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BODY SIZE DIVERSIFICATION IN *ANOLIS*: NOVEL ENVIRONMENT AND ISLAND EFFECTS

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Extreme morphologies of many insular taxa suggest that islands have unusual properties that influence the tempo and mode of evolution. Yet whether insularity per se promotes rapid phenotypic evolution remains largely untested. We extend a phylogenetic comparative approach to test the influence of novel environments versus insularity on rates of body size and sexual size dimorphism diversification in *Anolis*. Rates of body size diversification among small-island and mainland species were similar to those of anole species on the Greater Antilles. However, the Greater Antilles taxa that colonized small islands and the mainland are ecologically nonrandom: rates of body size diversification among small-island and mainland species are high compared to their large-island sister taxa. Furthermore, rates of diversification in sexual size dimorphism on small islands are high compared to all large-island and mainland lineages. We suggest that elevated diversifying selection, particularly as a result of ecological release, may drive high rates of body size diversification in both small-island and mainland novel environments. In contrast, high abundance (prevalent among small-island lizard communities) mediating intraspecific resource competition and male–male competition may explain why sexual size dimorphism diversifies faster among small-island lineages than among their mainland and large-island relatives.

KEY WORDS: ***Anolis* lizards, body size, ecomorphs, islands, morphological diversification rates, novel environments, phylogeny, sexual size dimorphism.**

The extremes and unusual diversity of morphological forms found on islands (Sondaar 1977; Case 1978), including dwarf and giant morphs of many taxa (Russell 1877; Hooijer 1967; Keogh et al. 2005; Hedges 2008), have prompted comparisons of the rate of trait evolution between insular and mainland taxa (Millien 2006; Harmon et al. 2008; Pinto et al. 2008). High rates of trait evolution on islands are commonly attributed to ecological release in which species' expand their resource use or habitat primarily because of a reduction in the number of competitors (Grant 1972). Rapid trait change driven by ecological release is expected to occur following colonization of a novel environment that has fewer potential competitors than the source (Grant 1972; Losos and De Queiroz 1997). This scenario is likely to be particularly prevalent for island colonization (Lister 1989; Dayan and Simberloff 1998; Meiri et al. 2005) because islands are often species poor. If ecological release is widespread among species following island colonization then we might expect morphological and ecological traits to diversify more rapidly among island species than their mainland counterparts.

High rates of evolution may also occur when colonizing a novel environment as a result of shifts in selection pressures driven by, for example, differences in climate, vegetation, resource base, competitors, or predators (Blondel 2000). In principle, this explanation is applicable to both novel island and novel continental habitats (Campbell and Echternacht 2003). However, Price (2008) suggests that the effects of differences in selection pressure will be more pronounced where there are multiple colonization events onto different islands rather than into different novel continental habitats. This is because the composition of island communities (in terms of species identity) is likely to be more heterogeneous (both between islands and through time) than the composition of novel continental communities (Price et al. 2009). Consequently, there should be greater variation in selection pressure between species that have colonized multiple islands than between species that have colonized a similar number of new areas of the mainland. This model therefore implies that there is greater potential for rapid trait divergence among species that have colonized islands than among species that have colonized mainland novel environments. Rates of phenotypic diversification, however, could be higher among species in both forms of novel environment than among the source pool of species.

Recent studies of Australasian birds, Caribbean anoles, and African chameleons have highlighted several systems in which islands are the source for mainland colonization (Raxworthy et al. 2002; Filardi and Moyle 2005; Nicholson et al. 2005; reviewed in Bellemain and Ricklefs 2008). The biogeographic history of Caribbean *Anolis* lizards (Nicholson et al. 2005) is well suited to the study of morphological evolution in novel environments versus islands per se. From a mainland South or Central American source, anoles diverged and speciated in situ and by dispersal between the islands of the Greater Antilles (Cuba, Hispaniola, Jamaica, and Puerto Rico). In turn, the adaptive radiation of Greater Antillean anoles has been the source of multiple colonization events onto smaller islands throughout the Caribbean, and of recolonization of the mainland (Schoener 1969; Glor et al. 2005; Nicholson et al. 2005). Anole communities on the Greater Antilles are species-rich and complex (Williams 1983; Losos et al. 2003) with as many as 14 or 15 species known to occur in sympatry in parts of Cuba (Diaz et al. 1998; Garrido and Hedges 2001). However, communities on small islands tend to be species-poor (with a maximum of four anole species) and consequently ecological opportunity is expected to be high for new colonizers. In contrast, mainland communities are more species-rich and contain many potential competitors including the sister-clade of Caribbean anoles (sometimes referred to as *Dactyloa*), and consequently have low expected ecological opportunity.

Island colonizers are expected to encounter low interspecific competition, but they may be subject to increased intraspecific competition due to density compensation (MacArthur et al. 1972). Density compensation describes the association between low species richness and increased population density and seems to be a common feature of insular lizard communities (Case 1975; Buckley and Jetz 2007). If increased population density elevates intraspecific competition, then there may be divergence in resource use within populations. This may lead to increased sexual dimorphism, particularly in body size or in the trophic apparatus (Selander 1966). If the population density varies among islands then we predict that sexual dimorphism should diversify more rapidly among islands (competitor-poor, both high and low abundance) than among novel mainland areas (competitor-rich, usually low abundance).

Our primary objective here is to compare rates of diversification in body size and sexual size dimorphism between Greater Antillean (large island source pool), small-island colonizing, and mainland colonizing anoles. However, several studies have suggested that anole lineages that dispersed away from the Greater Antilles are an ecologically and morphologically nonrandom set of species (Losos and De Queiroz 1997; Poe et al. 2007). This may be important in interpreting any differences in rates of morphological diversification. Greater Antillean anoles have been classified into six clearly defined ecological and morphological groupings or "ecomorphs" (Williams 1972, 1983; Losos 1994). Both body sizes (Schoener 1969; Williams 1983) and sexual dimorphism (Butler et al. 2000; Butler et al. 2007) differ substantially between ecomorphs. For example, "twig" anoles are typically small bodied and sexually monomorphic species, whereas "trunk-ground" and "trunk-crown" species tend to have intermediate body sizes and strong male-biased sexual size dimorphism. Most mainland species have not been assigned to ecomorphs (Irschick et al. 1997) but solitary species on small islands often resemble the "trunk-crown" or "trunk-ground" ecomorphs (Williams 1969; Losos and De Queiroz 1997). This may be because small-island (or mainland) colonizers are derived from the "trunk-crown" or "trunk-ground" ecomorphs. Alternatively, colonizing species may have converged on these two ecomorphs. If it is the former (as inferred by Poe et al. 2007) then it is interesting to ask whether rates of morphological diversification among small-island or mainland species exceed rates among large-island "trunk-crown" or "trunk-ground" species even if rates are not greater than all large-island species together. Therefore, morphological divergence of "trunk-crown" and "trunk-ground" species on the Greater Antilles may be constrained by competition with other anoles that would be absent from small islands or the mainland.

Here, we test whether colonizing lineages are nonrandom with respect to the ecomorph of the likely founding lineage. We then extend and apply a recent phylogenetic method (O'Meara et al. 2006; Thomas et al. 2006) to examine the influence of novel environments (mainland recolonizers) versus insularity per se (small-island colonizers) on rates of body size diversification in anoles.

Methods

NONRANDOM COLONIZATION AMONG ECOMORPHS

We tested for bias in the ecomorphs of anole lineages that have colonized small islands or the mainland by reconstructing the ancestral ecomorph states on a recent phylogeny of anoles (Nicholson et al. 2005). We classified each Greater Antillean anole species using the ecomorph (sensu Williams 1972) designations of Losos et al. (2006). Ecomorphs are named for the microhabitat they occupy: grass-bush, trunk, trunk-ground, trunk-crown, twig, and crown-giant. Some species do not fit into any of these six categories and are classified as unique (Supplementary Appendix S1 & S2). Two studies of 76 species in total (Supplementary Appendix S3) have shown that the six Greater Antilles ecomorphs form distinct clusters in morphospace (Losos et al. 1998; Beuttell and Losos 1999). Some species have not been subject to morphometric analyses but our main interest is in the ecological definition of ecomorph: definitions in Losos et al. (2006) were based on qualitative observations in the field and descriptions of species' habitat use from the literature (J. Losos, pers. comm.).

We used an ultrametric version of Nicholson et al's (2005) phylogeny with branch lengths proportional to time based on penalized likelihood downloaded from http://biosgi.wustl.edu/∼lososlab/anolis_mbg_2005/. We pruned the phylogeny to include only Greater Antillean species (that is, only the source pool species for which ecomorphs have been assigned; Supplementary Appendix S4). Ancestral ecomorphs were inferred using the maximum-likelihood Mk1 model in Mesquite version 2.0 (Maddison and Maddison 2006, 2007). This analysis confirmed that both small-island and mainland anoles are most likely derived from species of the trunk-crown and trunk-ground ecomorphs (Fig. 1 and Supplementary Appendix S4).

DATA

We categorized *Anolis* species as mainland, large-island, or small-island species (Supplementary Appendix S1) following Nicholson et al. (2005). Large islands (Cuba, Jamaica, Hispaniola, and Puerto Rico) are all $> 9000\ \mathrm{km}^2$ in area. Small islands are all $< 3500\ \mathrm{km}^2$. There are no Caribbean islands of intermediate area. Small-island status was only assigned to species endemic to small islands. Because small-island and mainland species are all derived from large-island lineages of the trunk-crown and trunk-ground ecomorphs (see above), we further divided large-island species into two ecomorph categories: species of the trunk-crown and trunk-ground ecomorphs, and species that are unique or fit one of the four remaining ecomorphs. Thus, we placed each species into one of four geographical and ecomorph categories: small-island species (scored as 0); large-island trunk-crown and trunk-ground species (1); large-island other ecomorph species (2); and, mainland species (3).

Lizards continue growing after reaching sexual maturity and the maximum, rather than mean, body size of a sample is often a more appropriate estimator of age-independent adult size (Stamps and Andrews 1992). Although maximum body size is likely to increase with sample size, around 20 individuals are considered sufficient to provide a reliable estimate of asymptotic body size with 25 individuals considered "adequate for most applications" (Stamps and Andrews 1992). We compiled sex-specific data on maximum snout vent length (SVL) of *Anolis* lizards from the literature and recorded sample sizes when available. All body size data, including sample sizes and sources, are provided in Supplementary Appendices S1 and S2. Our focus is on anoles including all Caribbean island species and their descendents that recolonized the mainland. We excluded species of *Dactyloa*, the mostly mainland-dwelling South American sister group of Greater Antilles anoles (Nicholson et al. 2005) and note that this group is extremely undersampled both morphologically and phylogenetically (Pinto et al. 2008). Although phylogenetic sampling of the species that have reinvaded the mainland is not complete, the sampled species are an unbiased representation of the diversity of body sizes found in this clade (see data in Meiri 2008).

Low intraspecific sampling can inflate variance across species and may influence estimates of relative morphological diversification rates. This is particularly important if sampling effort is inconsistent across groups. We used a chi-square test to examine sampling bias for male and female size across the four geographic and ecomorph categories. We divided species into those with good ($n \geq 20$) and poor ($n < 20$) sampling (following Stamps and Andrews 1992) and assumed that species with no sample sizes reported were poorly sampled ($n < 20$). We found no evidence for differences in the quality of sampling between the geographic and ecomorph classes (male SVL: $\chi^2 = 2.524$, df $= 3$, $P = 0.471$; female SVL: $\chi^2 = 1.795$, df $= 3$, $P = 0.616$). Using more stringent definitions for good sampling quality (minimum sample of 25, 30, 40, and 50 individuals), we still found no evidence for sampling bias. Nonetheless, we repeated all our main analyses on a subset of the data that included only species with maximum SVL based on at least 20 individuals (see below).

PHENOTYPIC DIVERSIFICATION RATES

The Brownian motion model of trait evolution describes a linear increase in phenotypic variance with distance from the root of the tree. The expected covariance among species can be described by the variance–covariance matrix (**V**) representation of the phylogenetic tree. The Brownian model is a suitable model of trait evolution under random genetic drift and also shares comparable expected covariance structures with directional, fluctuating, and punctuated evolution (Hansen and Martins 1996). Following Freckleton et al. (2002) the unbiased Brownian variance (σ^2) is given by

$$\sigma^2 = \frac{1}{(n-1)}(y - \hat{\alpha}\mathbf{X})^T \mathbf{V}^{-1}(y - \hat{\alpha}\mathbf{X}), \tag{1}$$

where n is the number of tips, y is an $n \times 1$ vector of trait values at the tips, α is an $n \times 1$ vector of the phylogenetic mean

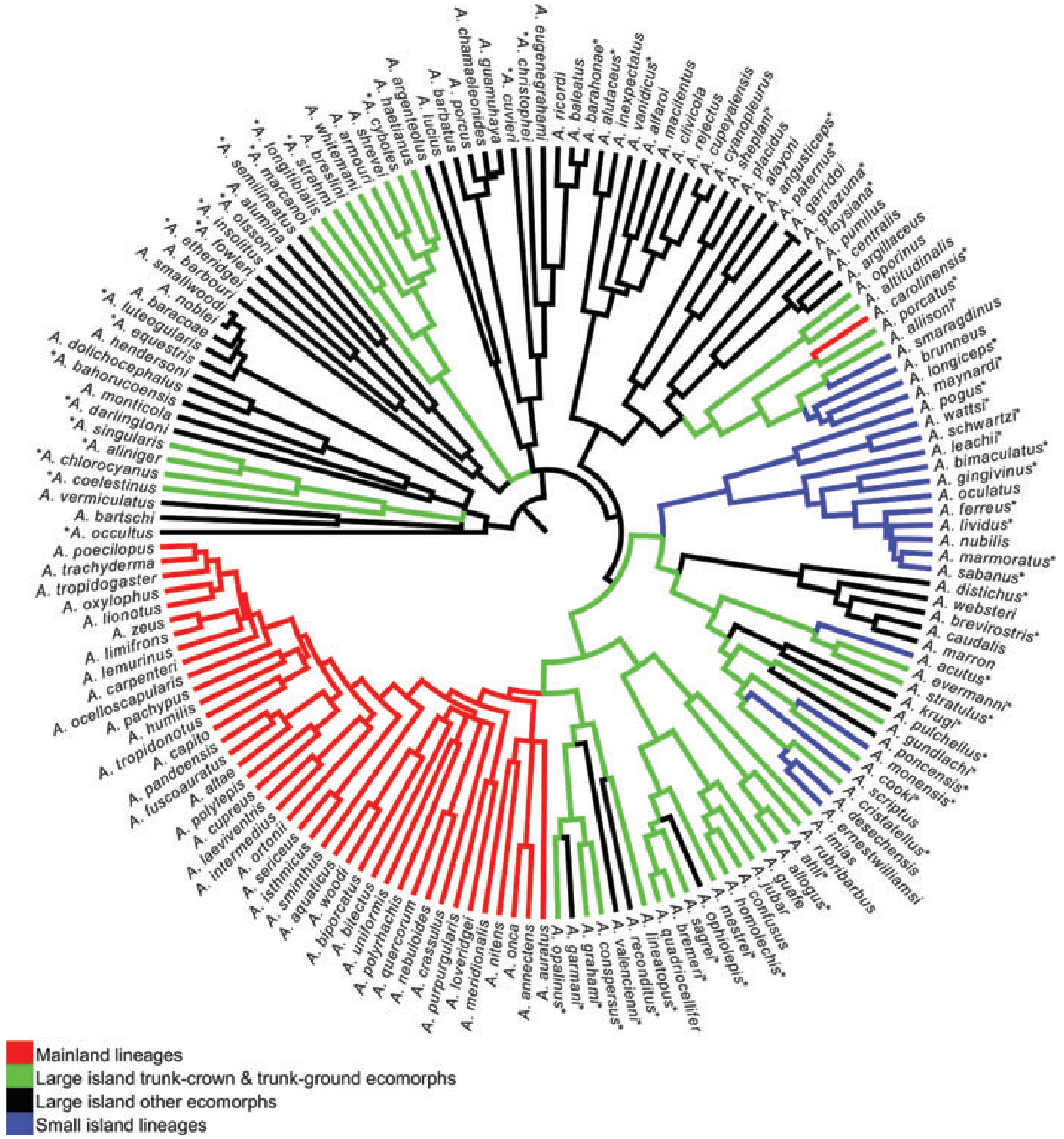

Figure 1. ***Anolis*** **phylogeny. Includes all species used in this study, after Nicholson et al. (2005). Lineages are colored according to geographic and ecomorph category. Asterisks indicate species that have been subject to morphometric analyses of ecomorphs (see Supplementary Appendix S3 for further details).**

for the trait, X is an $n \times 1$ design matrix in which all entries are set to one, and the superscript T shows that the transpose is calculated. The Brownian variance is an estimate of the minimum rate of evolutionary change (Garland 1992) and can therefore be considered a measure of the rate of phenotypic diversification. However, the Brownian model may incorrectly estimate the rate of evolution (distinct from the rate of diversification) if traits have evolved, for example, by directional, fluctuating, or punctuated evolution.

If the rate of phenotypic diversification is heterogeneous then the covariance among species may deviate from expectation derived from the phylogeny. Several methods have been proposed to test for rate heterogeneity among lineages (Garland 1992; McPeek 1995; Mooers et al. 1999; O'Meara et al. 2006; Thomas et al. 2006). The maximum-likelihood method proposed by Thomas et al. (2006) describes the expected covariance among species as the entry-wise sum of two matrices, $\mathbf{V}_0$ and $\mathbf{V}_1$, where $\mathbf{V}_0$ refers to branches of the phylogeny that share a binary character in state 0 and $\mathbf{V}_1$ refers to the branches the character in state 1. To derive the expected variance–covariance matrix, a scalar, θ, is applied to one of the two matrices such that $\mathbf{V} = \mathbf{V}_0 + \theta\mathbf{V}_1$ (note that the θ parameter in our model is not the same as the mean θ in Butler and King's (2004) Ornstein–Uhlenbeck model). The maximum-likelihood value of θ is then estimated where deviation from $\theta = 1$ indicates rate heterogeneity. Here we extend the Thomas et al. (2006) model to allow for multiple rate parameters such that $\mathbf{V} = \mathbf{V}_0 + \theta_1\mathbf{V}_1 + \cdots + \theta_{k-1}\mathbf{V}_{k-1}$ where k is the number of different parts of the tree such that the estimate of the Brownian variance (σ^2) is given by

$$\sigma^2 = \frac{1}{(n-k)}(y - \hat{a}\mathbf{X})^T(\mathbf{V}_0 + \theta_1\mathbf{V}_1 + \cdots + \theta_{k-1}\mathbf{V}_{k-1})^{-1}(y - \hat{\alpha}\mathbf{X}). \quad (2)$$

In contrast to equation (1), here X is an $n \times k$ design matrix describing a multilevel factor. Our approach differs from the "noncensored" method of O'Meara et al. (2006) because by including X as a design matrix, we allow a different phylogenetic mean (as well as a different rate) in each of the k parts of the tree rather than assuming a single phylogenetic mean across the tree. Because multiple means are estimated, the denominator $n - 1$ in equation (1) is replaced by $n - k$ in equation (2) (differing from O'Meara et al who use n in their noncensored method). The full derivation of the maximum-likelihood model is described in detail by Freckleton et al. (2002).

Although the inclusion of different means has been questioned (Revell 2008), we argue that most hypotheses postulating different rates imply different evolutionary regimes such that a difference in mean is also a likely outcome. Means could differ if trait evolution in one group is parallel (e.g., consistent shifts to small body size in elephant species on islands compared to their mainland sister species, Roth 1992; or the evolution of flightlessness in endemic rails, Trewick 1997), or if there is a single shift in trait values at the base of a clade (e.g., the clade-wide increase in bill length in Hawaiian honeycreepers, Lovette et al. 2001). A difference in means due to a single rapid change at the base of clade is a form of rate shift. However, although it may be possible to show that such a rate shift has occurred, it may not be possible to identify which group increased or decreased in rate. It is therefore informative to distinguish between a rate shift that is due to a change in mean and one that is due to differences in rates across all species in each group of interest. We show by simulation that models assuming a common mean can indicate a rate shift if the means of each group differ even if the Brownian variances within each group do not (see Supplementary Appendix S5). If the relevant hypothesis refers to differences in rates across all species in each group of interest then the inference of a rate shift due to differences in mean should be regarded as a type I error. Our model allows each group to effectively jump to different means but within each group the trait follows a Brownian model. Consequently, shifts in mean, but not in rates of whole groups, are not inferred as rate shifts (Supplementary Appendix S5).

RATES MODELS

We used the phenotypic diversification rate tests described above to compare rates of diversification in male maximum SVL, female maximum SVL, and sexual size dimorphism (SSD) across the four island type/ecomorph categories. We $\log_{10}$ transformed male (162 species) and female (163 species) SVLs prior to analysis and calculated sexual size dimorphism ($n = 160$ species) as $\log_{10}$ (male SVL / female SVL) following the recommendations of Smith (1999). Branches in the phylogeny were assigned to one of the four island type/ecomorph categories (Fig. 1) based on the ancestral state reconstruction described above and on Nicholson et al. (2005). The phylogeny with branch assignments as node labels is available in Supplementary Appendix S6. The most complex model of phenotypic diversification rates has four rates, one each for small-island lineages, large island trunk-ground and trunk-crown lineages, large island "other" lineages, and mainland lineages. In all models the parameter estimates were rescaled so that $\theta = 1$ for the small-island group to allow model averaging (see below). The simplest model is the null constant-rate Brownian model. We fitted each of the 12 possible models to male SVL, female SVL, and SSD in turn. We ranked models using the small-sample Akaike Information Criterion (AICc) and calculated both delta AICc and Akaike weights (Burnham and Anderson 2002). We used the Akaike weights to estimate model-averaged parameter estimates. We ran each set of 12 models four times using: (1) the full dataset and allowing different means in each group; (2) the full dataset and assuming a common mean; (3) the full dataset with different means in each group but after transforming the phylogeny according to the maximum-likelihood estimate of the branch length transformation kappa (see below); and (4) a reduced dataset including only species with SVL estimates based on samples of at least 20 individuals and allowing different means in each group. In the main text, we present only the first set of models and the results of the remaining three sets of models are available as Supporting Information (Supplementary Appendix S7). R code for the phenotypic diversification rate tests and an example analysis is available in Supplementary Appendices S8 and S9.

We also compared the maximum likelihood of each model with the likelihood of the constant-rate model using the likelihood-ratio statistic. This statistic is assumed to be asymptotically chi-square distributed with degrees of freedom equal to the difference in the number of parameters between the models (Edwards 1972). Previous studies based primarily on two-rate models indicate appropriate type I errors and that parameter estimates are unbiased (O'Meara et al. 2006; Thomas et al. 2006; Revell 2008), however, multiple parameter models have not previously been tested. We therefore simulated the evolution of a trait along the anole phylogeny with a single rate 10,000 times for each of the 12 models. We compared each model with the null to estimate type I error rates.

KAPPA TRANSFORMATION

If a trait evolves in a punctuated rather than gradual fashion (Eldredge and Gould 1972) then there could be a bias toward higher rates in one group if it has a predominance of short branches relative to the groups with which it is being compared. This is relevant here because short branches separate many small-island lineages and consequently high rates among these lineages could be an artifact of a speciational evolutionary process rather than a reflection of elevated rates of trait diversification on islands. We therefore tested for speciational evolution in our data by estimating the parameter κ (Pagel 1997) on the phylogeny for each of the three traits (male and female maximum SVL, and SSD) where $\kappa = 1$ indicates evolutionary change consistent with a Brownian model, $\kappa < 1$ indicates that there is evolutionary stasis in long branches, and $\kappa > 1$ indicates accelerated evolution in long branches. The maximum-likelihood estimate of κ can be compared with a model with $\kappa = 1$ using the likelihood-ratio statistic assuming a chi-square distribution with one degree of freedom.

Results

SIMULATIONS

Based on 10,000 simulations, we found very slightly elevated type I errors for most models (Supplementary Appendix S10). The maximum type I error rate across the full set of models was 0.058. Consequently, we also checked that models found to differ significantly from the null (constant rates) model using the likelihood-ratio tests were also significant based on the simulated distribution of the likelihood-ratio statistic. The qualitative interpretations of our results are not affected. However, we suggest that simulations should be used a matter of course when using the rates test, particularly when multiple rates are estimated.

MALE AND FEMALE SVL

The model-averaged parameter estimates for both male and female SVL show that the rate of phenotypic diversification is lower among large island trunk-ground and trunk-crown species than in the three other categories, which do not differ from one another (male SVL, Table 1; female SVL, Table 2). This is consistent with the single best-fitting model and the parameter estimates in the four-rate model (Table 1 and Fig. 2A; Table 2 and Fig. 2B). Models in which the rates of phenotypic diversification were equal for both large island categories but allowed to differ for mainland and/or small-island lineages were substantially worse than the best-fitting model (male SVL: ΔAICc > 8; female SVL ΔAICc > 11). This suggests that rates among small-island or mainland lineages do not exceed those of all large-island taxa but are higher than those of the large-island lineages from which they are derived.

Models in which we assumed a common mean (see Supplementary Appendix S7) typically have slightly lower AICc values than the equivalent multiple-means models, indicating that neither male SVL nor female SVL differs between groups. This is evident from the phylogenetically corrected 95% confidence intervals (based on model averaged variances) for male SVL in millimeters from the multiple means models: small-island species = 63.0–74.9; large-island trunk-crown and trunk-ground species = 67.9–73.4; large-island other ecomorph species = 59.3–71.3; and mainland species = 58.5–69.1. The equivalent 95% confidence intervals for female SVL are: small-island species = 48.8–56.6; large-island trunk-crown and trunk-ground species = 55.6–59.6; large-island other ecomorph species = 51.4–64.0; and mainland species = 52.0–61.9. The model averaged parameter estimates for the common mean models were consistent with the multimeans analyses (Supplementary Appendix S7). We found no evidence for long-branch stasis (male SVL: $\kappa = 0.841$; comparison with $\kappa = 1$: $\chi^2 = 1.820$, $P = 0.177$; female SVL: $\kappa = 1.054$; comparison with $\kappa = 1$: $\chi^2 = 0.219$, $P = 0.640$) and the model averaged parameter estimates were again similar when we first transformed the phylogeny according to the maximum-likelihood estimate of kappa (see Supplementary Appendix S7). This was also the case when we used the reduced dataset (see Supplementary Appendix S7). Overall, and regardless of the choice of analysis, rates among small-island or mainland lineages do not differ from those of all large-island taxa but are higher than those of the large-island lineages from which they are derived.

SEXUAL SIZE DIMORPHISM

The model-averaged parameter estimates for SSD show that the rate of phenotypic diversification is highest among small-island species with the lowest rates among both large-island other ecomorph species and mainland species. There is some evidence for intermediate rates among large-island trunk-crown and trunk-ground species (Table 3). This is consistent with the single best-fitting model and the parameter estimates in the four-rate model (Table 3; Fig. 2C).

Models in which we assumed a common mean (see Supplementary Appendix S7) typically have higher AICc values, indicating that SSD differs substantially between groups (phylogenetically corrected mean SSD ± 95% confidence intervals based on model averaged variance: small-island species = 0.097–0.130; large-island trunk-crown and trunk-ground species = 0.077–0.094; large-island other ecomorph species = 0.047–0.058; mainland species = 0.030–0.040). However, the model-averaged parameter estimates assuming a common mean were consistent with those allowing multiple means (Supplementary Appendix S7). The model-averaged

Table 1. Rates of diversification in male snout vent length. The maximum-likelihood estimates of θ with approximate 95% confidence intervals in parentheses for male snout vent lengths. Estimates of θ are shown for small-island, large-island trunk-ground and trunk-crown, large-island "other" ecomorph and mainland lineages. The models are ranked according to the small-sample Akaike Information Criteria (AICc): delta AICc shows the difference in AICc between the candidate model and the best-fitting model and wtAIC refers to the Akaike weights. The maximum likelihood of each model is also compared with the constant-rates Brownian model (which has five parameters: four means and one rate) using the likelihood-ratio statistic (χ^2) with degrees of freedom equal to the difference in the number of estimated parameters (k) and where * denotes $P<0.05$, ** denotes $P<0.01$, and *** denotes $P<0.001$. Models in which at least two rate categories are specified are named M1–M11 and the constant rate model is named All equal.

Model	Small islands	Large island TC & TG	Large island other	Mainland	deltaAICc	wtAIC	Maximum likelihood	*P* (k)
M5	1.000	0.409 (0.243–0.731)	1.000	1.000	0.000	0.389	122.539	** (6)
M3	1.000	0.379 (0.226–0.673)	1.000	0.809 (0.500–1.367)	1.598	0.175	122.833	* (7)
M4	1.000	0.445 (0.266–0.789)	1.214 (0.758–1.954)	1.000	1.625	0.173	122.820	* (7)
M9	1.000 (0.533–2.008)	0.415 (0.242–0.728)	1.018	1.018	2.183	0.131	122.541	* (7)
M1	1.000 (0.542–2.043)	0.409 (0.244–0.725)	1.115 (0.696–1.795)	0.879 (0.542–1.484)	3.724	0.060	122.877	* (8)
M11	1.000	1.000	1.455 (0.901–2.362)	1.000	6.233	0.017	119.423	NS (6)
All equal	1.000	1.000	1.000	1.000	6.430	0.016	118.246	(5)
M7	1.000 (0.828–3.152)	0.651	1.059 (1.009–2.636)	0.651	6.846	0.013	120.209	NS (7)
M2	1.000	1.000	1.741 (1.080–2.820)	1.421 (0.877–2.400)	6.961	0.012	120.152	NS (7)
M8	1.000 (0.658–2.520)	0.817	0.817	0.817	8.217	0.006	118.431	NS (6)
M10	1.000	1.000	1.000	1.041 (0.642–1.761)	8.562	0.005	118.258	NS (6)
M6	1.000 (0.673–2.574)	0.800	0.800	0.865 (0.667–1.828)	10.312	0.002	118.476	NS (7)
Model average	1.000	0.447	1.062	0.961				

Table 2. Rates of diversification in female snout vent length. Details follow Table 1.

Model	Small islands	Large island TC & TG	Large island other	Mainland	deltaAICc	wtAIC	Maximum likelihood	P (k)
M4	1.000	0.412 (0.245–0.734)	1.527 (0.956–2.451)	1.000	0.000	0.290	150.862	*** (7)
M5	1.000	0.337 (0.198–0.610)	1.000	1.000	0.483	0.228	149.529	*** (6)
M9	1.000 (0.337–1.308)	0.494 (0.184–0.563)	1.583	1.583	1.116	0.166	150.304	** (7)
M1	1.000 (0.533–2.069)	0.486 (0.289–0.867)	1.804 (1.130–2.895)	1.267 (0.782–2.139)	1.854	0.115	151.041	** (8)
M3	1.000	0.309 (0.183–0.556)	1.000	0.791 (0.489–1.336)	1.948	0.110	149.888	** (7)
M2	1.000	1.000	2.655 (1.654–4.283)	1.905 (1.177–3.217)	2.974	0.066	149.375	** (7)
M11	1.000	1.000	1.858 (1.154–3.010)	1.000	5.695	0.017	146.923	* (6)
M7	1.000 (0.583–2.316)	0.904	1.717 (1.180–3.076)	0.904	7.802	0.006	146.961	* (7)
All equal	1.000	1.000	1.000	1.000	10.037	0.002	143.673	(5)
M8	1.000 (0.422–1.700)	1.241	1.241	1.241	11.835	0.001	143.853	NS (6)
M10	1.000	1.000	1.000	1.057 (0.653–1.784)	12.147	0.001	143.697	NS (6)
M6	1.000 (0.425–1.712)	1.232	1.232	1.265 (0.634–1.734)	14.008	0.000	143.858	NS (7)
Model average	1.000	0.460	1.469	1.164				

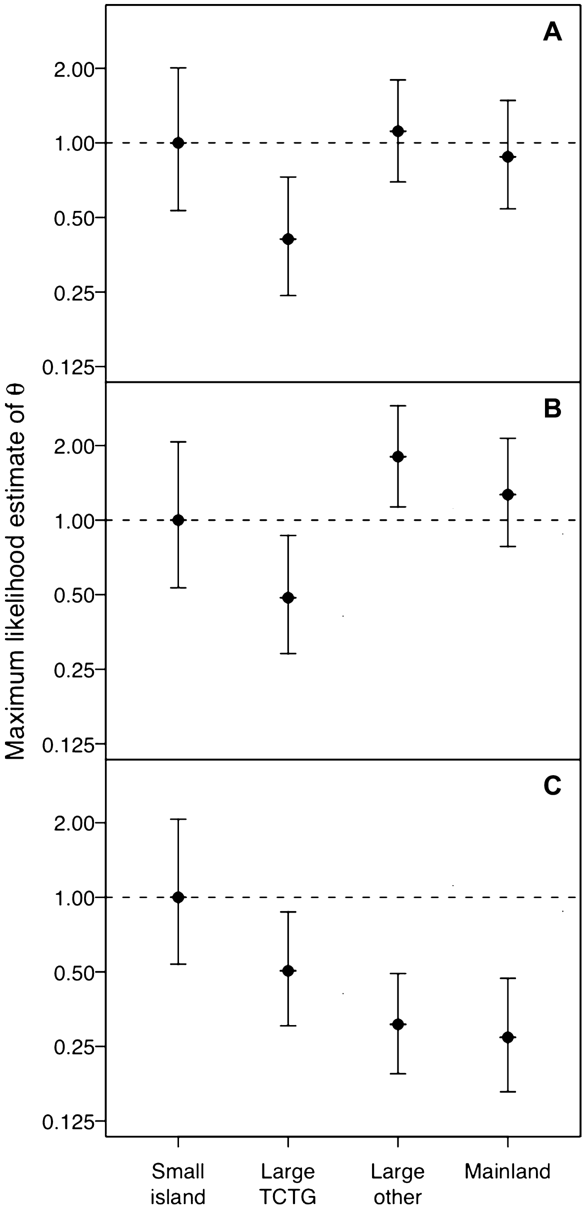

Figure 2. Rates of diversification of (A) male SVL, (B) female SVL, and (C) sexual size dimorphism among *Anolis* lizards. For the four ecomorph/island categories, the maximum-likelihood value of the relative rate estimates along with approximate 95% confidence intervals are shown for the full four-rate model. The four categories are labeled as: Small island (small-island species), Large TCTG (large-island trunk-ground and trunk-crown species), Large other (large-island species that are not trunk-ground and trunk-crown anoles), and Mainland (mainland species).

parameter estimates were also consistent when we first transformed the phylogeny according to the maximum-likelihood estimate of kappa, even though we found evidence for long-branch stasis ($\kappa = 0.666$; comparison with $\kappa = 1$: $\chi^2 = 5.081$, $P = 0.024$). The intermediate rates among large-island trunk-crown and trunk-ground species are not present when we used the

Table 3. Rates of diversification in sexual size dimorphism in snout vent length. Details follow Table 1.

Model	Small islands	Large island TC & TG	Large island other	Mainland	deltaAICc	wtAIC	Maximum likelihood	*P* (k)
M9	1.000 (1.831–7.047)	0.505 (1.032–2.981)	0.293	0.293	0.000	0.406	256.094	*** (7)
M8	1.000 (1.519–5.829)	0.354	0.354	0.354	1.855	0.160	254.072	*** (6)
M1	1.000 (0.537–2.067)	0.505 (0.303–0.873)	0.307 (0.194–0.492)	0.272 (0.164–0.471)	2.049	0.146	256.178	** (8)
M6	1.000 (1.400–5.382)	0.383	0.383	0.275 (0.432–1.246)	2.653	0.108	254.767	** (7)
M2	1.000	1.000	0.455 (0.288–0.730)	0.403 (0.244–0.697)	3.042	0.089	254.573	** (7)
M7	1.000 (1.386–5.318)	0.388	0.311 (0.506–1.283)	0.388	3.250	0.080	254.468	** (7)
M11	1.000	1.000	0.605 (0.382–0.970)	1.000	9.270	0.004	250.364	* (6)
M10	1.000	1.000	1.000	0.565 (0.341–0.982)	9.531	0.003	250.234	* (6)
M4	1.000	0.958 (0.576–1.651)	0.595 (0.376–0.954)	1.000	11.437	0.001	250.375	NS (7)
All equal	1.000	1.000	1.000	1.000	11.459	0.001	248.190	(5)
M3	1.000	1.049 (0.632–1.801)	1.000	0.574 (0.346–0.996)	11.689	0.001	250.249	NS (7)
M5	1.000	1.204 (0.726–2.068)	1.000	1.000	13.122	0.001	248.438	NS (6)
Model average	1.000	0.508	0.337	0.321				

reduced dataset: instead this group has a similar low rate to the large-island other ecomorph species and mainland species (see Supplementary Appendix S7). Taken together, these results strongly suggest exceptionally high rates of diversification in SSD among small-island species.

Discussion

Dispersal to novel, previously unoccupied, habitats can result in changes to both the strength and direction of selection pressures (Simpson 1944; Barton 1996; Blondel 2000; Herrel et al. 2008; Price 2008). Phenotypic change may be driven by differences in, for example, climate, community structure, and predation risk experienced by colonizing species (Blondel 2000; Blumstein 2002). Typically, studies of ecologically driven variation in rates of morphological evolution have considered islands as novel environments (Millien 2006; Harmon et al. 2008). Our results show that lineages of *Anolis* lizards that disperse to novel mainland environments have similar rates of body size diversification to lineages that dispersed to small-island (i.e., novel island) environments.

However, whether rates of trait diversification among mainland and small-island lineages differ from those of the (large-island) source pool depends on the definition of the source pool. Compared to all large-island taxa, rates of body size diversification on small islands or the mainland are not high: they are indistinguishable from the adaptive radiation of anoles on the Greater Antilles. Yet if the source pool is restricted to include only those lineages that appear to be ecologically predisposed to being successful dispersers and colonizers, that is the trunk-crown and trunk-ground ecomorphs (Poe et al. 2007), then rates of body size diversification are elevated among small-island lineages. Furthermore, rates of morphological diversification in sexual size dimorphism are high among small-island lineages, but not among mainland lineages, regardless of how the source pool is defined. We also note that large-island species of the other four ecomorphs have a higher rate of diversification in body size than large-island species of the trunk-crown and trunk-ground ecomorphs. This may imply that rather than high rates among small-island anoles, there is a low rate among large-island trunk-crown and trunk-ground species. Although we suggest that it is more parsimonious to infer high rates among small-island species, we also discuss the alternatives below.

A restricted definition of the source pool is valid and important in interpreting our results. Small-island and mainland taxa are similar to the trunk-crown or trunk-ground ecomorphs (Losos and De Queiroz 1997) because they are descended from them not because small-island or mainland lineages have converged toward these two ecomorphs (our Results and Poe et al. 2007). Why, then, are diversification rates higher in both small-island and mainland lineages than in the restricted source pool lineages? One explanation is that rates of diversification are low among trunk-crown and trunk-ground species because there is something unusual about these two particular ecomorphs. Male–male competition is known to be particularly strong with sexual selection favoring large male size in trunk-crown and trunk-ground anoles (Butler et al. 2000; Butler and Losos 2002; Butler et al. 2007). This may limit the extent to which ecological factors can influence diversification in body size. Indeed, a substantial proportion of morphospace occupancy in trunk-crown and trunk-ground anoles is determined by sexual dimorphism rather than by interspecific variation (Butler et al. 2007). Consequently, sexual selection may be a stronger constraint on body size divergence in trunk-crown and trunk-ground anoles than in the other ecomorphs. The difference in rates between our two groups of large-island ecomorphs may also be partly artefactual. Species' ecomorphs are designated on the basis of ecology, habitat use, and behavior but they also form distinct clusters in morphological space such that there are greater morphological difference between ecomorphs than within them (Losos et al. 1998; Beuttell and Losos 1999). When we compare the species that belong to the colonizing ecomorphs to the rest of the large island species, we are comparing two ecomorphs with four ecomorphs and unique species that do not fit to any particular ecomorph. Hence, a lower rate among the group of trunk-crown and trunk-ground species is not surprising because it captures little of the overall between ecomorph variation.

Although either of these explanations may explain the difference between the two ecomorph groupings of large island species, they cannot explain why small-island species have a much higher rate of body size diversification than the trunk-crown and trunk-ground ecomorphs. There is no evidence to suggest that species of any of the four other ecomorphs have successfully colonized small islands. We therefore suggest that the difference in rates that we identified between small-island species and trunk-crown and trunk-ground species is most likely due to net increases in rate among small-island species. One nonadaptive explanation that may apply over short periods of time is that founder effects (e.g., Mayr 1954; Carson and Templeton 1984) or random genetic drift acting on standing genetic variation (Kimura 1968) has resulted in elevated rates of trait diversification. However, this is unlikely to explain our results given that most field studies indicate that phenotypic differences between populations are generally best explained by selection rather than by purely neutral processes (e.g., Merilä and Crnokrak 2001; Clegg et al. 2002; Leinonen et al. 2008).

Two nonmutually exclusive ecological explanations may be important. First, the variation in selection pressure (particularly the direction of selection) encountered by lineages colonizing new environments may result in each colonizing species having distinct optima in each new environment (Price 2008). If this is the case, then variation in optima from one species or novel environment to the next will result in elevated rates of phenotypic diversification across species. However, variation in selection pressure is expected to be greatest among island settings, and will increase as island area decreases, due to greater variation in community composition (Price et al. 2009). The elevated rates among mainland taxa (compared to the restricted source pool) that we observed are therefore not expected in this model. One possible reason is that while species identity within communities may be variable in island settings and may link to variation in selection pressure, selection and trait optima may be influenced by other factors such as the greater complexity and variety of possible species interactions in the more species-rich mainland communities. The second, and most frequently invoked mechanism is that ecological opportunity is high on islands largely because some communities have few or no competitors, and this allows rapid trait diversification. If so, rates among small-island lineages may be high because they are not competing with smaller (twig ecomorphs) and larger (crown-giant ecomorph) competitors that may inhibit the size evolution of trunk-crown and trunk-ground species on species-rich large islands. In contrast, the mainland recolonizers may come into contact and compete with members of the species-rich *Dactyloa* sister clade (Nicholson et al. 2005). If there is variation in the direction of selection on different islands, as in the Price model (Price 2008), then ecological opportunity would elevate rates among small-island but not mainland anoles. A recent study by Pinto et al. (2008), however, suggests that anoles that have recolonized the mainland may not compete with *Dactyloa* anoles. They argue that Caribbean anoles and their descendents that recolonized the mainland have better-developed toe-pads than the *Dactyloa* species (Macrini et al. 2003; Velasco and Herrel 2007). The toe-pad may therefore be a key innovation or exaptation (Simpson 1944; Gould and Vrba 1982) that has increased ecological opportunity for the mainland colonizers. Our results are clearly consistent with this explanation and suggest a role for variation in the direction of selection as suggested by Price in combination with ecological opportunity both on small islands and the mainland. At present, there is insufficient phylogenetic data to test Pinto et al.'s (2008) hypothesis that the large clade of mainland recolonizers represents an adaptive radiation.

Our results for rates of diversification in body size are consistent with a reduction in the number of competitors and a role for unusual toe-pad evolution (Macrini et al. 2003; Velasco and Herrel 2007; Pinto et al. 2008). However, it has also been suggested that evolution in mainland anoles is regulated by predators whereas evolution in Caribbean anoles is regulated by intraspecific interactions (Andrews 1979; Pinto et al. 2008). Intraspecific interactions may be particularly important on small islands, where anole population densities are often exceptionally high (Lister 1976; Schoener and Schoener 1980; Wright 1981; Buckley and Jetz 2007). This may explain the relatively high rates of diversification in sexual size dimorphism on small islands in two ways, both related to the niche variation hypothesis (Van Valen 1965). First, high population density should, all else being equal, increase intraspecific competition and may promote resource partitioning between the sexes if the resource base is sufficiently large (Fitch 1981; Dayan and Simberloff 1998). Second, some islands have a narrow resource base such that males and females cannot diverge from one another, causing sexual size dimorphism to diminish (Lack 1947; Meiri et al. 2005). Increased trait diversification rates could therefore arise simply because species on some small islands become more dimorphic whereas species on other small islands become less dimorphic so the range of dimorphism across all small-island species increases. An alternative, although not mutually exclusive explanation, is that sexual selection that favors larger males in the battle for breeding territories may be intensified at high densities (Grant 1968; Stamps et al. 1997). The importance of sexual selection relative to ecological explanations is likely to depend on the colonizing lineages. Species of the trunk-crown and trunk-ground ecomorphs typically display more pronounced male–male competition than other ecomorphs (Butler et al. 2000; Butler and Losos 2002; Butler et al. 2007) and at high densities competition may be stronger. This implies that the high rate of diversification in SSD on small islands is at least partly due a combination of nonrandom colonization and increased sexual selection. This is further supported because species on small islands show, on average, more extreme male-biased dimorphism than large-island trunk-crown and trunk-ground species.

THE MULTIPLE RATES MODEL

The multiple rate method that we introduce here is a simple extension of Thomas et al's (2006) method for comparing rates of phenotypic diversification. It differs from the noncensored approach of O'Meara et al. (2006) by allowing each different partition of the phylogeny to have a different phylogenetic mean. We suggest that, contrary to Revell (2008), many hypotheses that infer different rates imply different evolutionary regimes and hence different means. This is not a trivial distinction because assuming a common mean can have serious consequences for the inferred differences in rates. Our simulations (Supplementary Appendix S5) show that models that assume a single mean (e.g., the noncensored test in O'Meara et al. 2006), but not our multiple-means model, can infer differences in rate even if only the means differ. Where there is no difference in means, or if that difference is small, then the common mean and multiple mean models are similar. When should each model be used? The common mean approach is appropriate if there is no mean difference between groups and the interest is in a net overall difference in rate between groups, or when means differ and the interest is in any form of rate shift. In contrast, the multiple means model is appropriate if the interest is in a net overall difference in rate between groups regardless of whether they differ in mean. In practice, it will often be informative to use both to explore whether observed differences between groups can be explained by differences in rates, means, or both. The common mean model is a special (nested) case of our multiple means model and they can be readily compared using maximum likelihood or AIC. In general, both the common mean and multiple mean models should be regarded as tests for differences in the net rate of phenotypic diversification but they may not reflect the true rate of evolution if, for example, there is parallel directional selection across lineages (where evolution can be fast, but diversification slow).

Our model also differs from the most frequently used implementation of the Ornstein–Uhlenbeck (OU) model in which different groups are allowed to have different optima but only a single rate (Butler and King 2004). OU models are designed primarily to test for evidence of stabilizing selection and each group has a parameter that reflects the strength of selection (sometime referred to the “rubber band” parameter) and a single drift parameter across all groups. In principle, it is possible to fit OU models with multiple drift parameters and explore nested models in which both optima and rate can vary (O'Meara et al. 2006). Our model is similar to this variant of the OU model except that we effectively set the strength of selection parameter to zero.

CONCLUSIONS

We have shown that in the light of nonrandom island colonization both properties of novel environments and ecological properties characteristic of small islands influence morphological diversification rates in anoles. Ecological opportunity may be high on small-islands as a result of a reduction in the number of competing species, most obviously the lack of the twig, trunk, crown-giant, and grass-bush ecomorphs. In contrast, on the mainland a unique toe-pad may allow colonizing species to minimize competition with *Dactyloa* and hence they also have enhanced ecological opportunity (Pinto et al. 2008). Ecological opportunity promotes morphological variation and if the direction of selection encountered by different colonizing species also varies then traits may diverge rapidly (Price 2008; Price et al. 2009). Although novel environments promote body size diversification in lineages relative to their ancestral stock, the evolutionary trajectories of males and females appear to differ depending on the properties of those novel environments. Where species richness is low and abundance is high (on small islands), the sexes diverge from one another. Where species richness and potential interspecific competition is high, and abundance is presumably lower (on the mainland) body sizes diverge but the sexes evolve in parallel with one another.

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Supporting Information

The following supporting information is available for this article:

Appendix S1. Data and Sample size (see separate tab-delimited text file).
Appendix S2. References for data sources.
Appendix S3. Species that have been subject to morphological analyses of ecomorph.
Appendix S4. Maximum likelihood reconstruction of *Anolis* ecomorphs.
Appendix S5. Common mean simulations.
Appendix S6. Phylogeny with ecomorph/geographic setting as node labels (see separate nexus file).
Appendix S7. Results of common mean, reduced dataset, and kappa-transformed analyses.
Appendix S8. Source code for rates analyses in R (see separate R file).
Appendix S9. Example of rates analyses (see separate R file).
Appendix S10. Multiple-rates simulations.

Supporting Information may be found in the online version of this article.
(This link will take you to the article abstract).

Additional results and discussion can be found in a document at http://www.repository.naturalis.nl/record/289893.