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Testing limiting similarity in Quaternary terrestrial gastropods

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Abstract.—The hypothesis of limiting similarity, which postulates that morphologically and/or ecologically similar species will differ enough in shape, size, or other variables to minimize competition, has been controversial among ecologists and paleoecologists. Many studies have reported the occurrence of limiting similarity in modern environments or in time-averaged fossil deposits; however, empirical high-resolution time series demonstrating limiting similarity over longer time scales are lacking. We have integrated radiocarbon-calibrated amino acid dating techniques, stable isotope estimates, and morphometric data to test the hypothesis of limiting similarity in late Quaternary land snails from the Canary Islands over a period of 42,500 years. We tested for both ecological character displacement (two closely related species will differ in size in order to minimize competition in sympatry and these differences will be minimized in allopatry) and community-wide character displacement (overdispersion of body size among competitors in a guild). Multiple proxies of body size consistently show that two endemic congeneric pulmonate gastropod species (*Theba geminata* and *T. arinagae*) maintained a difference in size from ~42,500 B.P. through the last occurrence of *T. arinagae* 14,900 B.P., with a concomitant trend of a decreasing body size. *Theba geminata* body size did not converge on that of *T. arinagae* and variation in *T. geminata* body size did not increase significantly following the extinction of *T. arinagae*; therefore, ecological character displacement and release did not occur. Community-wide character displacement was found in only one time bin over the last 42,500 years. These results suggest that limiting similarity is a transient ecological phenomenon rather than a long-term evolutionary process. This study not only demonstrates the problems inherent in biological ''snapshot'' studies and geological studies of time-averaged deposits to test limiting similarity adequately, but it also presents a more adequate research protocol to test the importance of interspecific competition in the history of life.

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Introduction

The theory of limiting similarity is an outgrowth of the competitive exclusion principle: species cannot make a living in identical ways and coexist (Brown and Wilson 1956; Hutchinson 1959; Macarthur and Levins 1967; Abrams 1983; Dayan and Simberloff 2005). One way that species can partition their niche is through altering their body size and/or the size of their feeding structures. Two types of limiting similarity have been identified: (1) ecological character displacement, e.g., increased size differences between two closely related sympatric species and (2) community-wide character displacement, e.g., overdispersion of body size of potentially competing species in the same guild (Simberloff and Boecklen 1981; Dayan and Simberloff 2005). Ecologists have uncovered the occurrence of limiting similarity in a wide array of organisms including butterfly larvae, ermine and weasels, diverse groups of birds, desert rodent communities, and sand dune floras (Dyar 1890; Hutchinson 1959; Schoener 1965; Bowers and Brown 1982; Cody 2000; Stubbs and Bastow Wilson 2004), though see Simberloff and Boecklen's (1981) rigorous statistical testing of previous claims of minimum size ratios between two species (vis-à-vis Hutchinson 1959) and constant size ratios between adjacent species in a group of three or more species ranked by size.

However, these examples lack a temporal

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dimension that might validate limiting similarity as an evolutionary process rather than a transient ecological phenomenon. And although paleoecologists have documented possible cases of limiting similarity in deep time—in such diverse groups as Ordovician brachiopods, Pleistocene land snails, and Devonian trilobites (Eldredge 1974; Schindel and Gould 1977; Hermoyian et al. 2002)—these fossil snapshots focused on individual sites rather than long-term time series that would allow us to examine limiting similarity in a temporal context. Limiting similarity seems ubiquitous in diverse biological systems today (as well as non-biological systems including musical instruments, bicycles, and skillets [Horn and May 1977]), but can it be traced persistently over longer time scales?

Fossil land snails represent an ideal system for addressing ecological hypotheses in deep time while minimizing the confounding factor of limited temporal resolution so common in many paleontological studies (Goodfriend and Gould 1996; Chiba 1998). In a study of land snails from the Bonin Islands, Chiba (2004) found that the shells of snails of the same species but with different feeding locations (arboreal, semi-arboreal, exposed ground, and sheltered ground) diverged significantly in morphology whereas the shells of allopatric species occupying similar feeding locations in distinct geographic areas were very similar to one another. Chiba (2004) also made the argument that although competitive interactions among continental land snails likely do not have an effect on morphological diversification, these competitive interactions are very important in the evolution of land snails thriving in the depauperate environments found on oceanic islands.

Here, we test for the occurrence and persistence of limiting similarity, as both ecological character displacement and community-wide character displacement in Quaternary terrestrial gastropods over a period of 42,500 years from the Canary Islands, an oceanic archipelago. Traditionally there have been two requirements for substantiating claims of ecological character displacement (Brown and Wilson 1956; Simberloff and Boecklen 1981; Dayan and Simberloff 2005). The first is character displacement, by which morphologies of sympatric species will diverge from one another. It is prudent to expand upon this prediction because our study incorporates the temporal element where previous studies did not. We also predict that this divergence will be maintained through time, and, that as shell size or morphology evolves, that difference will be maintained, resulting in parallel evolutionary trajectories. The second requirement is that character release, or the morphological convergence of one species toward the other following the removal of the other species, will occur if the species' ranges become allopatric in either time or space. We have included a third criterion that considers not only average size or morphology but that of variation: We postulate an increase in variation in the morphology of a species upon allopatry, due to the removal of morphological constraint imposed by the competing species. We test for community-wide character displacement by testing for over-dispersion of body size among all gastropod species during each individual time interval (Barton and David 1956; Simberloff and Boecklen 1981; Cody 2000). Our approach makes the assumption that size and morphology capture ecological information that is related to how these organisms acquire resources. Indeed this assumption is supported by the literature (Chiba 2004 and references therein), but admittedly these organisms could reduce competition by altering variables that would not be captured by size and shape (e.g., altering the time of day a species feeds).

Materials and Methods

Sampling.—The fossil gastropod samples were collected in the Chinijo Archipelago of the Eastern Canary Islands (Fig. 1) during 2002–2004. A total of four workers dry-sieved (with 1-mm mesh) the predominantly unconsolidated fossiliferous paleosols for two hours each along the outcrop at each sampling locality. In the rare cemented beds, where sieving was precluded, fossils were collected individually directly at the outcrop. Many species were sampled, but two gastropod species, *Theba geminata* (Mousson, 1957) and *Theba arinagae* Gittenberger and Ripken, 1987 (Fig. 2),

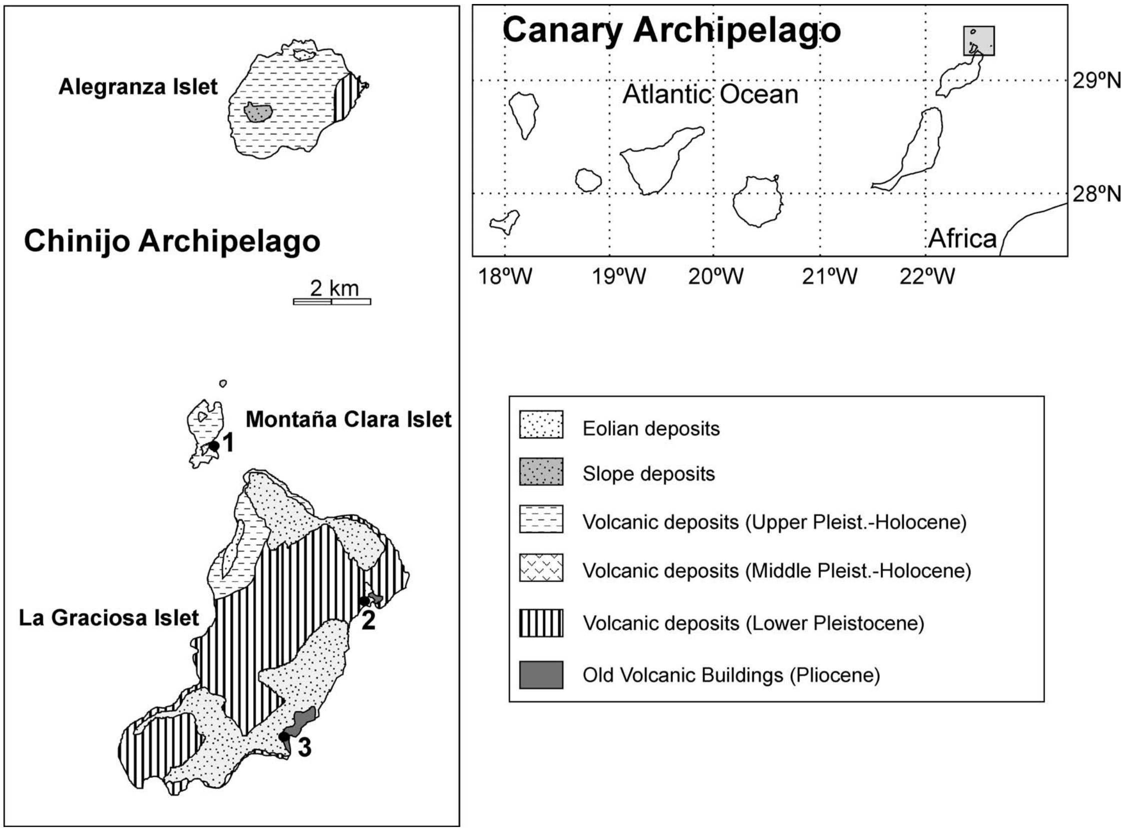

FIGURE 1. Map of the Canary Islands and the Chinijo Archipelago. Bulk samples were collected from La Graciosa and Montaña Clara Islets. 1, Caleta de Guzman-Llano del Aljibe section, Montana Clara Islet. 2, Morros Negros section, La Graciosa Islet. 3, Caleta del Sebo-Bahia del Salado section, La Graciosa Islet.

are the primary focus of this study because they are the most abundant species in the eastern Canary Islands (Gittenberger and Ripken 1987; Gittenberger et al. 1992), and because they both occur throughout all, or the majority, of the sampled fossil record (Castillo et al. 2002; Yanes et al. 2004) (Fig. 3). Both species of *Theba* are small helicoid gastropods with a globose shape. Although these species are restricted to the eastern islands and endemic to the Canary Archipelago, this genus is commonly represented by *T. pisana* (Müller, 1774) in Quaternary eolianite deposits from the Mediterranean, Western Europe, and Northern Africa (Kerney and Cameron 1979).

Dating.—We used radiocarbon-calibrated amino acid racemization (AAR) dating to estimate the age of a subset of the fossils collected (Ortiz et al. 2006). Amino acid racemization methods are one of the most efficient techniques for dating individual Quaternary shells (Goodfriend 1987a). Living organisms contain only L-amino acids, which gradually racemize (epimerize) into D-amino acids after death. Thus, the D/L ratio increases with time after death until it is equal to 1 (1.3 for isoleucine), that is, when equilibrium is reached. For details of our methodology see Ortiz et al. (2006) and Yanes et al. (2007).

The results of the radiocarbon-calibrated AAR dating provided us with a high-resolution geologic time series ideal for bridging the temporal gap between ecological and traditional paleontological studies. Seven statistically distinct intervals are available for study covering the last 42,500 years (0 Ka, 5.4 ± 1.1 Ka, 11.0 ± 4.0 Ka, 14.9 ± 3.6 Ka, 22.4 ± 4.5 Ka, 29.4 ± 4.8 Ka and 42.5 ± 6.0 Ka) (Ortiz et al. 2006).

Stable Isotope Analysis.—Carbon stable isotopes extracted from land snail shells generally provide an estimate of the proportion of C_3 and C_4 plants that snails consumed in their

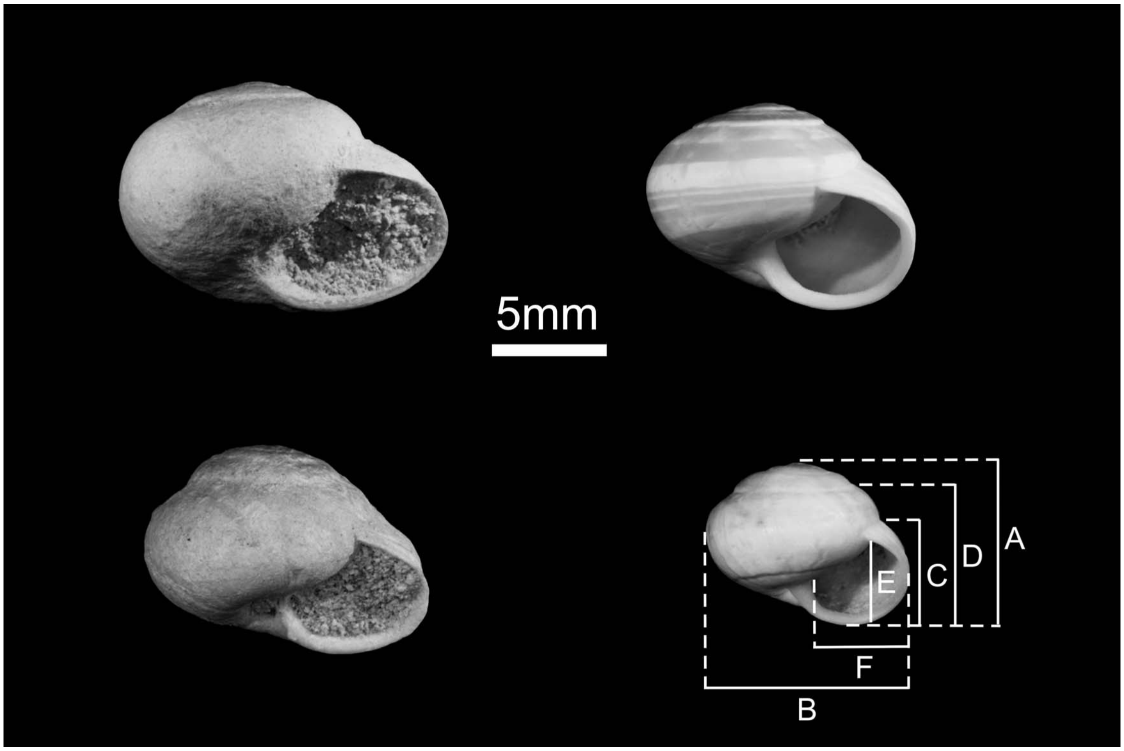

FIGURE 2. *Theba geminata* (top) and *T. arinagae* (bottom) with morphometric dimensions labeled. Ages of *T. geminata*: 42.5 Ka (left) and 5.4 Ka (right). Ages of *T. arinagae*: 42.5 Ka (left) and 14.9 Ka (right). Note how both species became smaller with time.

local habitat (Balakrishnan and Yapp 2004; Metref et al. 2003; Stott 2002). Because C_4 plants display more positive carbon isotope values on average (−12‰) relative to the international standard Vienna Pee-Dee Belemnite, or V-PDB, than C_3 plants (−27‰ V-PDB) (Farquhar et al. 1989), we are able to detect which type of plants were consumed by the land snails. Therefore, snails that show more positive values of carbon stable isotopes have consumed more C_4 plants whereas individuals with more negative results have ingested primarily C_3 plants. In addition, it has been shown that snails from carbonate-rich areas may ingest foreign inorganic carbonates from the surrounding sediments during their growing periods to build their own shells (Goodfriend 1987b), which can result in anomalies in radiocarbon analysis (Goodfriend 1987b; Ortiz et al. 2006). Ingested inorganic carbonate makes the carbon isotope values of the shells only slightly more positive (by a few units per mil) in the study area, so we can reconstruct the diet with reasonable confidence (Yanes et al. 2008a).

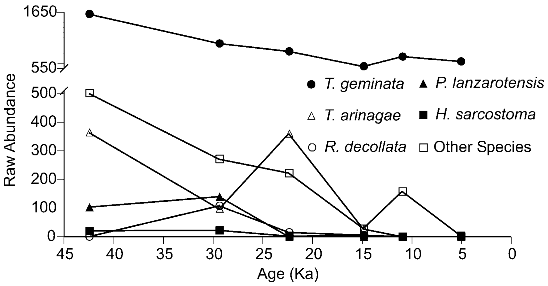

FIGURE 3. Raw abundance of gastropod species sampled in this study. Note the break in the vertical axis; black lines represent 100 before the break.

A total of 54 samples of fossil snail shells (32 *T. geminata* and 22 *T. arinagae*) from the eastern Canary Islands were analyzed in the Laboratory of Biogeochemistry of Stable Isotopes of the Estación Experimental del Zaidín–Consejo Superior de Investigaciones Científicas, or EEZ-CSIC (Granada, Spain) in order to determine their carbon stable isotope composition.

Carbon dioxide was evolved from the carbonates using 100% phosphoric acid for 24 hours in a thermostatic bath at 25°C. The CO_2 samples were analyzed on a Gas Bench II connected to IRMS Finnigan Delta Plus XL mass spectrometer. Values were calibrated against the international standard NBS-18 (carbonatite) and NBS-19 (limestone) (National Bureau of Standards). The precision of analyses based on the measurement of multiple standard aliquots during the run of samples is generally better than 0.1‰. The δ values are defined as

$$\delta^{13}C = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 1000 \text{ (in ‰ units)}$$

where $R = {}^{13}C/{}^{12}C$ ratios.

Theba geminata $\delta^{13}C$ values ranged from −8.7‰ to +2.5‰ (V-PDB) with a mean of −2.9‰ (V-PDB). *T. arinagae* $\delta^{13}C$ values ranged from −5.0‰ to −0.2‰ (V-PDB) with a mean of −3.6‰ (V-PDB). A marginally significant difference between the variances of $\delta^{13}C$ values of *T. geminata* and *T. arinagae* ($F = 2.30$, $p = 0.05$) precluded the use of the parametric *t*-test to assess the potential difference in means. Therefore, using PAST 1.39 (Hammer et al. 2001), we performed a Mann-Whitney *U*-test ($U = 282$, $p = 0.22$) and a Kolmogorov-Smirnov test ($D = 0.276$, $p = 0.23$) to assess potential differences between medians and between shapes of distributions, respectively. The $\delta^{13}C$ values of *T. geminata* and *T. arinagae* are statistically indistinguishable (Fig. 4).

Theba geminata and *T. arinagae* likely fed on common food sources, as reflected by their similar $\delta^{13}C$ values. The great variability of stable isotope values suggests that both species had a generalist diet that included C_3 plants, C_4 plants, and probably inorganic carbonates from the surrounding sediments. The larger variance of stable isotope values of *T. geminata* versus *T. arinagae* suggests that *T. geminata* had a slightly larger range of diet. *Theba* stable isotope values displayed no clear secular trends. Modern specimens of *T. geminata* from the eastern Canary Islands display a range of carbon isotope values at least as large as those of fossil *Theba* specimens (Yanes et al. 2008a).

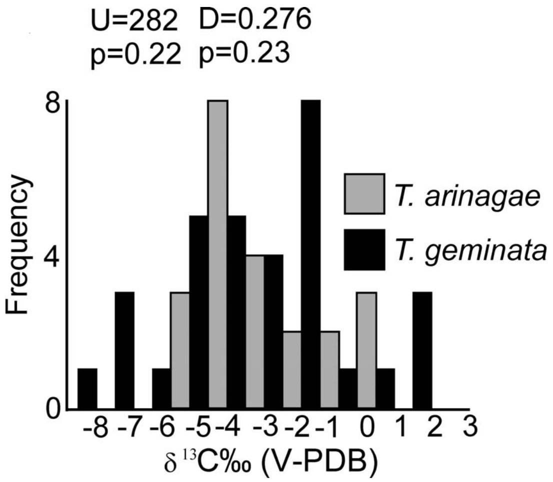

FIGURE 4. Comparison of $\delta^{13}C$ values of *T. geminata* and *T. arinagae*. The values are statistically indistinguishable. Mann-Whitney *U*-test for medians and Kolmogorov-Smirnov tests were completed in PAST 1.39 (Hammer et al. 2001).

In view of the evidence that the two *Theba* species were congeneric endemics, represented the two most abundant species sampled, and likely fed on common food sources, it is reasonable to infer that they were long-term competitors. They offer a model system to test for ecological character displacement.

Morphometric Analyses.—The standardized bulk sampling of dune and paleosol deposits and live collecting of modern snails resulted in a total of 760 specimens of *T. geminata*, *T. arinagae*, *Rumina decollata* (Linnaeus, 1758), *Pomatias lanzarotensis* (Wollaston, 1878), and *Hemicycla sarcostoma* (Webb and Berthelot, 1833) suitable for morphometric analysis.

Specimens that possessed four to five whorls were selected for morphometric analysis to minimize ontogenetic-related variation in size and shape. Traditional measurements were taken, rather than landmark data, because defining homologous landmarks on globose snails is difficult. The resulting matrix of six linear measurements (mm) (Fig. 2) from 642 *Theba* individuals was log-transformed and subjected to a principal components analysis (PCA) on a variance-covariance matrix using PAST 1.38b (Hammer et al. 2001). PC1 scores for each species were grouped a posteriori into age categories. Geometric means of log-transformed shell height and shell width were calculated for each individual as a second proxy of body size (Jablonski 1997).

For each age category, PC1 scores and geometric means were resampled with replacement 1000 times and mean scores were recomputed by using a balanced bootstrap module written in SAS/IML (Kowalewski et al. 1998). We used the percentile approach, or naïve bootstrap (Efron 1981), to calculate 95% confidence intervals (CI) from the bootstrapped sampling distributions by calculating the 2.5 and 97.5 percentile values.

Coefficient of variation (CV) of geometric mean was calculated for each age category. A randomization with 1000 iterations was performed in SAS/IML for each *Theba* species to determine the possible range of CV trends produced under the null model that CV fluctuated randomly through time (Huntley et al. 2006a,b). The geometric mean of each individual was randomly shuffled into each age category to replicate the original sampling structure. We calculated coefficient of variation for each age category and performed this randomization process for 1000 iterations. This resulted in 1000 CV estimates for each age category. From this sampling distribution we calculated the mean, 2.5 percentile, and 97.5 percentile values.

Repeated simulations suggest that 1000 iterations are sufficient to provide precise estimates of targeted parameters and associated probability values.

Barton-David Test Statistic for Community-Wide Character Displacement.—The Barton-David (B-D) test statistic calculates the probability that points along a line are distributed randomly whether they are scaled arithmetically or logarithmically. The null hypothesis is that points are distributed randomly and the alternative hypothesis is that the points are distributed uniformly (Barton and David 1956). We used B-D to calculate the probability that the mean body sizes of gastropod species within each time interval (that contained at least three species: 22.4 Ka, 29.4 Ka, and 42.5 Ka) were distributed randomly (Barton and David 1956; Simberloff and Boecklen 1981; Cody 2000; Dayan and Simberloff 2005). Mean body sizes (geometric mean of length and width) were calculated for each species separately by time interval. The gastropod species in each time interval were then sorted by mean body size. The differences in size between adjacent species were calculated and then sorted from smallest size difference to largest size difference. The B-D test statistic compares two of these size differences at a time to calculate the probability of random distribution of mean body sizes; we therefore calculated three test statistics for each time interval: G_{1n}, which compares largest and smallest size differences; G_{2n}, which compares largest and second smallest size differences; and $G_{1(n-1)}$, which compares second largest and smallest size differences. To make an argument for the presence of community-wide character displacement in a given time interval, at least one-half of the test statistics computed must display significant p-values ($\alpha = 0.05$) (Simberloff and Boecklen 1981).

Results

Morphometric Analysis.—The PCA ordination, based on linear dimensions, suggests that there are significant size-driven differences in morphology between *T. geminata* and *T. arinagae* (Fig. 5). The morphological history of the two congeneric species is remarkably concordant through time: whether estimated by the mean PC1 score or the mean geometric mean value (Fig. 5), the temporal trends in body size of two snails parallel each other perfectly. The two proxies of body size are stable between 42.5 and 29.4 Ka. Beginning at 29.4 Ka, both species undergo a reduction in body size. This trend ends at 14.9 Ka with the last occurrence of *T. arinagae*. Thereafter, *T. geminata* body size exhibits non-directional, though significant, fluctuation until the present. The average shift in body size (approximated by mean geometric mean) between sequential populations of *T. geminata* is twice as large following the last occurrence of *T. arinagae* (0.166) than sequential populations that co-occurred with *T. arinagae* (0.078).

Coefficient of variation fluctuated throughout the history of both *Theba* species (Fig. 6). There were no significant long-term trends in CV fluctuation, though there were times when CV was significantly lower than expected by random chance. *Theba geminata* and *T. arinagae*

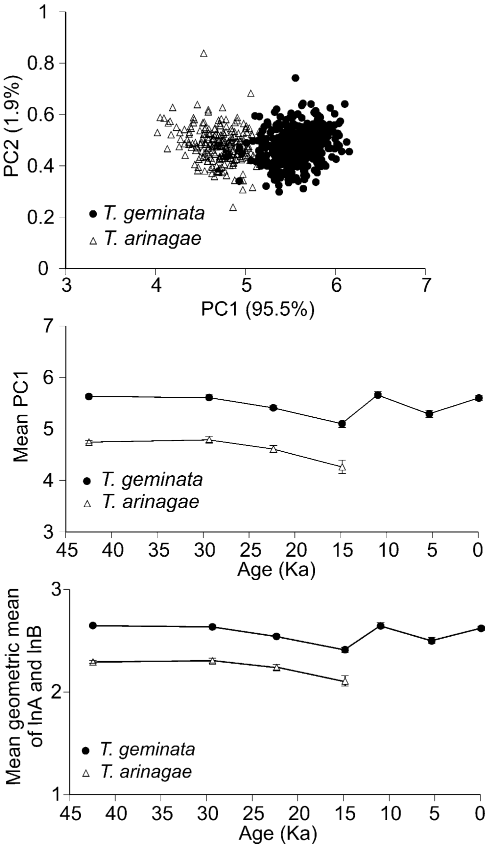

FIGURE 5. Morphometrics and size history of *T. geminata* and *T. arinagae*. Top panel, Scatterplot of PC1 and PC2 scores. The first principal component (PC1) accounts for 95.5% of the variation in the data matrix, whereas PC2 and PC3 account for 1.9% and 1.3% of the variation, respectively. The two species show the most separation along PC1. Variation along the first principal component has often been attributed to differences in size. Although this is an interpretation that should not be made without careful consideration, it especially seems to be true in this case, because all six morphological variables are highly positively correlated with PC1 values ($r > 0.96$). In addition PC1 is considered an appropriate proxy of body size in this case because it is a reflection of six linear measurements instead of one (e.g., length or width). PC2 is interpreted as an indicator of operculum shape and operculum size relative to body size. Middle panel, Mean PC1 score ± 95% bootstrap confidence intervals. Bottom panel, Mean geometric mean of natural log transformed shell height (A) and width (B) ± 95% bootstrap confidence intervals. Confidence intervals were calculated from 1000 iterations of bootstrapping procedure and are typically narrower than the symbol used to indicate body size.

had unexpectedly low CV at 42.5 Ka. *Theba geminata* displayed lower than expected CV at 22.4 Ka, 14.9 Ka, and 11.0 Ka (the sample immediately following the last occurrence of *T. arinagae*). The wide confidence interval at 14.9 Ka reflects a small sample size.

Barton-David Test Statistic for Community-Wide Character Displacement.—The 42.5 Ka, 29.4 Ka, and 22.4 Ka time intervals were the only intervals with body size data available for three or more species. Gastropod body sizes in the 29.4 Ka time interval were spaced more evenly than expected by random chance (two of three tests were significant; Table 1 and Fig. 7). This is considered evidence for community-wide character displacement. B-D test statistics calculated for the 42.5 and 22.4 Ka time intervals did not produce significant results. It appears that body sizes were randomly distributed during these time intervals.

Discussion

Ecological Character Displacement Prediction 1: Character Displacement.—The first prediction of ecological character displacement was confirmed; the morphology of the two species remained clearly distinct through time (Fig. 6). The parallel temporal tracking in shell size between the congeneric species and a synchronous reduction in their body size at a comparable rate is striking, and might seem to suggest that interspecific competition played an important role in controlling body size of *Theba* in the Canary Islands throughout the late Quaternary. However, the fulfilling of more criteria is required to support ecological character displacement.

Ecological Character Displacement Prediction 2: Character Release.—The second prediction of the hypothesis of ecological character displacement was not confirmed. Indeed one might mistakenly make a case for limiting similarity on the basis of the results of prediction 1 were it not for the exceptional stratigraphic resolution afforded by the radiocarbon-calibrated AAR dates that minimize the effects of time-averaging and allow us to test for character release on an ecologically relevant time scale. The morphology of *Theba geminata* did not converge on that of *Theba arinagae* following its extinction (Fig. 5); therefore character release did not occur, suggesting that interspecific competition was not the primary force controlling the evolution of these two snails.

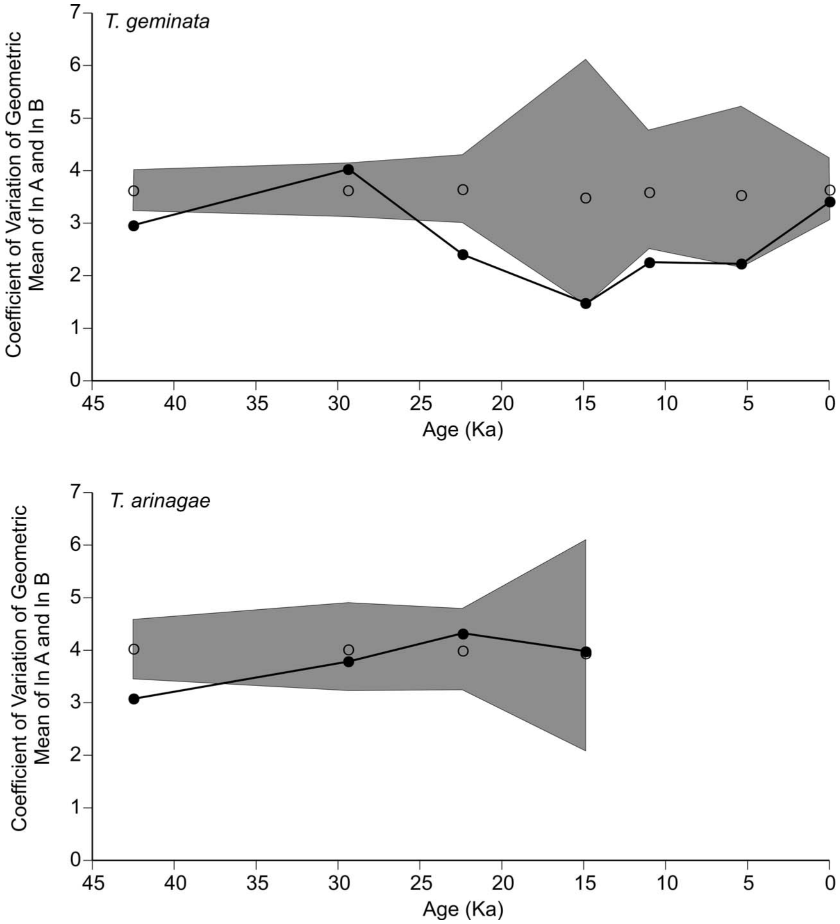

FIGURE 6. History of coefficient of variation (CV) of body size for *T. geminata* and *T. arinagae* and results of randomization. Solid circles represent actual CV values. Hollow circles represent mean CV values from randomization (1000 iterations). The gray envelope represents 95% confidence interval calculated from 2.5 and 97.5 percentile values of the sampling distributions produced from the randomization.

Ecological Character Displacement Prediction 3: Increase in Variation upon Allopatry.—The third prediction of the hypothesis of limiting similarity was not confirmed. Although the coefficient of variation of *T. geminata* body size did increase following the extinction of *T. arinagae*, it was not a significant increase. In fact, *T. geminata* body size CV was lower than expected by random chance before, during, and after the last occurrence of *T. arinagae* (Fig. 6). At no time was CV higher than expected by random chance. There is no relationship between abundance and CV. Trends in CV of both species are difficult to interpret, and the explanation of these periods of suppressed CV remains elusive.

Community-Wide Character Displacement.—Community-wide character displacement was detected in only one time interval in the last 42,500 years. It occurred when a new species, *R. decollata*, appeared in the 29.4 Ka time bin. There was little change in body size of the other species between the prior time bin (42.5 Ka) and the first appearance of *R. decollata*, suggesting that its presence did little to affect the body sizes of co-occurring gastropods. These

TABLE 1. Barton-David test statistic significance levels (p-values). Asterisk indicates significance at $\alpha = 0.05$.

Time interval	G_{1n}	G_{2n}	$G_{1(n-1)}$
22.4 Ka	$p = 0.053$	$p = 0.196$	$p = 0.159$
29.4 Ka	$p = 0.013$*	$p = 0.231$	$p = 0.025$*
42.5 Ka	$p = 0.391$	$p = 0.526$	$p = 0.452$

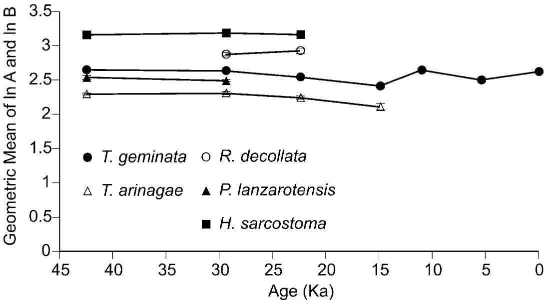

FIGURE 7. Body size history of all species for which body size data were available. Body size data were not collected from species whose taphonomic condition precluded measurement.

results suggest that, in this case study, limiting similarity is not an evolutionary process worked out over long periods of time, but merely a transient ecological phenomenon.

Alternative Perspectives and Explanations of Body Size Patterns.—The persistence of limiting similarity was not supported by our data. Ecological character displacement was not detected and community-wide character displacement was detected in only one time bin. However, there are clues that interspecific competition may have played a minor role in controlling the morphologic evolution of the two *Theba* species. Morphological shifts of *T. geminata* were of a higher magnitude and nondirectional in nature following the extinction of *T. arinagae*, perhaps suggesting some type of constraining force imposed during the temporal overlap of the two congeners.

When one considers the seemingly minor role that competition played in the evolution of terrestrial gastropods in the depauperate conditions of arid to semiarid oceanic islets, it is instructive to compare their morphological trends with changes in climatic conditions. The timing of the consistent multi-millennial decline in body size of *T. geminata*, *T. arinagae*, and *H. sarcostoma* (though not *R. decollata*) roughly corresponds to the last glacial maximum, which may suggest that snail body size was influenced by external environmental factors such as long-term increase in temperature and humidity at the end of the most recent glacial period (Kutzbach et al. 1996; Cronin 1999; Petit et al. 1999; Beyerle et al. 2003). This explanation would imply that these gastropods flourished in dry and cool conditions as opposed to humid and warm conditions. Goodfriend (1986) suggested that land snail individuals tend to display a larger shell size under wetter and warmer conditions, although others have not recorded any clear correlation between shell size and climatic factors (Hausdorf 2007). Indeed, the significant increase in *T. geminata* body size at 11 Ka coincides with the Younger Dryas, a geologically brief period characterized by cooler climate in Europe and North America (Cronin 1999). Moreover, increased climatic variability in the last 15,000 years could explain the increased variability in *T. geminata* body size during the same span of time just as well as loosened morphological constraints with the extinction of a competitor.

Predation pressure can be a strong shaper of communities (Paine 1966; Huntley and Kowalewski 2007), but the degree to which it affects this community of snails is unknown. Modern land snail communities from the eastern Canary Islands are affected by bird predation (Medina 1999). A quantitative taphonomic study of similarly aged deposits in Lanzarote (Canary Archipelago) suggests that bird predation was a factor in gastropod mortality (Yanes et al. 2008b). Thus, although it is reasonable to think that the land snail assemblages studied here have also experienced some degree of predation pressure, more work is needed to determine to what extent.

Conclusions

Our results suggest that limiting similarity, as seen in both ecological character displacement and community-wide character displacement, is a transient ecological phenomenon rather than a long-term evolutionary process. These results agree with recent theoretical and empirical arguments that competition is a weak force compared with other factors that shape communities, including predation and physical disturbance (Stanley 2008). It is likely that competition as an evolutionary force is not equally important across environments and trophic tiers; perhaps it is more important in the terrestrial realm, where resource availability and environmental conditions alter quite rapidly, and in higher trophic tiers for which resources are more limited and needed consistently to sustain high-energy physiologies (though, of course there are exceptions [McKinney 1995]). Even though these gastropods are terrestrial, as primary consumers they are in a low trophic tier.

Future research should include stable isotope estimates from all gastropod species within a guild in order to better understand the diets of potentially competing species. This information could shed new insight into the dynamics of community-wide character displacement. This study was restricted to deposits in the Eastern islets of the Canary Islands, and forthcoming studies would benefit by expanding geographic coverage to include deposits from across the entire archipelago and into western Africa. A firm grasp of the role of predation on these gastropods is needed as well.

This study also highlights the difficulties of testing the evolutionary role of interspecific competition. Studies focused on modern biological systems, though they have exhibited many interesting patterns, are found wanting because they lack a temporal element. Many geological studies, with the advantage of deep time, are often limited by the effects of time-averaging. The late Quaternary and Holocene fossil record provides unique opportunities to bridge the temporal gap between traditional biological and paleontological studies in order to test evolutionary paradigms. Advances in radiocarbon-calibrated amino acid racemization dating techniques allow for the assembly of high-resolution chronologies and an assessment of the extent of time-averaging within strata—all with a minimal sample size of carbonate per specimen ($\sim$1 mg) (Kaufman and Manley 1998) and at relatively low cost. Comprehensive ecological and environmental data are readily available through stable isotope and trace element analyses. Indeed, our ability to address significant questions about the pattern and process of evolution is enhanced when these geochemical techniques are combined with traditional morphometric approaches and our more thorough knowledge of the modern biota.

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