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Note

Comparison of Natural and Nonnative Two-Species Communities of *Anolis* Lizards

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abstract: Human-mediated colonizations present an informative model system for understanding assembly of organismal communities. However, it is unclear whether communities including naturalized species are accurate analogs of natural communities or unique combinations not present in nature. I compared morphology and phylogenetic structure of natural and naturalized two-species communities of *Anolis* lizards. Natural communities are phylogenetically clustered, whereas naturalized communities show no significant phylogenetic structure. This result likely reflects differences in colonization pools for these communities—that is, invasion from anywhere for naturalized communities but from proximal and thus phylogenetically close lineages in natural communities. Both natural and naturalized communities each include pairs of species that are significantly similar to each other in morphology, and both sets of communities are composed of species that possess traits of good colonizers. These similarities suggest that the formation of natural and naturalized communities may be at least partially governed by similar processes. Human-mediated invasions may be credibly viewed as modern incarnations of natural colonizations in this case.

Keywords: *Anolis*, community assembly, invasion, naturalization, phylogeny.

Introduction

The study of invasive or naturalized species may inform our views of historical ecological and evolutionary phenomena (Sax et al. 2007). Invasive species illustrate classic ecological processes of establishment (e.g., Fridley et al. 2007), competition (e.g., Brown et al. 2002), and range expansion (e.g., Short and Petren 2011). We may attempt to reconstruct the characteristics and circumstances that facilitated ancient colonizations, but there is no substitute for observing and documenting colonizations in real time. Invasive species, whatever their economic or aesthetic detriment (Pimentel et al. 2000), are a gold mine of ecological and evo-

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lutionary experiments in nature (e.g., Richardson et al. 2004).

One area of study that naturalized species may inform is community assembly (Diamond 1975; Weiher and Keddy 1999). There is much interest in understanding whether communities are formed through predictable or at least nonrandom processes (e.g., Götzenberger et al. 2011). Community assembly traditionally has been studied using observational tests based on null models (e.g., Connor and Simberloff 1979), historical studies (Losos et al. 1998; Gillespie 2004), colonization studies following defaunation (from, e.g., volcanic activity: Whittaker et al. 1989) or experimental manipulations (e.g., Burke and Grime 1996). Each of these approaches has contributed greatly to our understanding of community formation processes and patterns, but each also has its weaknesses. Null model approaches depend on appropriate designation of species pool, species taxonomy (Gotelli and Graves 1996), and phylogenetic information (Cavender-Bares et al. 2009); historical studies are dependent on these factors and imprecise ancestral reconstructions (e.g., Losos 1999); defaunation and subsequent recolonization studies usually are single data points; and experimental studies necessarily ignore the complexity of natural communities (Morin 2001).

The study of communities of naturalized species solves some of these problems while creating others. Historical factors such as colonization history (e.g., timing of arrival) often are known for naturalized species. Clades with multiple instances of naturalized communities create replicated experiments so examination of general trends is possible. Species that become naturalized have been found to be morphologically similar to ancient colonizers (Thompson et al. 1995; Poe et al. 2011). Thus, recently formed naturalized communities may be the result of processes that formed ancient communities. These positive study aspects of naturalized communities for understanding natural communities are countered by the decidedly unnatural mode of dispersal in naturalized species (i.e., human

mediated) and the frequent occurrence of naturalized communities in purportedly unnatural environments such as agricultural areas and city parks.

Instances and implications of invasions are well documented in animals and plants (Elton 1958; articles in *Biological Invasions*), but the structure of resulting combinations including naturalized species has not received much attention (but see, e.g., Lord et al. 2000; Maitner et al. 2011). No studies have directly compared structure in natural and naturalized communities, although such comparisons are implicit in the above-cited articles. The comparison of naturalized and natural communities has the potential to elucidate basic concepts in community formation and invasion biology. If natural and naturalized communities are similar despite their different modes of colonization, then some similarity of assembly rules may be hypothesized. Also, the standard distinction between "alien" and "natural" could be questioned (Davis et al. 2011). For if there is no way to objectively distinguish natural from naturalized communities or species, what is the point in entertaining the alien/natural distinction? Alternatively, if natural and naturalized communities are different, then perhaps colonization mode is critical in the early formation of communities, human interaction is strongly shaping the establishment of naturalized species, and/or not enough time has passed for recently established communities to evolve resemblance to natural communities.

Anolis lizards (anoles) are an excellent system for addressing issues in community assembly and invasion. The ecology and evolutionary history of a complex community of anoles has been elucidated (Losos et al. 2003; Rodriguez-Schettino et al. 2010), simple one- and two-species communities have been the subject of dozens of ecological studies (see Roughgarden 1995 for review), and colonization in anoles is becoming well studied (Williams 1969; Losos et al. 1993; Latella et al. 2011; Poe et al. 2011).

Here I ask whether two-species communities of anoles that include naturalized species are structured morphologically and/or phylogenetically similarly to natural two-species communities. I ask whether natural and naturalized communities each include species that significantly differ or are similar and whether the species of each set of communities can be distinguished from each other and/or from *Anolis* as a whole. I discuss these results in light of competition, environmental filtering, community assembly, and our interpretation of native and alien species.

Material and Methods

Species and Characters

Powell and Henderson (2012) list the herpetological species content of all islands in the Caribbean and whether each listed population is invasive (=naturalized, for our purposes). I culled sympatric species pairs of *Anolis* lizards from this list and included personal observations and communications regarding Bermuda and Florida (table 1). I divided two-species communities into naturalized—composed of at least one nonindigenous species—and natural assemblages and included each unique species combination as a data point. Certainly several other two-species communities of *Anolis* occur in addition to those analyzed here, for example, those on the fringes of multispecies communities. The sample analyzed here represents all communities that I could confirm as being composed of just two *Anolis* species, either through the presence of just two species recorded on an island (cases from Powell and Henderson) or from intensive repeated surveys and literature records (Bermuda, Florida, Grand Bahama). The two-species environments range from potentially very large (e.g., all of Florida) to tiny (some islands with two-species communities are smaller than 1 km^2). Many of these environments, for example, the smaller islands, are beach habitats, whereas others include diverse and relatively complex habitats (e.g., Florida). I see no obvious habitat or climate differences between areas with natural species pairs and those with naturalized pairs.

Virtually all comparative studies of community structure suffer from some degree of nonindependence due to species that are shared across communities (e.g., Hurlbert 1984; Stone et al. 2011). Workers have adopted various means to address this issue, including sampling from localities spaced some minimum distance apart (e.g., Harmon-Threatt and Ackerly 2013) and from ecologically isolated habitats such as separate lakes for aquatic species (e.g., Helmus et al. 2007). Here I address this concern by analyzing only unique combinations of species. Each species combination is counted as a single data point, even though many of these combinations occur at multiple localities resulting from independent invasions (e.g., the *Anolis sagrei–Anolis carolinensis* pair is found in both Florida and Taiwan). If one considers the unit of community analysis to be an independently formed community, then data-related biases in this article are likely toward low power (i.e., fewer data points are analyzed than could be used) rather than pseudoreplication.

I accumulated a data set of 166 (morphological values) to 179 (phylogenetics) comparative *Anolis* species in order to assess significance of recovered values for the analyzed two-species communities. Species were selected based on available data for morphology and phylogenetics. The use of this null pool essentially assumes equal probability of colonization for each species. This assumption is not completely realistic, as clearly some kinds of species colonize better than others (Latella et al. 2011). However, this pool

Table 1: Two-species communities of *Anolis* lizards analyzed here (most from Powell and Henderson 2012)

Community	Location and area (km²)
A. aeneus/*A. sagrei**	Canouan, Southern Lesser Antilles (7)
A. carolinensis/*A. sagrei**	Florida
A. oculatus/*A. cristatellus**	Dominica, Lesser Antilles (751)
*A. distichus**/*A. smaragdinus**	Great Abaco, Bahamas (1,681)
A. sagrei ordinatus/*A. distichus**	Grand Bahama, Bahamas (1,373)
A. sagrei ordinatus/*A. equestris**	Grand Bahama, Bahamas (1,373)
A. conspersus/ *A. sagrei**	Grand Cayman, Cayman Islands (197)
A. gingivinus/*A. carolinensis**	Anguilla, Lesser Antilles (91)
*A. extremus**/*A. grahami**	Bermuda, North Atlantic (53)
A. luciae/*A. extremus**	St. Lucia, Lesser Antilles (616)
A. extremus/*A. sagrei**	Barbados, Lesser Antilles (430)
*A. grahami**/*leachi**	Bermuda, North Atlantic (53)
A. luciae/*A. wattsi**	St. Lucia, Lesser Antilles (616)
A. aeneus/*A. richardi*	Sugar Loaf, Lesser Antilles (0.07)
A. angusticeps/*A. sagrei*	Cayo Lanzanillo, north Cuba (2)
A. bimaculatus/*A. schwartzi*	St. Kitts, Lesser Antilles (170)
A. brevirostris/*A. longitibialis*	Isla Beata, south Hispaniola (42)
A. brunneus/*A. sagrei*	Crooked Island, Bahamas (252)
A. brunneus/*A. scriptus*	West Plana, Bahamas (9)
A. conspersus/*A. luteosignifer*	Cayman Brac, Cayman Islands (38)
A. cristatellus/*A. poncensis*	Isla Magueyes, south Puerto Rico (0.07)
A. cristatellus/*A. pulchellus*	Cabeza de Perro, east Puerto Rico (0.1)
A. cristatellus/*A. stratulus*	Bovoni Cay, east Puerto Rico (0.2)
A. distichus/*A. sagrei*	Musha Cay, Bahamas (0.5)
A. fairchildi/*A. sagrei*	Cay Sal, Bahamas (1)
A. gingivinus/*A. pogus*	St. Bart, Lesser Antilles (22)
A. grahami/ *A. lineatopus*	Careening Island, south Jamaica (0.2)
A. griseus/ *A. trinitatis*	St. Vincent, Lesser Antilles (350)
A. homolechis/ *A. jubar*	Cayo Bahia de Cadiz, north Cuba (6)
A. jubar/*A. lucius*	Cayo Cueva, north Cuba (0.1)
A. jubar/*A. sagrei*	Cayo Cruz del Padre, north Cuba (12)
A. leachi/*A. forresti*	Barbuda, Lesser Antilles (160)
A. leachi/*A. wattsi*	Great Bird Island, Lesser Antilles (0.1)
A. sagrei/*A. lucius*	Cayo Aguado, north Cuba (3)
A. maynardi/*A. sagrei*	Little Cayman, Cayman Islands (28)
A. porcatus/*A. sagrei*	Cayo Levisa, north Cuba (1)
A. sagrei/*A. smaragdinus*	Great Stirrup Cay, Bahamas (1)

Note: Asterisk indicates naturalized species. Areas listed are examples; some species pairs occur in multiple areas.

affects only some of the analyses of this article (see below), and alternative pools (e.g., island species, species that best fit Latella et al.'s "colonization profile," invasive species, etc.) are fraught with no more realistic and much less parsimonious assumptions. These species were scored for maximum body size (snout to vent length, SVL); mean body (MBL), hindlimb (HLL), and head length (HDL); number of scales across the snout between the second canthal scales (SNSC); and sexual size dimorphism (maximum female/maximum male SVL; SSD). Each of these traits has been shown to possess some selective value for *Anolis* lizards. Body size and sexual size dimorphism affect many aspects of *Anolis* biology (e.g., Butler et al. 2000). Hindlimb length affects locomotor ability (e.g., Vanhooydonck et al. 2006). Head length is related to feeding habits (e.g., Schoener and Gorman 1968). Scale size is associated with moisture loss (e.g., Malhotra and Thorpe 1997). Data are from Latella et al. (2011), supplemented by unpublished observations.

DNA sequence data from the mitochondrial ND2 gene and flanking tRNAs (Nicholson et al. 2005) were obtained from GenBank and aligned by eye with reference to codon position and the pertinent regions of the mitochondrial genome of *A. carolinensis* (Castoe et al. 2008).

Analyses

Thirteen naturalized and 24 natural two-species *Anolis* communities are summarized in table 1. Of the 13 naturalized communities, 10 include one natural and one naturalized species and three include two naturalized species. Analyses excluding the three all-naturalized communities (not shown) produced similar results as those including all 13 naturalized communities. Four species were present in the studied communities but lacked phylogenetic and morphological data. *Anolis fairchildi* was scored using data from *Anolis smaragdinus*, its close relative and morphological near duplicate (Williams 1969, 1976). *Anolis luteosignifer* was scored as *A. sagrei*, with which it was formerly considered conspecific (Schwartz and Thomas 1975). *Anolis extremus* was scored as *Anolis roquet*, with which it was formerly considered conspecific (Grant 1959). *Anolis forresti* was scored as *Anolis wattsi*, with which it was formerly considered conspecific (Lazell 1972).

I performed a phylogenetic analysis of the DNA data using RaxML (Stamatakis 2006) with separate GTR + G models for each codon position and tRNAs, the "ML search" option, and *Polychrus acutirostris* and *Basiliscus plumifrons* as outgroups. Pairwise patristic distances were obtained from this tree.

Phylogenetic distances, maximum SVL, SSD, and SNSC were analyzed as untransformed values. Hindlimb length (HLL) and head length (HDL) were natural-log transformed and regressed against natural-log transformed mean SVL. Residuals were used in analyses.

For each species pair, I obtained absolute differences between species for each studied trait. I compared mean difference of naturalized communities to mean difference of natural communities for each trait using a Mann-Whitney U-test. I compared mean difference for each set of species (naturalized or natural) to *Anolis* as a whole using randomization. I compared mean difference for the 13 naturalized communities to mean differences for 999 random samples of 13 pairs of species from the entire *Anolis* pool and performed the same test with 24 pairs for natural communities. Species were sampled equiprobably without replacement.

Latella et al. (2011) ranked *Anolis* species according to a naturalization score based on a model that predicted colonization ability from traits shared by naturalized species of *Anolis*. In order to test whether species in two-species communities are similar to good colonizers, I compared the colonization rankings of species in two-species communities (natural, naturalized, and pooled) to rankings of other *Anolis* using a Mann-Whitney U-test. I also compared traits (SVL, SSD, SNSC, HLL, HDL) of species in natural two-species communities to traits of species in naturalized two-species communities.

Results

Traits for each species are summarized in the table in the Dryad Digital Repository, http://dx.doi.org/10.5061/dryad.dc976 (Poe 2014). The phylogenetic estimate obtained was nearly identical to results from other studies using these data (e.g., Nicholson et al. 2005) and thus is presented only in skeleton form (fig. 1).

Results of comparisons are summarized in table 2. For all morphological traits, the differences between members of naturalized communities are not significantly greater or less than the differences within natural communities. The phylogenetic comparison showed that natural communities include significantly closer relatives than naturalized communities.

For body size (SVL) and head scalation (SNSC), differences within both natural and naturalized communities are significantly less than differences between random samples of *Anolis*. Phylogenetic distances are significantly lower within natural communities than within *Anolis* generally (i.e., phylogenetic clustering; Webb et al. 2008; fig. 1*A*). Phylogenetic distances within naturalized communities are roughly representative of distances within *Anolis* generally (fig. 1*B*).

Species in two-species communities have significantly better colonization scores than other *Anolis* ($P = .0001$ for natural, naturalized and pooled natural + naturalized species samples). The species in natural communities are statistically indistinguishable from those in naturalized communities using the morphological traits studied here (SVL: $P = .09$; SNSC: $P = .46$; SSD: $P = .76$; HDL: $P = .48$; HLL: $P = .74$).

Discussion

Patterns within Natural and Naturalized Communities

Both natural and naturalized two-species communities of *Anolis* display significant morphological similarity between inhabitant species. Species in each kind of community are significantly similar in body size and head scalation (table 2). This pattern suggests that a combination of body size and head scalation rather than a single trait may be favored in two-species communities. Alternatively, one particular trait (e.g., body size) may be favored in the two-species environment and the other trait (e.g., head scalation) may correlate due to phylogenetic inertia or developmental constraints. The phylogenetic explanation is challenged by the lack of significant phylogenetic similarity among naturalized species pairs (table 2). The great morphological similarity of these species pairs in the absence of phylogenetic similarity suggest convergent occurrence of morphotypes that are suitable inhabitants of two-species communities (and provides a counterexample to the as-
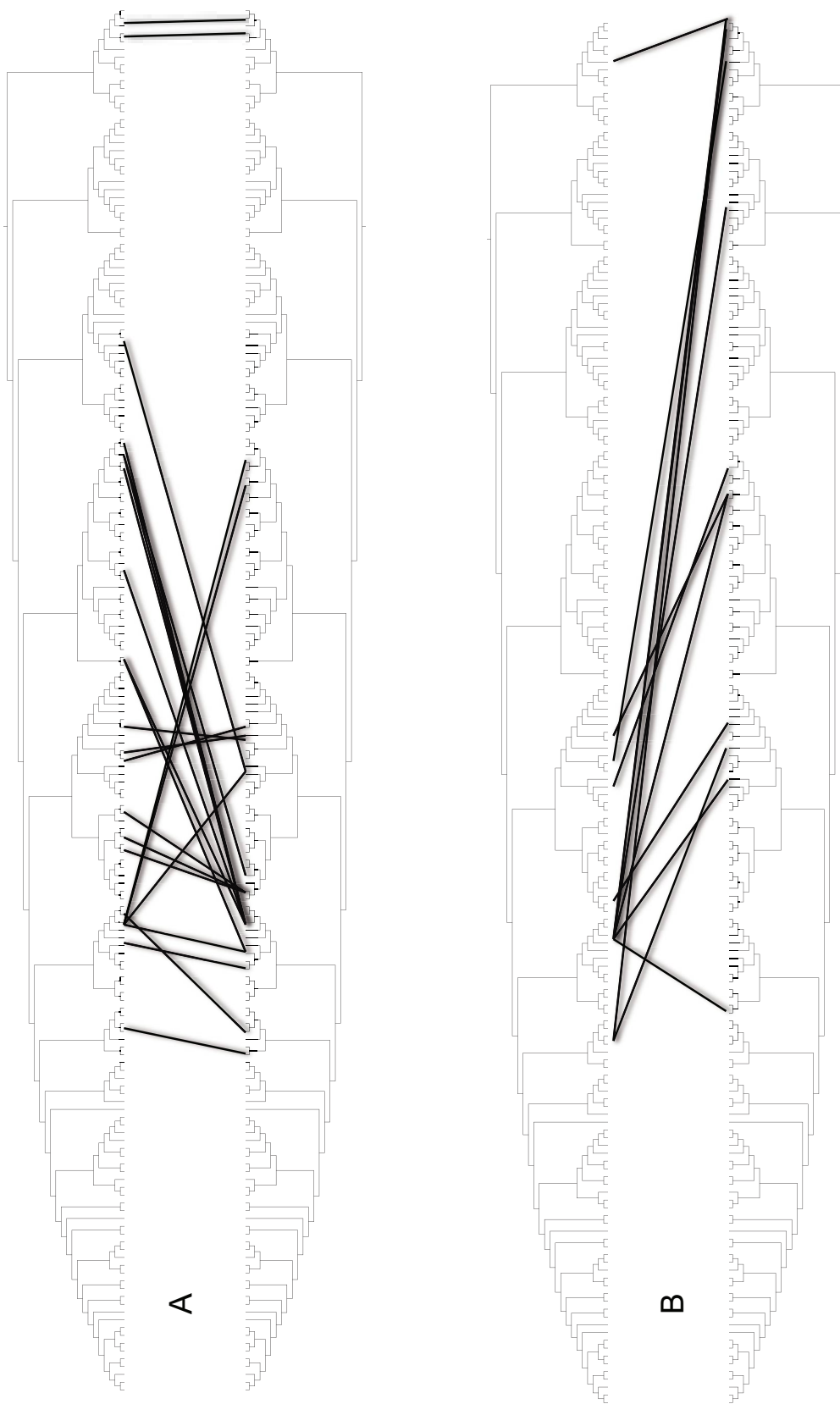
Figure 1: Phylogenetic distances among species pairs. Natural communities (*A*) include significantly close relatives (i.e., are clustered; Webb et al. 2008), whereas naturalized communities (*B*) show no significant pattern.

Table 2: Comparisons of mean differences in traits between sets of natural ($N = 24$) and naturalized ($N = 13$) species pairs in two-species communities, and between each of these groups and 166–178 species of *Anolis*

	Phylogenetic	Body size	No. scales across snout	Sexual size dimorphism	Hindlimb length	Head length
Natural pairs vs.	.53 (±.22)	23.08 (±22.8)	.92 (±.72)	.13 (±.09)	.12 (±.02)	.09 (±.03)
Naturalized pairs	.74* (±.21)	20.5 (±32.7)	1.31 (±1.42)	.13 (±.08)	.17 (±.02)	.11 (±.02)
Natural pairs vs.	.53 (±.22)	23.08 (±22.8)	.92 (±.72)	.13 (±.09)	.12 (±.02)	.09 (±.03)
All pairs of *Anolis*	.75* (±.16)	35.12* (±36.1)	2.45* (±2.09)	.13 (±.09)	.15 (±.11)	.09 (±.07)
Naturalized pairs vs.	.74 (±.21)	20.5 (±32.7)	1.31 (±1.42)	.13 (±.08)	.17 (±.02)	.11 (±.02)
All pairs of *Anolis*	.75 (±.16)	35.12* (±36.1)	2.45* (±2.09)	.13 (±.09)	.15 (±.11)	.09 (±.07)

Note: Table entries are mean differences with standard deviations in parentheses. Comparison of natural and naturalized communities was done using the Mann-Whitney U-test. Comparison of natural versus all *Anolis* and naturalized versus all *Anolis* were done using a randomization test (see text).

* Significant at .01.

sumption that phylogeny is an appropriate proxy for trait clustering/dispersion).

Similarity among species in a community may be interpreted as evidence of habitat filtering (Weiher and Keddy 1999), but competition also could lead to species similarity (Mayfield and Levine 2010). The island environments studied here may be invadable by a particular colonizing type of *Anolis* (Williams 1969), that is, a superior competitor that is suitable for the habitat. This inference is supported by the good colonization scores of species in both natural and naturalized two-species communities. However, the resulting communities of good invaders may be formed by mixed ecological types. Losos (1999) drew from earlier authors (e.g., Williams 1983) to categorize Greater Antillean *Anolis* by "ecomorph" type. Two of these types—"trunk-crown" and "trunk-ground"—appear to be superior invaders, and ecological differences between these forms may allow them to coexist (Losos et al. 1993; Losos and de Queiroz 1997). This inference of competitive structuring is supported by the pattern of ecomorph pairs in two-species communities. None of the species pairs include two of the same ecomorph, in spite of several trunk-ground ($N = 27$) and trunk-crown ($N = 15$) species among the 35 species pairs (ecomorph designations from Losos 2009). This pattern of ecomorph repulsion is highly nonrandom even if the available pool is considered to be only those species in two-species communities (i.e., $P \ll .01$).

Natural species pairs share both morphologic and phylogenetic similarity (table 2). In this case, the phylogenetic similarity is likely attributable to the species pool available for colonization. For example, Careening Island is located just off the south coast of Jamaica. Jamaican anoles, most of which evolved in a single intraisland adaptive radiation (Etheridge 1959; Nicholson et al. 2005), form the pool of potential colonizers. Presumably, two of the appropriate morphotype colonized from this pool of close relatives and

a two-species community of phylogenetically and morphologically similar species resulted.

There was no evidence of natural or naturalized communities being composed of significantly differing species morphologically or phylogenetically (table 2). Differences within communities usually are interpreted as evidence of competition (MacArthur and Levins 1967), and thus this result may be surprising given the extensive literature demonstrating that interspecific competition is a driving force in *Anolis* evolution (Losos 1994). Two aspects suggest that competition may actually be an important factor shaping at least some of these communities. First, competition may be structuring these communities according to traits not studied here (see ecomorph discussion above). Second, it must be noted that there are exceptions to the general trend of pair similarity. Williams (1972) described Schoener's (1969) discovery of body size patterns among West Indian anoles as "Schoener rules." Pertinent to the current case, Schoener (1969) noted that two-species communities tend to be composed of one small and one large species. The four Lesser Antillean communities that spawned the Schoener rules each display size disparities, as does one of the naturalized communities (*Anolis sagrei–Anolis equestris*). Each of these Schoener-rules communities is otherwise typical, that is, similar in head scalation and, in the case of the natural communities, including close relatives. The Schoener-rules communities are unusual in that their species are not naturally found in multispecies communities elsewhere. Thus, whereas other two-species communities may experience gene flow from conspecific populations in multispecies areas that dampens competitive pressures of the two-species community, the Schoener-rules species are free to evolve in response only to their sympatric congeners. It is probable that character displacement in size is the result (Williams 1972; Losos 1990).

Comparison of Natural and Naturalized Communities

Natural and naturalized two-species communities are similarly morphologically structured and thus may have been assembled via similar ecological processes. This generality of structure across different modes of dispersal (natural vs. human mediated) and phylogenetic levels (clustered vs. random; fig. 1; table 2) suggests some similarity to the assembly process in these cases. Perhaps the early stages of colonization are dominated by particular colonizing morphotypes that may invade and even coexist in suitable habitats. Naturalized species obviously are recent colonizers, but some populations of natural species may result from repeated (i.e., recent) colonizations as well as cycles of local extinction (e.g., due to hurricanes) and replacement. Regardless of process, the observable morphological structure of natural and naturalized communities is similar.

The resemblance of natural and naturalized communities extends beyond the comparable levels of dissimilarity of traits between species in a pair. The species in the studied two-species communities have unusually high colonization scores, and comparisons of morphological traits for species in natural versus naturalized communities are all nonsignificant (see above). The statistical importance of the latter result is colored by the difficulty of interpreting a nonsignificant result and rampant nonindependence—some two-species community members are in both natural and naturalized communities (table 1), and many analyzed species are close relatives (fig. 1). But these results are compatible with the idea of a colonizing type in *Anolis* (Williams 1969; Poe et al. 2011; this article). That is, species such as those in table 1 may be adept at spreading to new island environments, even if there is a (similar) anole species already present in the invaded area and especially if the incumbent is of a different ecological type (see above).

Conclusions and Implications

The similarity of natural and naturalized two-species communities of *Anolis* has implications for community formation and our interpretations of invasive species. The composition of natural and naturalized communities may be governed by similar processes in *Anolis* lizards. This result suggests the possibility of general rules for community formation apart from human influences. Anole community evolution may begin with species such as those listed in table 1 and proceed through character displacement and adaptive radiation when enough time and/or space is available (Williams 1972; Losos and de Queiroz 1997). Adaptive radiation is undeniably important in anole community evolution (Williams 1969; Losos 1994), but perhaps habitat filtering (Weiher and Keddy 1999) and

varying kinds of competition (Mayfield and Levine 2010) dominate the earliest stages of diversification.

Current discussions of the interpretation of naturalized species have been contentious (Brown and Sax 2005; Cassey et al. 2005; Davis et al. 2011; Simberloff 2011). The results of this article may inform this discussion. For the morphological traits examined here, human-mediated two-species communities of anoles are indistinguishable from communities that formed during millions of years of evolution in the absence of modern humans. The species in each set of communities are of the same type (i.e., good colonizers) and the community structure of each set is similar. As humans we may view ourselves as destructive, with massive effects on some ecosystems that may confer upon us some "nonnatural" status. Alternatively, some see us as just another species, acting according to our evolved behaviors as any species does (Simberloff 2003; Vining et al. 2008). Regardless of how we view communities that we label as naturalized or natural, these categories are morphologically indistinguishable in the current case.

Literature Cited

Brown, B. J., R. J. Mitchell, and S. A. Graham. 2002. Competition for pollination between an invasive species (purple loosestrife) and a native congener. Ecology 83:2328–2336.

Brown, J. H., and D. F. Sax. 2005. An essay on some topics concerning invasive species. Austral Ecology 30:481–483.

Burke, M. J. W., and J. P. Grime. 1996. An experimental study of plant community invasibility. Ecology 77:776–790.

Butler, M. A., T. W. Schoener, and J. B. Losos. 2000. The relationship between sexual size dimorphism and habitat use in Greater Antillean *Anolis* lizards. Evolution 54:259–272.

Cassey, P., T. M. Blackburn, R. P. Duncan, and S. Chown. 2005. Concerning invasive species: reply to Brown and Sax. Austral Ecology 30:475–480.

Castoe, T. A., Z. J. Jiang, W. Gu, Z. Wang, and D. D. Pollock. 2008. Adaptive evolution and functional redesign of core metabolic proteins in snakes. PLoS ONE 3:e2201.

Cavender-Bares, J., K. Kozak, P. Fine, and S. Kembel. 2009. The merging of community ecology and phylogenetic biology. Ecology Letters 12:693–715.

Connor, E. F., and D. Simberloff. 1979. The assembly of species communities: chance or competition. Ecology 60:1132–1140.

Davis, M. A., M. K. Chew, R. J. Hobbs, A. E. Lugo, J. J. Ewel, G. J. Vermeij, J. H. Brown, et al. 2011. Don't judge species on their origins. Nature 474:153–154.

Diamond, J. M. 1975. Assembly of species communities. Pages 342–344 *in* M. L. Cody and J. Diamond, eds. Ecology and evolution of communities. Harvard University Press, Cambridge, MA.

Elton, C. S. 1958. The ecology of invasions by animals and plants. Methuen, London.

Etheridge, R. 1959. The relationships of the anoles (Reptilia: Sauria: Iguanidae): an interpretation based on skeletal morphology. PhD dissertation, University of Michigan, Ann Arbor.

Fridley, J. D., J. J. Stachowicz, S. Naeem, D. F. Sax, E. W. Seabloom, M. D. Smith, T. J. Stohlgren, D. Tilman, and B. Von Holle. 2007. The invasion paradox: reconciling pattern and process in species invasions. Ecology 88:3–17.

Gillespie, R. 2004. Community assembly through adaptive radiation in Hawaiian spiders. Science 303:356–359.

Gotelli, N. J., and G. R. Graves. 1996. Null models in ecology. Smithsonian Institution, Washington, DC.

Götzenberger, L., F. de Bello, K. A. Brathen, J. Davison, A. Dubuis, A. Guisan J. Lepš, et al. 2011. Ecological assembly rules in plant communities: approaches, patterns and prospects. Biological Reviews 87:111–127.

Grant, C. 1959. Herpetology of Barbados, B.W.I. Herpetologica 15:97–101.

Harmon-Threatt, A. N., and D. D. Ackerly. 2013. Filtering across spatial scales: phylogeny, biogeography and community structure in bumble bees. PLoS ONE 8:e60446.

Helmus, T. J., J. Bland, C. K. Williams, and A. R. Ives. 2007. Phylogenetic measures of biodiversity. American Naturalist 169:E68–E83.

Hurlbert, S. H. 1984. Pseudoreplication and the design of ecological field experiments. Ecological Monographs 54:187–211.

Latella, I. M., S. Poe, and J. T. Giermakowski. 2011. Traits associated with naturalization in *Anolis* lizards: comparison of morphological, distributional, anthropogenic, and phylogenetic models. Biological Invasions 13:845–856.

Lazell, J. D. 1972. The anoles (Sauria: Iguanidae) of the Lesser Antilles. Bulletin of the Museum of Comparative Zoology 143:1–115.

Lord, J. M., J. B. Wilson, J. B. Steel, and B. J. Anderson. 2000. Community reassembly: a test using limestone grassland in New Zealand. Ecology Letters 3:213–218.

Losos, J. B. 1990. A phylogenetic analysis of character displacement in *Anolis* lizards. Evolution 44:558–569.

———. 1994. Integrative approaches to evolutionary ecology: *Anolis* lizards as model systems. Annual Review of Ecology and Systematics 25:467–493.

———. 1999. Uncertainty in the reconstruction of ancestral character states and limitations on the use of phylogenetic comparative methods. Animal Behaviour 58:1319–1324.

———. 2009. Lizards in an evolutionary tree: ecology and adaptive radiation of anoles. University of California Press, Berkeley.

Losos, J. B., and K. de Queiroz. 1997. Evolutionary consequences of ecological release in Caribbean *Anolis* lizards. Biological Journal of the Linnean Society 61:459–483.

Losos, J. B., T. R. Jackman, A. Larson, K. de Queiroz, and L. Rodríguez-Schettino. 1998. Historical contingency and determinism in replicated adaptive radiations of island lizards. Science 279:2115–2118.

Losos, J. B., M. Leal, R. E. Glor, K. de Queiroz, P. E. Hertz, L. Rodríguez-Schettino, A. Chamizo-Lara, T. R. Jackman, and A. Larson. 2003. Niche lability in the evolution of a Caribbean lizard community. Nature 424:542–545.

Losos, J. B., J. C. Marks, and T. W. Schoener. 1993. Habitat use and ecological interactions of an introduced and a native species of *Anolis* lizard on Grand Cayman, with a review of the outcomes of anole introductions. Oecologia (Berlin) 95:525–532.

MacArthur, R., and R. Levins. 1967. The limiting similarity, convergence, and divergence of coexisting species. American Naturalist 101:377–385.

Maitner, B. S., J. A. Rudgers, A. E. Dunham, and K. D. Whitney. 2011. Patterns of bird invasion are consistent with environmental filtering. Ecography 35:614–623.

Malhotra, A., and R. S. Thorpe. 1997. Microgeographic variation in scalation of *Anolis oculatus* (Dominica, West Indies): a multivariate analysis. Herpetologica 53:49–62.

Mayfield, M. M., and J. M. Levine. 2010. Opposing effects of competitive exclusion on the phylogenetic structure of communities. Ecology Letters 13:1085–1093.

Morin, P. J. 2001. Realism, precision, and generality in experimental ecology. Pages 50–70 *in* W. J. Resetarits and J. Bernardo, eds. Experimental ecology: issues and perspectives. Oxford University Press, Oxford.

Nicholson, K. E., R. E. Glor, J. J. Kolbe, A. Larson, S. B. Hedges, and J. B. Losos. 2005. Mainland colonization by island lizards. Journal of Biogeography 32:1–10.

Pimentel, D., L. Lach, R. Zuniga, and D. Morrison, D. 2000. Environmental and economic costs of nonindigenous species in the United States. BioScience 50:53–65.

Poe, S. 2014. Data from: Comparison of natural and nonnative two-species communities of *Anolis* lizards. Dryad Digital Repository. http://dx.doi.org/10.5061/dryad.dc976

Poe, S., J. T. Giermakowski, I. M. Latella, E. W. Schaad, E. P. Hulebak, and M. J. Ryan. 2011. Ancient colonization predicts recent naturalization in *Anolis* lizards. Evolution 65:1195–1202.

Powell, R., and R. W. Henderson. 2012. Island lists of West Indian amphibians and reptiles. Bulletin of the Florida Museum of Natural History 51:85–166.

Richardson, D. M., M. Rouget, and M. Rejmánek. 2004. Using natural experiments in the study of alien tree invasions: opportunities and limitations. Pages 180–201 *in* M. S. Gordon and S. M. Bartol, eds. Experimental approaches to conservation biology. University of California Press, Berkeley.

Rodríguez Schettino, L., J. B. Losos, P. E. Hertz, K. de Queiroz, A. R. Chamizo, M. Leal, and V. Rivalta González. 2010. The anoles of Soroa: aspects of their ecological relationships. Breviora 520:1–22.

Roughgarden, J. 1995. *Anolis* lizards of the Caribbean: ecology, evolution and plate tectonics. Oxford University Press, Oxford.

Sax, D. F., J. J. Stachowicz, J. H. Brown, J. F. Bruno, M. N. Dawson, S. D. Gaines, R. K. Grosberg, et al. 2007. Ecological and evolutionary insights from species invasions. Trends in Ecology and Evolution 21:465–471.

Schoener, T. W. 1969. Size patterns in West Indian *Anolis* lizards I: size and species diversity. Systematic Zoology 18:386–391.

Schoener, T. W., and G. C. Gorman. 1968. Some niche differences in three Lesser Antillean lizards of the genus *Anolis*. Ecology 49:819–830.

Schwartz, A., and R. Thomas. 1975. A checklist of West Indian amphibians and reptiles. Carnegie Museum of Natural History Special Publications 1:1–216.

Short, K. H., and K. Petren. 2011. Fine-scale genetic structure arises during range expansion of an invasive gecko. PLoS ONE 6:e26258.

Simberloff, D. 2003. Confronting introduced species: a form of xeno-phobia? Biological Invasions 5:179–192.

———. 2011. Non-natives: 141 scientists object. Nature 475:36.

Stamatakis, A. 2006. RAxML-VI-HPC: maximum likelihood-based phylogenetic analyses with thousands of taxa and mixed models. Bioinformatics 22:2688–2690.

Stone, G. N., S. Nee, and J. Felsenstein. 2011. Controlling for non-independence in comparative analysis of patterns across populations within species. Philosophical Transactions of the Royal Society B: Biological Sciences 366:1410–1424.

Thompson, K., J. G. Hodgson, and T. C. G. Rich. 1995. Native and alien invasive plants: more of the same? Ecography 18:390–402.

Vanhooydonck, B., A. Herrel, and D. J. Irschick. 2006. Out on a limb: the differential effect of substrate diameter on acceleration capacity in *Anolis* lizards. Journal of Experimental Biology 209:4515–4523.

Vining, J., M. S. Merrick, and E. A. Price. 2008. The distinction between humans and nature: human perceptions of connectedness to nature and elements of the natural and unnatural. Human Ecology Review 15:1–11.

Webb, C. O., D. D. Ackerly, and S. W. Kembel. 2008. Phylocom: software for the analysis of phylogenetic community structure and character evolution. Bioinformatics 24:2098–2100.

Weiher, E., and P. Keddy. 1999. Ecological assembly rules, perspectives, advances, retreats. Cambridge University Press, Cambridge.

Whittaker, R. J., M. B. Bush, and K. Richards. 1989. Plant recolonization and vegetation succession on the Krakatau Islands, Indonesia. Ecological Monographs 59:59–123.

Williams, E. E. 1969. The ecology of colonization as seen in zoogeography of anoline lizards on small islands. Quarterly Review of Biology 44:345–389.

———. 1972. The origin of faunas. Evolution of lizard congeners in a complex island fauna: a trial analysis. Evolutionary Biology 6:47–89.

———. 1976. West Indian anoles: a taxonomic and evolutionary summary 1. Introduction and a species list. Breviora 440:1–21.

———. 1983. Ecomorphs, faunas, island size, and diverse end points in island radiations of *Anolis*. Pages 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.

Anolis cristatellus awakened on a leaf. Photo credit: Tom Kennedy, University of New Mexico.