Bloch 2004, Willig *et al.*, 2007). One might therefore expect snail assemblages in the LEF to be in equilibrium and to display morphological patterns consistent with a history of competitive interactions. Nonetheless, this prediction is not supported by patterns of body size among species, and species do not exhibit density compensation (Bloch, 2004). These analyses, however, failed to incorporate intraspecific variability in morphology or body size; therefore, only competition that is pervasive throughout the assemblage and strong among adults would be evident. In addition, competitive effects may manifest in some species by reducing growth rates, rather than survivorship (Tanaka *et al.*, 1999), thereby being difficult to detect in studies of assemblage structure. Such effects have not been evaluated for snails in the

LEF. As such, the role of competition in this assemblage remains unresolved.

If competitive interactions are strong, they can reduce growth rates and adult sizes of terrestrial snails. Growth of individuals may be reduced at high densities of conspecifics or competitors because of reduced resource quality or availability (Baur & Baur, 1990), or because interference by competitors reduces access to resources (Cameron & Carter, 1979; Smallridge & Kirby, 1988). In the LEF, *Caracolus caracolla* (L.) is an ideal species with which to test these hypotheses. This caenid is among the most abundant and widespread gastropods in the forest (Heatwole & Heatwole, 1978; Willig *et al.* 1998). In addition, it is long-lived (up to 10–15 years; Heatwole & Heatwole, 1978; M.R. Willig *et al.* unpubl.) and attains large size (up to 65 mm in diameter of shell; Heatwole & Heatwole, 1978). Therefore, if competition reduces growth of terrestrial snails in the LEF, such effects should be evident for *C. caracolla*. We assessed growth rates and body sizes of *C. caracolla* in the LEF to quantify the effects of both intra- and interspecific competition, and did so from both spatial and temporal perspectives.

MATERIAL AND METHODS

Long-term censuses of terrestrial gastropods were done on 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 & Whitmore, 1973) found below elevations of 600 m. Terrain and soil types are varied (Thompson *et al.*, 2002, 2004). Precipitation is substantial throughout the year. 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).

Forty circular plots of 3-m radius were spaced evenly within a rectilinear grid such that 60-m separated adjacent points along a row or column. Beginning in the summer of 1995 and continuing until 2003, gastropod surveys were conducted twice annually, in March (dry season) and during the summer (wet season). The sole exception was the dry season of 1999, when

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sampling was conducted in January rather than March to assess the short-term effects of Hurricane Georges. Each plot was sampled four times per season, except for the dry season of 2003 (two surveys). A minimum of 2 days was maintained between sampling periods so that gastropods could recover from displacement during previous surveys. All surveys were conducted at night (1930–0300 h) to coincide with peak snail activity (Heatwole & Heatwole, 1978; Willig *et al.*, 1998).

Each time a plot was sampled for snails and slugs, two 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 *c.* 5 m. To prevent excessive disturbance to long-term study sites, substrate was not manipulated during the search for specimens. All gastropods were identified to species in the field. Each captured *Caracollus caracolla* was marked with a numbered plastic circle affixed to the shell with superglue, and measured from the lip of the aperture to the most distal part of the shell (i.e. diameter) to the nearest 0.1 mm using dial callipers. All individuals were returned, within minutes, as closely as possible to the point of capture (and always within the plot of capture).

Mean growth rate of each *C. caracolla* was estimated by subtracting the diameter at first capture from the diameter at final capture and dividing by the number of sampling seasons (essentially representing 0.5 years) between captures. Negative values were assumed to be a function of shell breakage or measurement error and were considered zero growth for analyses. Although this approach to estimating growth rates implicitly assumes that growth is constant throughout the life of the snail – probably an unrealistic assumption (Williamson, 1976) – it is necessary because most individuals were captured only sporadically throughout the study period, preventing the development of a more accurate growth curve. Nevertheless, to test the realism of this assumption, ordinary least squares (OLS) linear regression was used to test for a relationship between initial diameter and growth for individuals captured during consecutive seasons. This method is appropriate when the goal of the analysis is to identify significant associations between variables, although it underestimates the slope of the relationship if both variables are measured with error (Warton *et al.*, 2006). To minimize bias due to non-independence of data, individuals captured in more than two consecutive seasons were included in this analysis only once, using one randomly selected time interval.

Population abundance of each species within each plot in each season was estimated as the mean number of individuals captured during the successive samples within that season. Although this measure underestimates true density, it has advantages over other measures. It does not require marking of individuals for subsequent identification (a technique that is difficult or impossible to use for small or shell-less species), 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 highly significantly correlated with mark-recapture estimates of density for two species (*C. caracolla* and *Nenia tridens* (Schweigger)), suggesting that average number of captures is a reasonable index for changes in density of these snails over time (Bloch, 2004).

OLS linear regression was used to test for a temporal association between shell diameter and population density of *C. caracolla*. For each season, one value of shell diameter (the median of the diameters of all individuals) and one value of population density (median of the 40 plots) existed ($n = 17$). The degree of temporal association between size of *C. caracolla* and total density of all other species in the assemblage was assessed using the same method.

Spatial association between shell diameter of *C. caracolla* and density of potential competitors also was assessed. The spatial

distribution of density for *C. caracolla* and for total snails remains similar over time (Bloch, 2004). Thus, a plot harbouring a high density of snails in 1 year generally maintained high snail densities in most seasons of the study, relative to other plots. If density of competitors inhibits growth of *C. caracolla*, then shell diameter should be lower in high-density plots than in low-density plots. OLS regression was used to test this hypothesis using median shell diameter within each plot (over all seasons of the study) and median population size within plots. Similarly, OLS regression was used to test the hypothesis that growth rates of *C. caracolla* decrease with increasing density of conspecifics or other species. Individuals captured only once and those that had clearly achieved full adult size (>50 mm in diameter and with a thickened apertural lip of the shell) at the time of first capture were excluded from analyses of growth rates.

RESULTS

A total of 17 species of terrestrial gastropods was captured on the LFDP from 1995 to 2003 (Fig. 1). Of these species, *Caracollus caracolla* was the most abundant in 10 of 17 seasons, and always one of the three most abundant. Shell diameter averaged 41.8 mm during the study (range: 12.5–65.9 mm). Mean growth rate per season was 2.72 ± 2.45 (SD) mm. Growth rates declined with increasing initial size ($b_0 = 5.50$, $b_1 = -0.09$, $P < 0.001$), although this relationship displayed a great deal of variability ($r^2 = 0.27$) and was driven largely by decreased growth in the largest adults (Fig. 2). If these individuals were excluded from the analysis, initial size retained virtually no power to predict growth rates ($r^2 = 0.03$).

No significant association existed between shell diameter and population density of *C. caracolla* over time ($r^2 = 0.07$, $df = 1,15$, $F = 1.04$, $P = 0.32$; Fig. 3A). Also, diameter of *C. caracolla* was unrelated to total density of other species of terrestrial gastropods ($r^2 = 0.01$, $df = 1,15$, $F = 0.13$, $P = 0.73$; Fig. 3B). Results were qualitatively the same if analyses included only adults.

Diameter of *C. caracolla* was positively associated spatially with density of conspecifics ($r^2 = 0.18$, $b_0 = 38.46$, $b_1 = 0.95$, $df = 1,38$, $F = 8.33$, $P = 0.01$; Fig. 3C); individuals generally were largest at sites where density of *C. caracolla* was highest. If only adults were included in the analysis, no significant relationship remained ($r^2 < 0.01$, $P = 0.74$). Size of *C. caracolla* was not significantly associated with density of all other gastropods ($r^2 = 0.05$, $df = 1,38$, $F = 1.82$, $P = 0.19$; Fig. 3D). Elimination of juveniles from the analysis did not affect this outcome. Growth rates of *C. caracolla* were not significantly associated with population density of *C. caracolla* ($r^2 = 0.02$, $df = 1,38$, $F = 0.84$, $P = 0.37$) or with density of other gastropods ($r^2 = 0.001$, $df = 1,38$, $F = 0.03$, $P = 0.88$).

DISCUSSION

Crowding, both interspecific and intraspecific, inhibits growth of some terrestrial gastropods (Herzberg, 1965; Pomeroy, 1969; Williamson, Cameron & Carter, 1976; Cameron & Carter, 1979; Smallridge & Kirby, 1988; Baur & Baur, 1990; Tanaka *et al.*, 1999). Two mechanisms can account for this effect: exploitative competition for resources or interference. In gastropods, interference does not result solely from physical confrontations among individuals. Rather, chemical cues in mucus trails may be proximate causes of growth inhibition (Cameron & Carter, 1979; Tattersfield, 1981; Baur & Baur, 1990). Such effects often manifest in laboratory situations, which frequently involve greater than natural densities of snails, but are not ubiquitous in natural populations (Baur, 1993; Cook, 2001).

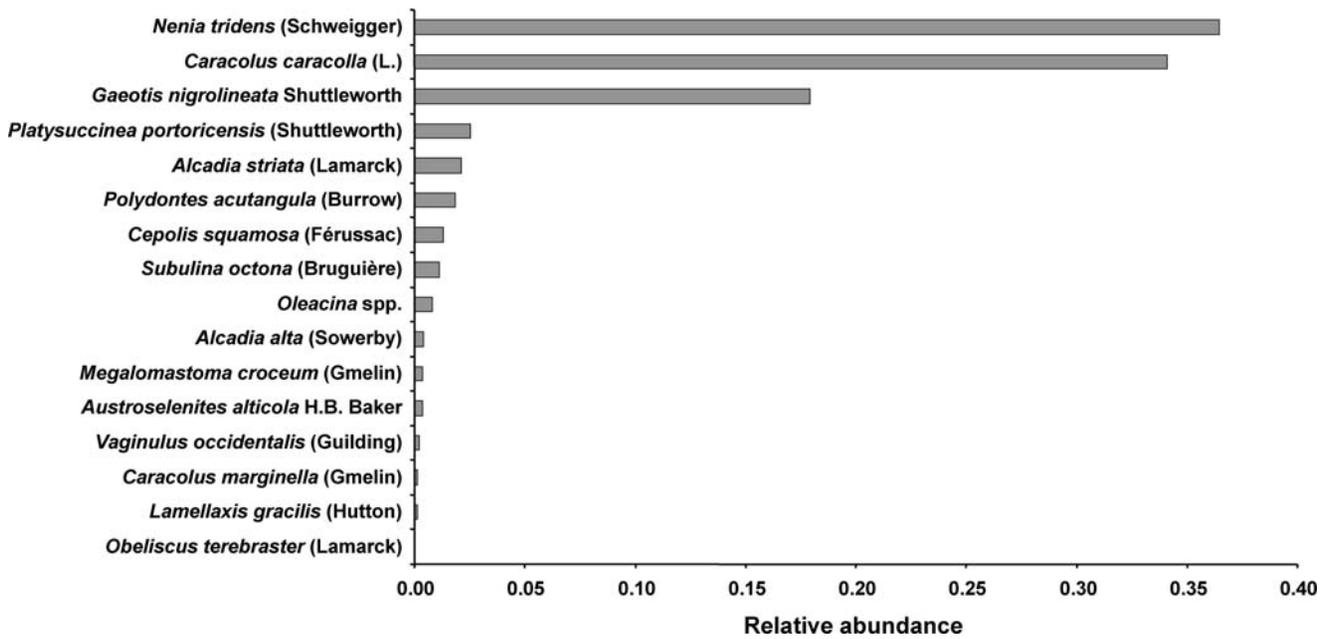


Figure 1. Proportional abundances of gastropod taxa on the Luquillo Forest Dynamics Plot from 1995 to 2003. Data are pooled across all sampling seasons. *Oleacina* spp. includes *O. glabra* (Pfeiffer), *O. interrupta* (Shuttleworth) and *O. playa* (H.B. Baker).

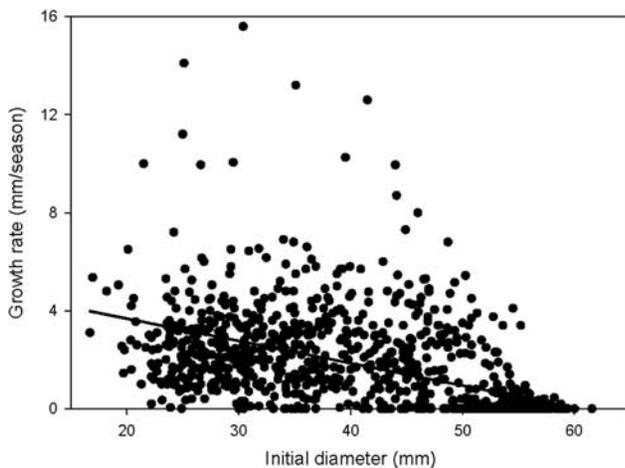


Figure 2. Growth rates of *Caracolus caracolla*, in mm per sampling season, as a function of initial shell diameter.

On the LFDP, no evidence existed for inhibition of growth of *C. caracolla*, irrespective of mechanism. Although it is difficult to demonstrate conclusively that competition is unimportant or does not occur, especially in observational (as opposed to experimental) studies, this set of results suggests that the effects of exploitative competition are weak in this system. Several factors could explain a lack of strong competition for resources. First, *C. caracolla* is a generalist that feeds on a wide variety of macroscopic and microscopic food items (Heatwole & Heatwole, 1978). This breadth and flexibility of diet probably reduces the potential for competition. Second, productivity in the LEF is high (Wang *et al.*, 2003), suggesting that food sources, especially fungi and algae, replenish rapidly. Third, the LEF is subject to a complex disturbance regime (Willig & Walker, 1999; Thompson *et al.*, 2002). Two extensively studied disturbance types in the LEF are treefalls and hurricanes. These two kinds of disturbance influence gastropod populations in two ways: altering microclimate and translocating

resources from the canopy to the forest floor (Alvarez & Willig, 1993; Willig *et al.*, 1998; Bloch & Willig, 2006). The former effect may limit densities of *C. caracolla* below a threshold at which competition would become evident, and the latter may reduce or eliminate resource limitation. Another factor, mortality by predation, has been suggested as a potential mechanism preventing the attainment of densities great enough to promote strong competition in mixed-species colonies of terrestrial snails (Perry & Arthur, 1991). Several taxa consume gastropods in the LEF, including several species of birds, the black rat, *Rattus rattus*, frogs of the genus *Eleutherodactylus*, lizards of the genus *Anolis* (Reagan & Waide, 1996) and carnivorous snails of the genus *Oleacina* (C.P. Bloch, personal observation). Nevertheless, the extent to which predation influences population densities of *C. caracolla* remains unclear.

Interference is less easy to discount than exploitative competition. Nonetheless, it is inconsistent with our results. Median size of *C. caracolla* increased with increasing density of conspecifics and displayed no association with density of other gastropods (although mean diameter did correlate positively with density). This probably reflects an increased proportion of adults compared with juveniles at high-density plots, as the pattern disappeared if only adults were included in the analysis. Regardless, high density of potential competitors clearly did not decrease body size of *C. caracolla*. Moreover, individuals often aggregated in large groups (often including multiple species and size classes) on a single substrate. Thus, dominant individuals, it would seem, do not physically exclude potential competitors.

It remains unclear whether the mucus of *C. caracolla* contains growth-inhibiting compounds. At least one other species in the LEF, *Polydotes luquillensis* (Shuttleworth), may secrete toxins in its mucus (Heatwole & Heatwole, 1978). Nonetheless, if such compounds exist in *C. caracolla* or any species with which it coexists on the LFDP, they either are not present in sufficient quantity in the environment or are not sufficiently persistent (e.g. washed away by frequent rains) to show an appreciable effect on *C. caracolla*. Median diameter of *C. caracolla* was greatest at sampling plots with high densities of conspecifics and was unaffected by density of other gastropods. Similarly,

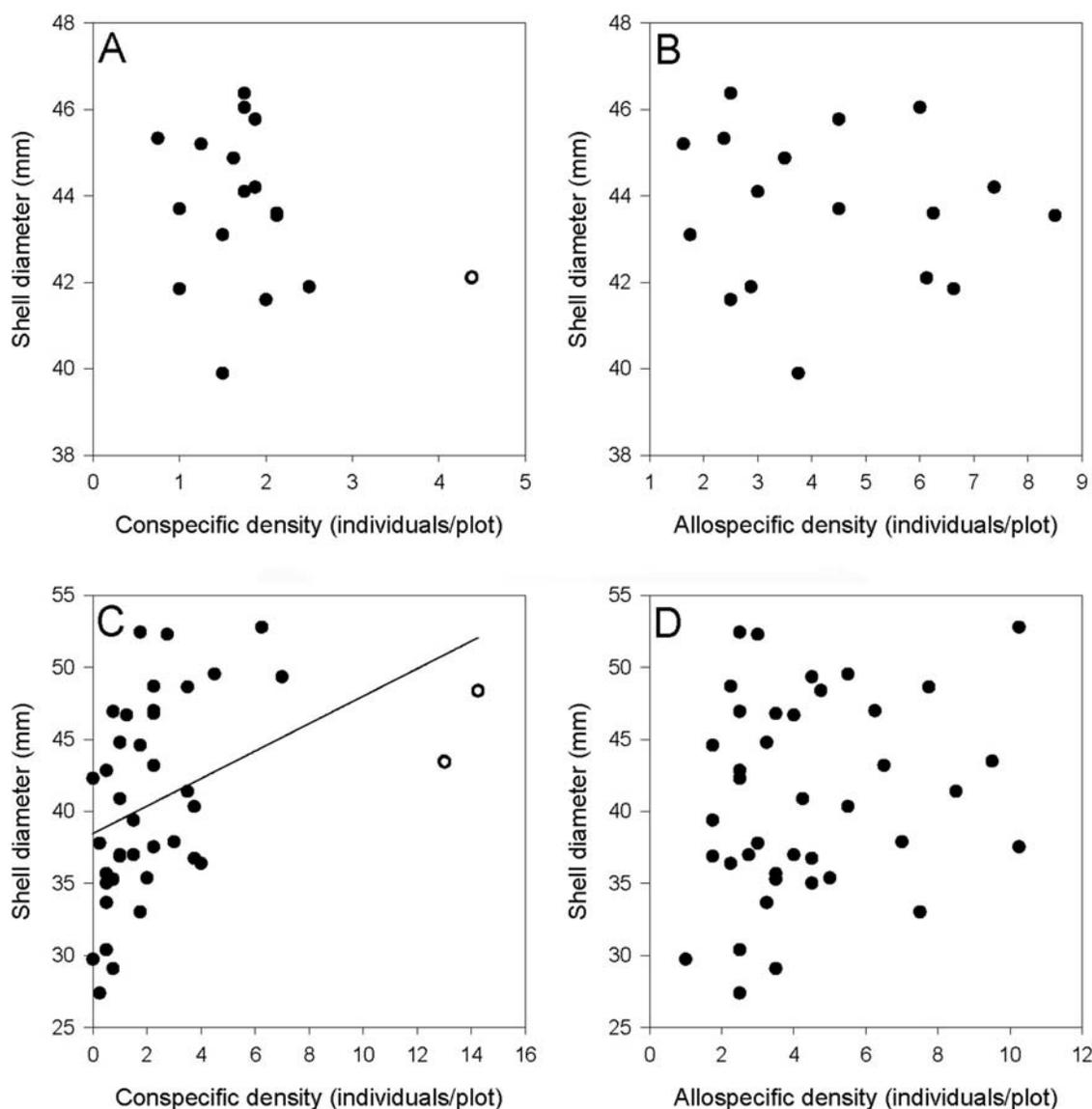


Figure 3. The effects of population density (individuals/plot) on shell diameter (mm) of *Caracollus caracolla*. **A.** Shell diameter as a function of density of conspecifics, from a temporal perspective (i.e. each data point represents median shell diameter and median population density among 40 sampling plots within a single season). **B.** Shell diameter as a function of total density of other gastropod species, from a temporal perspective. **C.** Shell diameter as a function of density of conspecifics, from a spatial perspective (i.e. each data point represents median shell diameter and median population density for a single sampling plot over the length of the study). **D.** Shell diameter as a function of total density of other gastropod species, from a spatial perspective. A few points in (A) and (C) represent unusually large values of population density (indicated by open circles); however, omitting these data does not alter the outcome of analyses.

growth rates were uncorrelated with density of potential competitors. This suggests a minor role for intra- or interspecific competition on *C. caracolla*.

The greatest effect of chemical cues in mucus is likely to be on juvenile snails (Cook, 2001). The smallest *C. caracolla* captured, however, was 12.5 mm in diameter. Although neither intra- nor interspecific density affected sizes of *C. caracolla* larger than this, no data exist with which to draw conclusions about potential effects on the smallest individuals (i.e. hatchlings). Nevertheless, body size clearly is an ecologically important characteristic for *C. caracolla* because it drives age-specific behaviour, distribution and mortality (Heatwole & Heatwole, 1978). It probably also correlates with the ability of individuals to survive in disturbed environments.

Age-specific microhabitat preferences in *C. caracolla* suggest the possibility of competitive interactions between adults and

juveniles. Juveniles typically reside under rocks, in crevices, or under fallen palm petioles, whereas adults commonly use tree trunks or the leaf litter. Most likely, juveniles select microhabitats as refugia from desiccation (Heatwole & Heatwole, 1978) or perhaps predation, rather than in response to competition from adults. Nevertheless, additional work is necessary to assess the relative influence of competition *vs* climate or disturbance on growth and survival of juvenile snails.

Regardless of interspecific interactions, temperature and humidity can exercise strong constraints on body size and shell morphology of terrestrial snails (Machin, 1967; Riddle, 1983; Goodfriend, 1986). The LEF is subject to intense, recurrent disturbances, with major hurricanes striking every 50–60 years on average and smaller storms occurring more frequently (Scatena & Larsen, 1991). Hurricanes influence both temperature and humidity by producing large gaps in the forest

canopy. Within such gaps, microclimate is characterized by elevated soil and air temperatures, increased rates of evaporation and decreased humidities compared with those of undisturbed forest (Denslow, 1980). Desiccation, especially of eggs and young individuals, is a principal cause of snail mortality (Riddle, 1983; Solem, 1984; Baur & Baur, 1993) and could be an important stressor for snails that inhabit frequently disturbed environments such as the LEF.

Just as natural selection promotes character divergence to mitigate the negative consequences of competition, it may lead to adaptations that decrease susceptibility to environmental correlates of disturbance. For example, *Nenia tridens*, a species that has higher population densities in treefall gaps than in undisturbed forest, may reduce water loss by having a much smaller shell aperture than does *C. caracolla*, which attains higher densities in undisturbed forest than in gaps (Alvarez, 1991; Alvarez & Willig, 1993). Moreover, disturbance can reduce competitive pressure by reducing densities of superior competitors (Grime, 1973; Connell, 1978). Therefore, in frequently disturbed systems, competition may have relatively little effect on morphology.

Disturbance probably influences growth of *C. caracolla* in the LEF more strongly than does competition. Cary (1992) found significant differences in size class distributions between seasons and among localities that differed with respect to damage by Hurricane Hugo. In contrast, size distributions were stable over time in the same forest years earlier (Heatwole & Heatwole, 1978). Disturbance history may explain this discrepancy, as the former study commenced only 1 year after Hurricane Hugo struck the LEF, whereas the latter study was conducted decades after the most recent major hurricane (Scatena & Larsen, 1991).

Caracolus caracolla typically grows for only about half of the year, and the length of the growth period may be influenced by rainfall (Heatwole & Heatwole, 1978). Decreased humidity in canopy gaps resulting from disturbance may therefore influence the length of the growing season for *C. caracolla*, especially for the smallest individuals, which are the least mobile and most susceptible to desiccation (Heatwole & Heatwole, 1978). This microclimatic harshness probably contributes to decreased population size of *C. caracolla* in gaps as compared with sites under intact canopy (Alvarez & Willig, 1993). In contrast, increased resource availability within gaps may help to offset the effects of microclimate. Fallen trees in gaps provide abundant resources for snails and some of their food sources (e.g. fungi). Snails that are able to survive in disturbed environments may be able to exploit a superabundant resource base. This explains their ability to grow more rapidly in more disturbed plots than on a less disturbed plot during the first few years after Hurricane Hugo (Cary, 1992).

Although terrestrial gastropods in the LEF boast only modest species richness (Van Der Schalie, 1948; Garrison & Willig, 1996), population densities are high relative to those in mainland tropical forests (Bloch, 2004). Nevertheless, neither densities of conspecifics nor those of other gastropods reduced growth of *C. caracolla*. This result suggests that competition is relatively unimportant in this assemblage, as it is for most terrestrial gastropod assemblages. Other factors such as predation, disturbance, climate and the distribution of important resources such as calcium are probably more important influences than competition on populations and assemblages of terrestrial gastropods in the LEF.

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REFERENCES

- ALVAREZ, J. 1991. *The effects of treefall gaps on a tropical land snail community*. MSc thesis, Texas Tech University.
- ALVAREZ, J. & WILLIG, M.R. 1993. Effects of treefall gaps on the density of land snails in the Luquillo Experimental Forest. *Biotropica*, **25**: 100–110.
- BARKER, G.M. & MAYHILL, P.C. 1999. Patterns of diversity and habitat relationships in terrestrial mollusc communities of the Pukeamaru Ecological District, northeastern New Zealand. *Journal of Biogeography*, **26**: 215–238.
- BAUR, A. 1993. Effects of food availability and intra- and inter-specific interactions on the dispersal tendency in the land snail *Chondrina clienta*. *Journal of Zoology*, **230**: 87–100.
- BAUR, B. 1988. Microgeographical variation in shell size of the land snail *Chondrina clienta*. *Biological Journal of the Linnean Society*, **35**: 247–259.
- BAUR, B. & BAUR, A. 1990. Experimental evidence for intra- and interspecific competition in two species of rock-dwelling land snails. *Journal of Animal Ecology*, **59**: 301–315.
- BAUR, B. & BAUR, A. 1993. Climatic warming due to thermal-radiation from an urban area as possible cause for the local extinction of a land snail. *Journal of Applied Ecology*, **30**: 333–340.
- BLOCH, C.P. 2004. *Long-term responses of snail populations and communities to disturbance in the Luquillo Experimental Forest, Puerto Rico*. PhD thesis, Texas Tech University.
- BLOCH, C.P. & WILLIG, M.R. 2006. Context-dependence of long-term responses of terrestrial gastropod populations to large-scale disturbance. *Journal of Tropical Ecology*, **22**: 111–122.
- BOYCOTT, A.E. 1934. The habitats of land Mollusca in Britain. *Journal of Ecology*, **22**: 1–38.
- BROWN, S., LUGO, A.E., SILANDER, S. & LIEGEL, L. 1983. *Research history and opportunities in the Luquillo Experimental Forest*. General Technical Report SO-44. United States Department of Agriculture, Forest Service, New Orleans.
- CAMERON, R.A.D. & CARTER, M.A. 1979. Intra- and interspecific effects of population density on growth and activity in some helioid land snails (Gastropoda: Pulmonata). *Journal of Animal Ecology*, **48**: 237–246.
- CAMERON, R.A.D. & COOK, L.M. 2001. Madeiran snails: faunal differentiation on a small island. *Journal of Molluscan Studies*, **67**: 257–267.
- CARY, J.F. 1992. *Habitat selection, home range, and population dynamics of Caracolus caracolla in the Luquillo Experimental Forest of Puerto Rico*. MSc thesis, Texas Tech University.
- CHASE, J.M. & LEIBOLD, M.A. 2003. *Ecological niches: linking classical and contemporary approaches*. University of Chicago Press, Chicago.

- CONNELL, J.H. 1978. Diversity in tropical rain forests and coral reefs. *Science*, **199**: 1302–1310.
- COOK, A. 2001. Behavioural ecology: on doing the right thing, in the right place at the right time. In: *The biology of terrestrial molluscs* (G.M. Barker, ed.), pp. 447–487. CAB International, Wallingford.
- COOK, L.M. 2007. Species richness in Madeiran land snails, and its causes. *Journal of Biogeography*, **35**: 647–653.
- DE WINTER, A.J. & GITTENBERGER, E. 1998. The land snail fauna of a square kilometer patch of rainforest in southwestern Cameroon: high species richness, low abundance and seasonal fluctuations. *Malacologia*, **40**: 231–250.
- DENSLAW, J.S. 1980. Gap partitioning among tropical rainforest trees. *Biotropica*, **12**: 47–55.
- EMBERTON, K.C. 1995. Land-snail community morphologies of the highest-diversity sites in Madagascar, North America, and New Zealand, with recommended alternatives to height-diameter plots. *Malacologia*, **36**: 43–66.
- EWEL, J.J. & WHITMORE, J.L. 1973. The ecological life zones of Puerto Rico and the United States Virgin Islands. Forest Service Research Paper ITF-18. International Institute of Tropical Forestry, Río Piedras, Puerto Rico.
- GARRISON, R.W. & WILLIG, M.R. 1996. Arboreal invertebrates. In: *The food web of a tropical rain forest* (D.P. Reagan & R.B. Waide, eds), pp. 183–245. University of Chicago Press, Chicago.
- GOODFRIEND, G.A. 1986. Variation in land-snail shell form and size and its consequences. *Systematic Zoology*, **35**: 204–223.
- GRIME, J.P. 1973. Competitive exclusion in herbaceous vegetation. *Nature*, **242**: 344–347.
- HEATWOLE, H. & HEATWOLE, A. 1978. Ecology of the Puerto Rican camaenid tree-snails. *Malacologia*, **17**: 241–315.
- HERZBERG, F. 1965. Crowding as a factor in growth and reproduction of *Helix aspersa*. *American Zoologist*, **5**: 254.
- MACHIN, J. 1967. Structural adaptation for reducing water-loss in three species of terrestrial snail. *Journal of Zoology*, **152**: 55–65.
- MAGNIN, F. 1993. Competition between two land gastropods along altitudinal gradients in south-eastern France: neontological and palaeontological evidence. *Journal of Molluscan Studies*, **59**: 445–454.
- PERRY, R. & ARTHUR, W. 1991. Shell size and population density in large helioid land snails. *Journal of Animal Ecology*, **60**: 409–421.
- POMEROY, D.E. 1969. Some aspects of the ecology of the land snail, *Helicella virgata*, in South Australia. *Australian Journal of Zoology*, **17**: 495–514.
- REAGAN, D.P. & WAIDE, R.B. (eds) 1996. *The food web of a tropical rain forest*. University of Chicago Press, Chicago.
- RIDDLE, W.A. 1983. Physiological ecology of land snails and slugs. In: *The Mollusca*. Vol. 6. *Ecology* (W.D. Russell-Hunter, ed.), pp. 431–461. Academic Press, Orlando.
- SCATENA, F.N. & LARSEN, M.C. 1991. Physical aspects of Hurricane Hugo in Puerto Rico. *Biotropica*, **23**: 317–323.
- SCHILTHUIZEN, M. & RUTJES, H.A. 2001. Land snail diversity in a square kilometre of tropical rainforest in Sabah, Malaysian Borneo. *Journal of Molluscan Studies*, **67**: 417–423.
- SMALLRIDGE, M.A. & KIRBY, G.C. 1988. Competitive interactions between the land snails *Theba pisana* (Müller) and *Cermea virgata* (Da Costa) from South Australia. *Journal of Molluscan Studies*, **54**: 251–258.
- SOLEM, A. 1984. A world model of land snail diversity and abundance. In: *World-wide snails: biogeographical studies on non-marine Mollusca* (A. Solem & A.C. van Bruggen, eds), pp. 6–22. E.J. Brill, Leiden.
- SOLEM, A. 1985. Simultaneous character convergence and divergence in Western Australian land snails. *Biological Journal of the Linnean Society*, **24**: 143–163.
- SOLEM, A., CLIMO, F.M. & ROSCOE, D.J. 1981. Sympatric species diversity of New Zealand land snails. *New Zealand Journal of Zoology*, **8**: 453–485.
- TANAKA, K., WATANABE, T., HIGUCHI, H., MIYAMOTO, K., YUSA, Y., KIYONAGA, T., KIYOTA, H., SUZUKI, Y. & WADA, T. 1999. Density-dependent growth and reproduction of the apple snail, *Pomacea canaliculata*: a density manipulation experiment in a paddy field. *Population Ecology*, **41**: 253–262.
- TATTERSFIELD, P. 1981. Density and environmental effects on shell size in some sand dune snail populations. *Biological Journal of the Linnean Society*, **16**: 71–81.
- TATTERSFIELD, P. 1996. Local patterns of land-snail diversity in a Kenyan rain forest. *Malacologia*, **38**: 161–180.
- THOMPSON, J., BROKAW, N., ZIMMERMAN, J.K., WAIDE, R.B., EVERHAM, E.M., III, LODGE, D.J., TAYLOR, C.M., GARCÍA-MONTIEL, D. & FLUET, M. 2002. Land use history, environment, and tree composition in a tropical forest. *Ecological Applications*, **12**: 1344–1363.
- THOMPSON, J., BROKAW, N., ZIMMERMAN, J. K., WAIDE, R.B., EVERHAM, E.M. & SCHAEFER, D.A. 2004. Luquillo Forest Dynamics Plot. In: *Tropical forest diversity and dynamism: results from a long-term tropical forest network* (E. Losos & E.G. Leigh, eds), pp. 540–550. University of Chicago Press, Chicago.
- TILMAN, D. 1982. *Resource competition and community structure*. Princeton University Press, Princeton.
- VAN DER SCHALIE, H. 1948. The land and fresh-water mollusks of Puerto Rico. *Miscellaneous Publications of the Museum of Zoology of the University of Michigan*, **70**: 1–134.
- WALDÉN, H.W. 1981. Communities and diversity of land molluscs in Scandinavian woodlands. High diversity communities in taluses and boulder slopes in SW Sweden. *Journal of Conchology*, **30**: 351–372.
- WANG, H., HALL, C.A.S., SCATENA, F.N., FETCHER, N. & WU, W. 2003. Modeling the spatial and temporal variability in climate and primary productivity across the Luquillo Mountains, Puerto Rico. *Forest Ecology and Management*, **179**: 69–94.
- WARTON, D.I., WRIGHT, I.J., FALSTER, D.S. & WESTOBY, M. 2006. Bivariate line-fitting methods for allometry. *Biological Reviews*, **81**: 259–291.
- WILLIAMSON, P. 1976. Size-weight relationships and field growth rates of the landsnail *Cepaea nemoralis* L. *Journal of Animal Ecology*, **45**: 875–885.
- WILLIAMSON, P., CAMERON, R. A. D. & CARTER, M. A. 1976. Population density affecting adult shell size of snail *Cepaea nemoralis* L. *Nature*, **263**: 496–497.
- WILLIG, M.R., SECREST, M.F., COX, S.B., CAMILO, G.R., CARY, J.F., ALVAREZ, J. & GANNON, M.R. 1998. Long-term monitoring of snails in the Luquillo Experimental Forest of Puerto Rico: heterogeneity, scale, disturbance, and recovery. In: *Forest biodiversity in North, Central, and South America and the Caribbean: research and monitoring* (F. Dallmeier & J. Comisky, eds), pp. 293–322. UNESCO and Parthenon Press, Carnforth.
- WILLIG, M.R., BLOCH, C.P., BROKAW, N., HIGGINS, C., THOMPSON, J. & ZIMMERMANN, C.R. 2007. Cross-scale responses of biodiversity to hurricane and anthropogenic disturbance in a tropical forest. *Ecosystems*, **10**: 834–838.
- WILLIG, M.R. & WALKER, L.R. 1999. Disturbance in terrestrial ecosystems: salient themes, synthesis, and future directions. In: *Ecosystems of disturbed ground* (L.R. Walker, ed.), 747–767. Elsevier Press, Amsterdam.