


VOLUME 65, NUMBER 4, APRIL 2011

EVOLUTION

INTERNATIONAL JOURNAL OF ORGANIC EVOLUTION



Toward a general species
concept

Evidence that sex reduces
genetic variation

Power, corruption and the
evolution of cooperation

Published by the Society
for the Study of Evolution



ANCIENT COLONIZATION PREDICTS RECENT NATURALIZATION IN *ANOLIS* LIZARDS

Steven Poe,^{1,2} J. Tomasz Giermakowski,¹ Ian Latella,¹ Eric W. Schaad,¹ Erik P. Hulebak,¹ and Mason J. Ryan¹

¹Department of Biology and Museum of Southwestern Biology, University of New Mexico, Albuquerque, New Mexico 87131

²E-mail: anolis@unm.edu

Received February 25, 2009

Accepted January 7, 2011

The distributions and characteristics of naturalized species may be explained by novel anthropogenous aspects of world biogeography such as the creation of favorable transport environments for propagules on ships. Conversely, the unprecedented connectivity of humans may simply accelerate omnipresent ecological and evolutionary forces, for example, ships may allow species that are generally good dispersers to disperse more quickly. As a null hypothesis, there may be no human component to species naturalization. The first hypothesis predicts that naturalized species will possess unusual characteristics specific to interactions with humans. The latter two hypotheses predict similarity between ancient colonizers and recently naturalized species. In this article, we present a test of the latter hypotheses and show how they may be reconciled with the former. We show that species of *Anolis* lizard that are ancient solitary colonizers share characteristics of size, shape, scalation, and phylogeny with naturalized species of *Anolis*. Characteristics of ancient solitary colonizers predict naturalization approximately as well as characteristics of naturalized species themselves. These results suggest the existence of a general colonizing type of *Anolis*, and that contemporary patterns of naturalization are at least partially explained by abilities that are unrelated to interactions with humans.

KEY WORDS: Evolution, invasion, natural processes, nonnative, solitary species.

Invasive species are a global concern due to resulting economic losses and extinction of indigenous wildlife. Much of invasion biology focuses on identifying common characteristics of invasions, including intrinsic (e.g., asexual reproduction) (Rejmanek and Richardson 1996) and extrinsic (e.g., suitable habitat for invasion) (Williamson 1996) factors, with two goals in mind (Rice and Sax 2005). First, such information may be used to erect a predictive framework of likely invasive species for conservation, health, and economic purposes. Second, knowledge of the characteristics of recent invaders may give insight into general ecological and evolutionary processes.

In this article, we examine whether the reverse inference, of evolutionary biology informing invasion biology, is also possible. We studied an ancient evolutionary colonization pattern, the so-called “solitary” *Anolis* lizards, to gain insight into the characteristics that determine recent naturalization success. We study naturalization—the establishment of a population outside of its

native range, rather than invasion—the spread of a naturalized species beyond its point of introduction (Richardson et al. 2000), because naturalization is a necessary precursor to invasion and invasion is more difficult to demonstrate than naturalization.

Anolis lizards are an ideal system for studying naturalization. Nineteen of 374 (5%) *Anolis* species include naturalized populations. For example *A. sagrei* is native to Cuba but has established populations in Belize, Grenada, Guam, Jamaica, Mexico, Taiwan, and the United States (Lever 2003). Naturalized species of *Anolis* share unusual characteristics of anatomy, environment, ecology, and phylogeny (Latella et al. 2010).

Anolis is also a model system for studies of ancient evolutionary colonization (Williams 1969; Nicholson et al. 2005), that is, nonhuman-mediated naturalizations that occurred millions of years ago. Solitary *Anolis*—species historically endemic to islands lacking congeners (note that this definition excludes the dozens of *Anolis* species that are sole inhabitants of some islands

but historically sympatric with congeners in other parts of their range)—are probably all overwater colonizers. Solitary species inhabit either oceanic islands (e.g., *A. agassizi*), so are necessarily colonizers, or landbridge islands and are phylogenetically recent derivatives (e.g., *A. desechensis* [Rodríguez-Robles et al. 2007]), indicating recent colonization rather than vestigial vicariant existence.

The 26 species of solitary *Anolis* share traits of size, sexual dimorphism, limb length, head scalation, and toe scalation, and the similarities among solitary species in each of these traits except toe scalation evolved earlier than the transition to solitary existence (Schoener 1969; Poe et al. 2007; Poe unpubl. data). That is, these traits did not evolve as adaptive responses to solitary existence, but rather evolved earlier and apparently facilitated colonization as exaptations. This lack of postcolonization evolutionary change in studied traits is what allows us to consider extant solitary species as proxies for the ancient colonizing versions of themselves—there is no reason to reconstruct ancestral states, because ancestral states will tend to be the same as current states in solitary species for the traits we are studying.

Naturalized species have been viewed as models for evolutionary colonization at least since Darwin (1859). However, the appropriateness of naturalized species as models to test ancient evolutionary processes has never been tested. If this supposition holds true, then ancient colonizers (i.e., solitary species) and naturalized species would be expected to share unusual characteristics that facilitate colonization and/or establishment. We hypothesized that solitary and naturalized species are especially similar to each other and differ from other *Anolis* in the same ways. We test this contention using randomized contingency tests. If solitary and naturalized species are found to be nonrandomly similar according to these tests, we should be able to construct a model that predicts naturalization based on either solitary or naturalized species, and both solitary and naturalized parameterizations should yield good fit to the model. We construct such models using both phylogenetic logistic regression (Ives and Garland 2010) and logistic regression incorporating a parameter for phylogenetic distance to naturalized species (Jiang et al. 2010). Our goal is to test whether it is possible to predict naturalization using information from ancient evolutionary colonizers.

Materials and Methods

DATA

We measured body length from snout to vent, head length from anterior edge of ear to tip of snout, and femoral length from ventral midline to knee of 242 species of *Anolis* ($n = 1\text{--}15$ specimens per species). We recorded maximum male and female snout to vent length, median number of head scales across the snout between the second canthals, and median number of lamellae under

the fourth toe from personal observation of 242 species of *Anolis*, Williams et al. (1995), and original species descriptions. Each of these traits has been shown or suggested to reflect performance differences in *Anolis* (Losos 2009). All variables were natural-log transformed before analyses. Maximum snout to vent length was used as a measure of body size (henceforth: SVL). Sexual size dimorphism was measured as maximum female SVL divided by maximum male SVL ($=SSD$). Head length, femoral length, and lamellae number were found to be strongly correlated with snout to vent length and so regression residuals were used in analyses. Mean head length and femoral length were regressed against mean snout to vent length measured for the same specimens of each species. Median lamellae number was regressed against SVL for each species. Residuals for these regressions are henceforth abbreviated as HL (head length), FL (femoral length), and LM (lamellae). Naturalized status of species was determined based on Lever (2003). Solitary status of species was based on Losos and de Queiroz (1997) and Williams et al. (1995). Data are listed in Table S1.

PHYLOGENETICS

We performed a parsimony analysis of data from Nicholson et al. (2005; mitochondrial DNA, nuclear ITS DNA) and Poe (2004; morphology) and unpublished morphological data (45 additional species scored beyond Poe [2004]) for 252 species of *Anolis* and eight outgroups using the parsimony ratchet (Nixon 1999) on PAUP (Swofford 2002). Data coverage varied from all 1267 parsimony-informative characters scored to 52 characters for some species scored only for external morphology. This analysis resulted in 1344 most parsimonious trees. Mixed-model Bayesian methods were attempted but convergence to optimal trees was not obtained in spite of multiple lengthy searches (up to three months of computer time).

To obtain branch lengths to measure phylogenetic distances between species, we performed a separate analysis of the mitochondrial dataset of Nicholson et al. (2005) using the topology obtained in parsimony analyses of the entire dataset. We used the AIC in Modeltest (Posada and Crandall 1998) to select a model of evolution for likelihood analysis in PAUP. The model (GTR + G + I) was applied in a likelihood analysis of a randomly selected optimal topology with species that were not scored for mtDNA excluded and branch lengths constrained to enforce a molecular clock. The resulting branch lengths were grafted onto this topology of all 252 species using the BladJ program in Phylocom (Webb et al. 2007), which interpolates node times by evenly spacing undated branchpoints between dated nodes.

We also obtained a tree from analysis of the mtDNA data alone. We added a sequence from *A. apletophallus* to the dataset of Nicholson et al. (2005) and performed a Bayesian phylogenetic analysis of 187 *Anolis* species and two outgroups using

MrBayes (Huelsenbeck and Ronquist 2001) under the following parameter/Markov Chain Monte Carlo values: GTR + I + gamma, two runs of four heated chains, heating temp = 0.1 (a value obtained by trial and error while attempting to reach the acceptance rate of the Metropolis proposals recommended by the authors, i.e., 10–70%), 10,000,000 generations, sampling every 500 generations, 1000 burnin trees. We confirmed postburnin convergence between runs by comparing plots of likelihood values for stability and examining the standard deviation of split frequencies. We obtained clocklike branch lengths on the most probable tree using penalized likelihood in r8s (Sanderson 2003).

SIMILARITY OF SOLITARY AND NATURALIZED SPECIES

We tested whether solitary and naturalized species are significantly similar and unrepresentative of *Anolis* in SVL, SSD, HL, FL, HS, and LM using a contingency metric:

$$G = (x_{\text{sol},i} - x_{\text{all},i}) \times (x_{\text{nat},i} - x_{\text{all},i}), \quad (1)$$

where x refers to mean for $i = \text{SVL, SSD, HL, FL, HS, or LM}$ for solitary (x_{sol}), naturalized (x_{nat}), or all (x_{all}) *Anolis* species. G is large and positive if solitary and naturalized species are similar to each other and unrepresentative of *Anolis* and small or negative if they are each representative of *Anolis* or differ from *Anolis* in different ways. We compared the test statistics from solitary and naturalized means to a null distribution of values calculated for 999 random samples of 26 (corresponding to solitary) and 19 (corresponding to naturalized) species selected without replacement from the total pool of species.

We tested whether naturalized species tend to come from the same clades as solitary species using Webb et al's (2007) COMDIST approaches. These methods test whether the mean (COMDIST) or nearest neighbor (COMDISTNT) phylogenetic distances between sets of species are significantly smaller (or greater) than the distribution of such distances from randomly selected sets of species.

NATURALIZATION MODELS

We wanted to test whether naturalization was predictable based on a model that is independently parameterized to predict evolutionary colonization to a solitary environment. We performed logistic regression analyses using naturalization as the dependent variable and, in separate analyses, using solitary existence as the dependent variable. If naturalization can be predicted based on species traits, then models based on naturalized species are expected to have maximal predictive ability for naturalization, as such models are parameterized using those species that have actually become naturalized. However if solitary characteristics are good predictors of naturalization, then models predicting naturalization and

models predicting solitary existence should be correlated. That is, they should both identify the same species as likely invaders.

We used two logistic regression approaches, stepwise elimination of parameters incorporating a parameter for phylogenetic distance between taxa (Jiang et al. 2010) and phylogenetic logistic regression (Ives and Garland 2010), which explicitly accounts for shared phylogenetic history via a variance–covariance matrix. For the former approach, we started with a model including all independent variables (SVL, SSD, HL, FL, LM, HS; and PHY, defined below) and reduced this model in a stepwise fashion by sequentially removing the variable that had the least effect on the likelihood of the model. Phylogenetic distance (PHY) was measured as the branch length connecting a species to its closest naturalized relative. Our stopping rule was to obtain a model wherein all remaining variables were significant at $P < 0.05$. These analyses produced models that predicted naturalization and solitary existence. For the phylogenetic logistic regression (which currently does not allow stepwise procedures), we constructed models using the same parameters identified in the stepwise procedure (excluding PHY), and also using all parameters that were found to be individually significant under separate univariate phylogenetic logistic regression analyses. Our use of phylogenetic logistic regression followed the implementation of Ives and Garland (2010).

Results of a logistic regression analysis may be summarized as continuous values from the linear model (i.e., a “naturalization score”) or as discrete classifications of those values (i.e., prediction of naturalized if model score is positive, or nonnaturalized if negative). The absolute fit of the model is generally evaluated with a Classification Table, which summarizes the percentage of species that are correctly classified by the model. Interpretation of logistic regression results for our analysis using naturalization as the dependent variable is clear—results show the ability of the model to predict naturalization and which parameters are the best predictors of naturalization. But a comparison of these results to the performance of solitary species as naturalization predictors is not straightforward. To compare results from the analysis using solitary existence as the dependent variable to the naturalization results, we interpreted the values of the linear solitary model as naturalization scores rather than solitary scores. Thus, a positive model score was interpreted to indicate classification as naturalized rather than as solitary, and fit of the model was evaluated by whether the scores for the solitary colonization model accurately predicted naturalization rather than solitary existence.

We compared continuous scores of these models (naturalization, solitary) using a bivariate plot, the Spearman's signed ranks correlation test, and simple linear regression. A significant result suggests that these models are describing similar phenomena; that is, that ancient solitary colonization can predict recent naturalization.

We compared logistic regression results predicting solitary and naturalized species using five approaches: (1) All 242 species, including all 19 naturalized and 26 solitary species, using the phylogenetic tree obtained with parsimony analysis and Phylocom branch lengths and stepwise regression including PHY as a parameter; (2) 237 species, including only statistically independent solitary ($n = 21$) and naturalized ($n = 14$) species (i.e., excluding the five species that are both solitary and naturalized), using the parsimony tree with phylocom branch lengths and stepwise regression using PHY as a parameter; (3) 187 species, including only those species scored for mtDNA (20 solitary, 19 naturalized), using the Bayesian mtDNA tree and stepwise regression including PHY as a parameter.; (4) all 242 species, using the parsimony tree with phylocom branch lengths and phylogenetic logistic regression using the parameters chosen in (1), excluding PHY; (5) all 242 species, using the parsimony tree with phylocom branch lengths and phylogenetic logistic regression under models incorporating all parameters that are individually significant in univariate phylogenetic logistic regression, excluding PHY.

Results

SIMILARITY OF SOLITARY AND NATURALIZED SPECIES

Solitary and naturalized species of *Anolis* are significantly similar and differ from other *Anolis* in SVL ($P = 0.001$), SSD ($P = 0.001$), HL ($P = 0.024$), HS ($P = 0.002$), and LM ($P = 0.001$) (Table 1). Figure 1 shows phylogenetic clustering of solitary and naturalized species ($P = 0.001$).

Table 1. Means and standard deviations (in parentheses) of traits. For each set of entries, first row shows raw values (measurements in millimeters unless otherwise noted), second row shows ln-transformed and/or size-corrected values used in analyses.

	All <i>Anolis</i> ($n = 242$)	Solitary <i>Anolis</i> ($n = 26$)	Naturalized <i>Anolis</i> ($n = 19$)
Body size	72.1 (32.5)	76.3 (19.2)	91.2 (32.8)
(SVL)	4.20 (0.38)	4.31 (0.25)	4.46 (0.31)
Sexual size	0.89 (0.12)	0.77 (0.11)	0.75 (0.11)
dimorphism	-0.13 (0.14)	-0.27 (0.14)	-0.30 (0.15)
(SSD)			
No. headscapes	8.6 (3.0)	7.3 (1.6)	7.1 (1.5)
(HS)	2.10 (0.33)	2.00 (0.21)	1.94 (0.19)
No. lamellae	20.4 (5.6)	23.6 (4.0)	24.5 (4.4)
(LM)	0.00 (0.16)	0.11 (0.09)	0.07 (0.13)
Femoral length	17.5 (7.6)	19.0 (3.3)	20.4 (6.9)
(FL)	0.00 (0.14)	0.03 (0.07)	0.01 (0.07)
Head length	17.3 (8.2)	18.8 (3.6)	21.0 (7.8)
(HL)	0.00 (0.09)	0.02 (0.08)	0.03 (0.10)

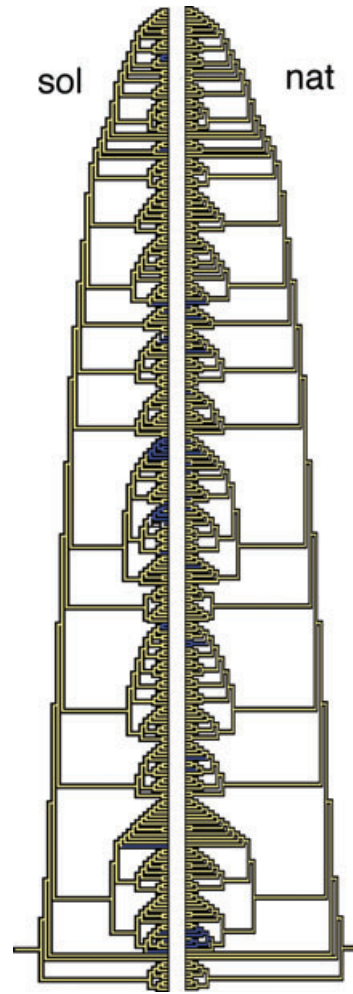


Figure 1. Similarity of phylogenetic position for solitary and naturalized species of *Anolis*. Dark branches show solitary (left) and naturalized (right) species. Tree is one of the optimal trees from phylogenetic analyses.

COLONIZATION MODEL

The final logistic regression model for the analysis of all 242 species using stepwise regression incorporating the PHY parameter, with naturalization as dependent variable, is:

$$N = -6.23 (\text{SSD}) - 3.03 (\text{PHY}) - 2.43. \quad (2)$$

This model accurately classifies 92.2% of species. Model scores for naturalized species (mean = -1.54) are significantly greater than scores for nonnaturalized species (mean = -3.35 ; $P < 0.0001$, Mann-Whitney U test).

The final logistic regression model for the analysis of all 242 species, with solitary existence as dependent variable, is:

$$S = -4.07 (\text{SSD}) + 5.77 (\text{FL}) + 5.72 (\text{LM}) - 4.01 (\text{PHY}) - 1.65. \quad (3)$$

This model accurately classifies 89.8% of species as naturalized or nonnaturalized. Model scores for naturalized species

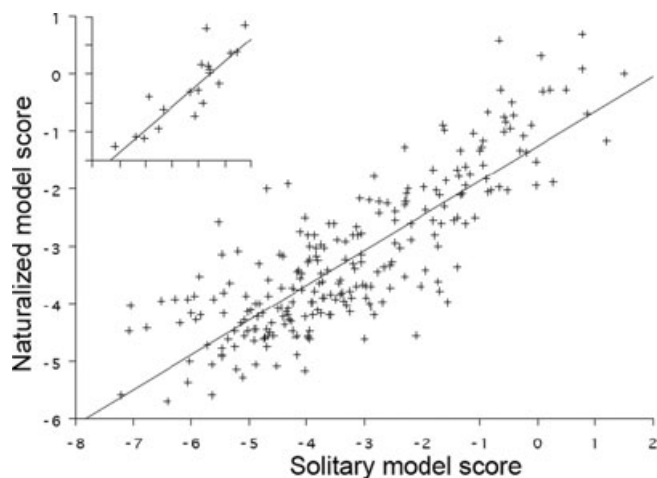


Figure 2. Similarity of scores from models predicting naturalization under parameterizations using solitary and naturalized species of *Anolis*. Inset graph shows a comparison of scores for the 19 naturalized species.

(mean = -1.24) are significantly greater than scores for nonnaturalized species (mean = -3.39 ; $P < 0.0001$, Mann–Whitney U test).

Scores for these two models are strongly correlated (Fig. 2; $P < 0.0001$, Spearman's signed ranks test). Solitary model score explains 69% of the variance in naturalized model score (R^2 , simple regression). The correlation is strong among the 19 naturalized species (Fig. 2, inset; $R^2 = 0.74$).

Results using subsets of statistically independent taxa, phylogenetic logistic regression, and the mtDNA phylogenetic tree are qualitatively identical to those shown here (Figs. S1–S4). In all cases, naturalization and solitary models both significantly predict naturalization and are strongly correlated with each other ($P < 0.0001$ for each comparison; Spearman's signed ranks test).

Discussion

Solitary anoles share several unusual characteristics with naturalized species (Table 1). These results reflect the close phylogenetic relationship of solitary and naturalized species (Fig. 1) and suggest the potential utility of these traits for demonstrating similarity between these groups using the phylogenetically corrected modeling procedures discussed below. See Latella et al. (2010) for a discussion of how each of these traits may function in dispersal and establishment of species.

Models based on solitary parameterization predict naturalization approximately as well as models based on naturalized species themselves (Fig. 2, Figs. S1–S4). The correlation of model scores among naturalized species (Fig. 2, inset) is especially telling, as it indicates that naturalization and solitary models consider the same species to be typical (e.g., *A. carolinensis*) and surprising

(e.g., *A. equestris*) invaders. Both naturalized and solitary models display good absolute predictability of naturalization as evidenced by high classification percentages (Analysis 1: 89.8, 92.2), significantly greater model scores in naturalized versus nonnaturalized species ($P < 0.0001$ in each case), and significant variables in all models.

The consistency of the modeling results across five analyses including four combinations of taxa, two phylogenetic estimates, and two statistical techniques (Fig. 2, Figs. S1–S4) suggests robustness of these results within this dataset. The full dataset includes five species that are both solitary and naturalized as well as several naturalized and solitary species that share recent phylogenetic history with other naturalized or solitary species. Although these issues invite obvious statistical complications, we prefer results from the full dataset because we believe the potential statistical issues are outweighed by biological considerations. Rather than being problematic, the existence of species that are both solitary and naturalized actually supports the conclusions of this article. Consider the hypothetical extreme case of statistical nonindependence where all solitary species produced naturalized populations and all naturalized species invaded from solitary localities. In such a case, the conclusion of this article of similarity between solitary and naturalized species would be obvious and the statistical analyses presented here would be superfluous. Regardless, though, the analysis using only unshared species obtains the same results as the full dataset (compare Fig. 2 and Fig. S1).

The different analyses included two logistic regression approaches, one explicitly correcting for phylogeny (Ives and Garland 2010; Figs. S3 and S4) and one that incorporated phylogeny through an additional regression parameter (Jiang et al. 2010; Fig. 2, Figs. S1 and S2). We view the Jiang et al. (2010) approach of allowing phylogeny to compete with other explanatory parameters roughly equally via the PHY parameter as a best attempt at fulfilling the human goal of prediction of naturalization. Conversely, we interpret the Ives and Garland (2010) phylogenetic correction as an attempt at biological explanation for naturalization ability. Although we wish to point out that, unlike typically analyzed traits in comparative biology (i.e., morphological, ecological), all instances of species naturalization are in fact nonhomologous—they occurred after each species had achieved phylogenetic independence from sister species—and therefore the phylogenetic correction is accounting for inertial tendency rather than homologous similarity. Regardless of one's preferred interpretation, for our purposes of comparing prediction of naturalization using solitary versus naturalized species, results using the Jiang et al. (2010) and Ives and Garland (2010) approaches are qualitatively identical (compare Fig. 2, Figs. S1, S2 to Figs. S3, S4). That is, all analyses show a significant positive relationship between naturalized and solitary parameterizations and thus that naturalization can be predicted using solitary species.

The similarities between solitary and naturalized species suggest reciprocal insight. Recent invasions have long been considered a model for natural evolutionary colonization (Darwin 1859). Our use of evolutionarily solitary species as a model system allows the first test of this assumption. The shared characteristics of solitary and naturalized species indicate that this assumption is warranted, at least in this case.

The recent naturalization success of species with solitary characteristics may be explained by these same characteristics being favored in solitary environments where successful and failed colonization attempts are ubiquitous throughout evolutionary history. Islands with solitary species are environmentally homogeneous, not large enough to support multiple species, and geographically close to source islands so attempted invasions are likely to be common (MacArthur and Wilson 1967; Rand 1969). The solitary species that inhabit these islands probably possess characteristics that favor competitive ability over congeners (to repel attempted invaders or replace previous inhabitants), persistence in a volatile (i.e., hurricane affected), homogeneous, spatially limited environment, and initial colonizing ability into such environments. These same characteristics contribute to modern invasive success. Williams (1969) presents an early exposition of this idea of a “colonizing type.”

The evolution of a colonizing type of *Anolis* is supported by at least two contemporary patterns of naturalization. First, among 41 instances of establishment for 19 naturalized species, only one of these involves invasion from the mainland to an island (Lever 2003). Most of the approximately 200 species of mainland *Anolis* evolved in situ (Nicholson et al. 2005) within multispecies communities (Köhler 2003). Thus, mainland diversification has been shaped by evolutionary forces of vicariance, adaptation to complex environments, and community competition rather than of colonization and direct competition for limited homogeneous space as in solitary species. The characteristics of mainland species allow coexistence in multispecies communities but apparently are not conducive to naturalization. That is, there are no colonizing types found among the vicariantly evolved mainland communities.

Second, the two ecological types (“ecomorphs”; Williams 1983, Losos et al. 1998) that are predominant among both solitary and naturalized species, trunk-crown and trunk-ground (Losos and de Queiroz 1997), are also the most abundant types around human habitations where other types are nearly absent (Schwartz and Henderson 1991; Lever 2003; a contingency test similar to equation (1) with ecomorph type as a dependent variable is significant at $P = 0.001$, $n = 107$). As in other exotic species (Elton 1958), naturalized *Anolis* are often most abundant, or even restricted to, human-altered environments (Lever 2003). If disturbed environments are the only available habitats for invasion (due to, e.g., niche-packing [MacArthur and Levins 1967]), then those species

that are exapted for such environments will be the most successful invaders (Lozon and Isaac 1997). Species with trunk-ground and trunk-crown ecologies such as solitary and naturalized *Anolis* appear to be so exapted. That is, trunk-ground and trunk-crown species fit the colonizing type.

The similarities between historical colonizers and recent invaders suggest that the success or failure of particular introduced species may not be attributable to the peculiarities of humans (Brown and Sax 2005). For example, the specialized morphologies of naturalized *Anolis* are unlikely to be due to these traits being exaptations for stowage in ship or airplane cargo because solitary species possess the same morphologies, and they became established long before ships and planes existed. More likely is the possibility that species that are especially good dispersers anyway are fortuitously able to disperse more efficiently due to the speed and scope of modern human travel. Similarly, human habitations may be amenable to invasion because they imitate ancient invadable environments, perhaps as areas that are unsuitable for specialized local species and/or lack competing species due to eradication of natural habitat. Disturbed habitats thus may allow only modern invaders that are similar to ancient invaders. Colonizations may be proceeding more frequently now due to the greater connectivity of humans, but the colonization ability of particular species appears unrelated to human influence, at least in the case of *Anolis*.

Conclusions

Recently naturalized species of *Anolis* lizard share unusual characteristics with solitary species that colonized environments before human history. Logistic regression models based on solitary species predict naturalization with similar effectiveness to those based on naturalized species themselves (Fig. 2, Figs. S1–S4). These results suggest that invasions occurring during modern human history are similar to ancient prehuman colonizations. There is no need to invoke special interactions with humans to explain which species will become naturalized, as the same colonizing “type” of *Anolis* occurs anciently and in modern times.

Naturalized species have been considered model systems to test general ecological and evolutionary principles at least since Darwin (1859). The results presented here validate this assumption in the case of characteristics that are correlated with colonization, as naturalized species appear to be recent incarnations of forms that have been successful colonizers over evolutionary time. Future work is likely to forge additional links between ancient natural processes and recent phenomena we view as human-mediated. Humans clearly are altering the global environment at a rapid rate, sometimes with catastrophic consequences. But such alterations may simply change the tempo, rather than the essence, of omnipresent natural processes.

ACKNOWLEDGMENTS

We thank C. Webb for help with Phylocom, and A. Ives and T. Garland for providing the PLogReg program. J. Brown and T. Lowrey reviewed earlier versions of this manuscript and provided useful comments. This research was funded by NSF grant DEB 0844624 to SP.

LITERATURE CITED

- Brown, J. H., and D. F. Sax. 2005. An essay on some topics concerning invasive species. *Aust. Ecol.* 30:481–483.
- Darwin, C. 1859. *On the origin of species*. Harvard Univ. Press, Cambridge, MA.
- Elton, C. S. 1958. *The ecology of invasions by animals and plants*. Methuen, London.
- Huelsenbeck, J. P., and F. Ronquist. 2001. MRBAYES: Bayesian inference of phylogeny. *Bioinformatics* 17:754–755.
- Ives, A. R., and T. Garland, Jr. 2010. Phylogenetic logistic regression for binary dependent variables. *Syst. Biol.* 59:9–26.
- Jiang, L., J. Tan, and Z. Pu. 2010. An experimental test of Darwin's naturalization hypothesis. *Am. Nat.* 175:415–423.
- Kohler, G. 2003. *Reptiles of Central America*. Herpeton, Offenbach, Germany.
- Latella, I. M., S. Poe, and J. T. Giermakowski. 2010. Traits associated with naturalization in *Anolis* lizards: comparison of morphological, distributional, anthropogenic, and phylogenetic models. *Biol. Inv.*, doi: 10.1007/s10530-010-9873-x [Epub ahead of print].
- Lever, C. 2003. *Naturalized reptiles and amphibians of the world*. Oxford Univ. Press, New York.
- Losos, J. B. 2009. *Lizards in an evolutionary tree: ecology and adaptive radiation of anoles*. Univ. of California Press, Berkeley and Los Angeles, CA.
- Losos, J. B., and K. de Queiroz. 1997. Evolutionary consequences of ecological release in Caribbean *Anolis* lizards. *Biol. J. Linn. Soc.* 61:459–483.
- Losos, J. B., T. R. Jackman, A. Larson, K. de Queiroz, and L. Rodríguez Schettino. 1998. Contingency and determinism in replicated adaptive radiations of island lizards. *Science* 279:2115–2118.
- Lozon, J. D., and H. J. Mac Isaac. 1997. Biological invasions: are they dependent on disturbance? *Environ. Rev.* 5:131–144.
- MacArthur, R. H., and R. Levins. 1967. The limiting similarity, convergence and divergence of coexisting species. *Am. Nat.* 101:377–385.
- MacArthur, R. H., and E. O. Wilson. 1967. *The theory of island biogeography*. Princeton Univ. Press, Princeton, NJ.
- Nicholson, K. E., R. E. Glor, J. J. Kolbe, A. Larson, S. B. Hedges, and J. B. Losos. 2005. Mainland colonization by island lizards. *J. Biogeogr.* 32:1–10.
- Nixon, K. 1999. The parsimony ratchet, a new method for rapid parsimony analysis. *Cladistics* 15:407–414.
- Poe, S. 2004. Phylogeny of anoles. *Herp. Monogr.* 18:37–89.
- Poe, S., J. R. Goheen, and E. P. Hulebak. 2007. Convergent exaptation and adaptation in solitary island lizards. *Proc. R. Soc. Lond. B* 274:2231–2237.
- Posada, D., and K. A. Crandall. 1998. MODELTEST: testing the model of DNA substitution. *Bioinformatics* 14:817–818.
- Rand, A. S. 1969. Competitive exclusion among anoles (Sauria: Iguanidae) on small islands in the West Indies. *Breviora* 319:1–16.
- Rejmanek, M., and D. M. Richardson. 1996. What attributes make some plant species more invasive? *Ecology* 77:1655–1661.
- Rice, W. R., and D. F. Sax. 2005. Testing fundamental evolutionary questions at large spatial and demographic scales. Pp. 291–308 in D. F. Sax, J. J. Stachowicz, and S. D. Gaines, eds. *Species Invasions: insights into ecology, evolution and biogeography*. Sinauer, Sunderland, MA.
- Richardson, D. M., P. Pysek, M. Rejmanek, M. G. Barbour, F. Dane Panetta, and C. J. West. 2000. Naturalization and invasion of alien plants: concepts and definitions. *Diversity and Distributions* 6:93–107.
- Rodríguez-Robles, J., T. Jezkova, and M. A. García. 2007. Evolutionary relationships and historical biogeography of *Anolis desechensis* and *Anolis monensis*, two lizards endemic to small islands in the eastern Caribbean Sea. *J. Biogeogr.* 34:1546–1558.
- Sanderson, M. J. 2003. r8s: inferring absolute rates of evolution and divergence times in the absence of a molecular clock. *Bioinformatics* 19:301–302.
- Schoener, T. W. 1969. Size patterns in West Indian *Anolis* lizards: I. Size and species diversity. *Syst. Zool.* 18:386–391.
- Schwartz, A., and R. W. Henderson. 1991. *Amphibians and reptiles of the West Indies*. Univ. of Florida Press, Gainesville, FL.
- Swofford, D. L. 2002. PAUP*: Phylogenetic Analysis Using Parsimony (*and Other Methods). Sinauer, Sunderland, MA.
- Webb, C. O., D. D. Ackerly, and S. W. Kembel. 2007. Phylocom: software for the analysis of community phylogenetic structure and character evolution, Version 3.41, Available at; <http://www.phylodiversity.net/phylocom/>.
- Williams, E. E. 1969. The ecology of colonization as seen in the zoogeography of anoline lizards on small islands. *Quart. Rev. Biol.* 44:345–389.
- Williams, E. E. 1983. Ecomorphs, faunas, island size, and diverse end points in island radiations of *Anolis*. Pp. 326–370 in R. B. Huey, E. R. Pianka, and T. W. Schoener, eds. *Lizard ecology: studies of a model organism*. Harvard University Press, Cambridge, MA.
- Williams, E. E., H. Rand, A. S. Rand, and R. J. O'Hara. 1995. A computer approach to the comparison and identification of species in difficult taxonomic groups. *Breviora* 502:1–47.
- Williamson, M. 1996. *Biological Invasions*. Chapman and Hall, London.

Associate Editor: J. Vamosi

Supporting Information

The following supporting information is available for this article:

Figure S1. Plot of prediction of naturalized model score by solitary model score using only statistically independent species, with phylogenetic distances from parsimony tree with Phylocom branch lengths (i.e., analysis 2).

Figure S2. Plot of prediction of naturalized model score by solitary model score using only species scored for mtDNA, with phylogenetic distances from Bayesian mtDNA analysis (i.e., analysis 3).

Figure S3. Plot of prediction of naturalized model score by solitary model score using all species and phylogenetic logistic regression with models incorporating parameters determined to be significant in stepwise analysis (i.e., analysis 4).

Figure S4. Plot of prediction of naturalized model score by solitary model score using all species and phylogenetic logistic regression with models incorporating all parameters that were individually significant (i.e., analysis 5).

Table S1. Data.

Supporting Information may be found in the online version of this article.

Please note: Wiley-Blackwell is not responsible for the content or functionality of any supporting information supplied by the authors. Any queries (other than missing material) should be directed to the corresponding author for the article.