

Empirical test of the native–nonnative distinction: Native and nonnative assemblages of *Anolis* lizards are similar in morphology and phylogeny

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Abstract

1. Nonnative (“invasive,” “exotic,” “naturalized”) species frequently are vilified. However, some philosophers and ecologists have questioned whether nonnative species and assemblages are objectively, ahistorically identifiable as different entities relative to native species and assemblages, once selection biases are taken into account.
2. We used an unprecedented dataset of morphology, phylogeny and assemblage content for 336 species of *Anolis* lizard to compare morphological and phylogenetic characteristics of variability and central tendency between native assemblages and those that include nonnative species.
3. Equivalence tests demonstrated significant similarity between native and nonnative assemblages in trait variability, phylogenetic dispersion and mean trait values except for body size; logistic and zero-inflated regression failed to distinguish native and nonnative assemblages. For most traits, similarity was not due to assemblages being structured randomly but rather to both native and nonnative assemblages including similar species.
4. Without historical information, a naïve observer would be unable to identify *Anolis* assemblages as native or nonnative based on morphological assemblage structure or most mean assemblage trait values, but would have some success categorizing assemblages based on average body size of species in the assemblage.
5. Significant phylogenetic and morphological clustering in native assemblages likely reflects source pools composed of close relatives that share traits, as well as some environmental filtering effects; the slightly less phylogenetically clustered but equally morphologically clustered nonnative assemblages are less constrained to proximal source pools but still probably subject to filtering. Differences between native and nonnative assemblages in mean body size likely reflect assemblage youth. The ontological status of nonnative species is discussed in the light of these results.

KEYWORDS

assemblage, community, invasion, lizard, naturalized, nonnative

1 | INTRODUCTION

Debate over the ethical, economic and aesthetic status of “nonnative” species continues unabated. One view (e.g., Russel & Blackburn, 2017; Simberloff, 2011, 2013) suggests that all nonnative species should be targets of eradication due to the potential detrimental effects of these forms. Another view (e.g., Davis & Chew, 2017; Davis et al., 2011; Thompson, 2014) contends that each nonnative species should be judged based on its potential for detrimental effects. Critically for these arguments, what is considered detrimental is subjective and related to the value we place on affected entities (e.g., Dietz, Fitzgerald, & Shwom, 2005). But virtually all would agree that human health or financial loss is bad and probably most would agree that extinction of native species is undesirable. Many nonnative species are universally and, under conventional ethical standards, justifiably vilified (e.g., the Brown Tree Snake on Guam), whereas others display no apparent effects that would be considered negative and may even be considered beneficial if viewed through an objective lens (see examples in Schlaepfer, Sax, & Olden, 2011; Thompson, 2014; Pearce, 2015).

An important and understudied aspect of the nonnative species issue is frequently overshadowed by the commonly discussed cost–benefit concerns described above (where the costs and benefits may be economic or connected to other valued entities such as “biodiversity”). This aspect is the objective identification of what is considered nonnative relative to what is considered native. If a naïve conscious observer were to visit earth from another planet, could it distinguish “natural” from nonnative assemblages of species? If the distinction of these systems is impossible using objective, ahistorical means, then the status of this distinction as a basis for judgement of sets of organisms may be questioned.

We refer to the objective identification of nonnative species as “Sagoff’s question” after the philosopher Mark Sagoff, who has asked of native and nonnative systems:

Can ecologists tell which is which simply by examining the two systems and their species without knowledge of their history? Is there any biological, as distinct from historical, fact that would tip off the ecologist that he or she is studying a colonized and, in that way, corrupted or disrupted system? Sagoff (2002: 7)

The question was presented as a philosophical one, but there are biological repercussions here as well. Nonnative species are considered model systems in ecology and comparison of native and nonnative systems provides information on basic ecological processes of dispersal, establishment and community assembly (Sax et al., 2007). Nonrandom similarities between native and nonnative systems suggest some shared processes and fail to support the hypothesis of humans as agents effecting novel biological patterns. Differences are compatible with some explanatory role for human involvement (Poe, 2014), although they do not indicate human cause with any certainty. As in other areas of ecology, precise identification of shared or disparate processes of community assembly is not possible from

comparative studies of pattern alone (e.g., Gerhold, Cahill, Winter, Bartish, & Prinzing, 2015; Kraft et al., 2015), but such comparisons are a frequent and perhaps necessary starting point for understanding such processes (Levin, 1992).

Clearly, there are species cohabiting now that have not previously been sympatric. These “novel ecosystems” (Chapin & Starfield, 1997; Hobbs et al., 2006) may be taken as prima facie evidence of humans’ unprecedented alteration of the biosphere (whether such alterations are “bad” is a separate question). But ecologists are aware that many species can fill a niche, and evolutionary biologists are familiar with the phenomenon of essentially duplicate species replacing each other along some geographical gradient. In testing for true novelty in ecosystems, the appropriate question is not who is there, but rather what kinds of things are there.

The *Anolis* lizards have become an informative system for native/nonnative comparisons (e.g., Helmus et al., 2016). Twenty species of *Anolis* have established dozens of nonnative populations (Lever, 2003), and these species display a nonrandom set of characteristics (Latella, Poe, & Giermakowski, 2011). However, nonnatives share characteristics with ancient colonizers (Poe et al., 2011), and simple and probably evolutionarily recent native two-species assemblages are morphologically indistinguishable from two-species assemblages that include nonnative species (Poe, 2014). A strong ecology–morphology link has been established in *Anolis* (e.g., Calsbeek & Irschick, 2007; Collette, 1961; Losos, 1990; Rand & Williams, 1969; Williams, 1983), so although these studies do not directly address nonmorphological aspects of assemblages, their results suggest that nonnative assemblages might be ecological equivalents to native assemblages.

Here we compare the morphological and phylogenetic structure (i.e., variability, clustering, dispersion) of naturally formed assemblages of *Anolis* to the structure of assemblages that include nonnative species using simple equivalence tests and logistic and zero-inflated multiple regression. We also compare morphological central tendencies among native and nonnative assemblages. The multifaceted human invasion effects (e.g., disparate invasion sources; see Ricciardi, 2007; Table 1) might suggest an expectation of greater dispersion within nonnative assemblages. Conversely, the existence of community “assembly rules” (Diamond, 1975) would predict similarity among native and nonnative assemblages. We predict that Sagoff’s question will be answered in the negative. That is, assemblages including nonnative species will be contemporarily indistinguishable from naturally formed assemblages in spite of vastly different assembly processes (i.e., human-mediated vs. “natural”), but will display a phylogenetic (i.e., historical) fingerprint that is different from natural assemblages.

2 | MATERIALS AND METHODS

2.1 | Data

We collected four characters of morphology from one to 15 specimens of 336 species of *Anolis* (a recent study (Armstead & Poe,

2015) suggests $n = 1$ is an adequate sample size for our purposes). Body size (snout vent length, SVL) was measured from tip of snout to anterior edge of cloaca. Hindlimb length (HLL) was measured from ventral longitudinal midline laterally to knee as thigh is extended from the body at a right angle. Head length (HDL) was measured from tip of snout to anterior extent of ear opening. Size of head scales (HDS) was measured as number of scales across the snout at the level of the second canthal scales. These traits have theoretical or demonstrated functional utility for lizards. For example, head length may be related to feeding habits (e.g., Verwajen, van Damme, & Herrel, 2002), limb length correlates with microhabitat use (e.g., Irschick, 2002), scale size is related to desiccation rate (e.g., Soulé & Kerfoot, 1966), and body size affects many if not most life-history traits (e.g., Peters, 1983). Hindlimb length and head length obviously are strongly correlated with overall size, and thus, this trait was collected in units of SVL. Ratios sometimes are considered undesirable for size correction (e.g., Packard & Boardman, 1988) so many authors use residuals from linear regression on some measure of body size (e.g., body length or first principal component [PC] score or body weight) instead of our approach. However, for our data, body size ratios are nearly completely correlated with body length residuals (example shown in Supporting Information Figure S1), so we use ratios for practical reasons (e.g., it is not necessary to perform a new regression every time a new data point [species] is added).

In this study, we focus on results from individual traits, but acknowledge that composite treatments of morphology are possible (e.g., PCs, Mahalanobis distances) and favoured by some. We have reservations about using these composite measures due to known phylogenetic effects (Revell, 2009) and the difficulty with correcting for these (Uyeda, Caetano, & Pennel, 2015), as well as additional effects that indicate other biases. All such composite corrections implicitly assume constancy of trait relationships across included species, but this assumption appears clearly to be violated in the current case. For example, PC scores are vastly different when calculated separately for mainland and island species (Supporting Information Appendix S1). Furthermore, in addition to these bias issues, results from individual traits are much more easily interpretable than, for example, PC scores. Given these reservations, we believe it is more informative to present results from individual traits and interpret these in the light of expected trait correlations (with phylogeny, body size, etc.) than to present biased, uninterpretable PC scores.

We compiled a new dataset of *Anolis* species content at 167 localities with unique combinations of two to six species, including 137 “natural” assemblages and 30 assemblages that include at least one established nonnative species (Supporting Information Appendices S2 and S3). Analyses were also performed on a smaller dataset including only those 23 assemblages that are composed of at least 50% nonnative species; see below). This limit of six species was chosen because the largest nonnative assemblage includes six species, and we were concerned that inclusion of larger native assemblages might introduce biases related to the number of taxa—that is, for example, it seems likely that larger assemblages might tend towards more variance (regardless, analyses using the full dataset produced

nearly identical results to those presented here; results not shown). We have visited (i.e., “ground-truthed”) 111 of these assemblages and verified the species composition at those localities.

For comparative phylogenetic analyses, we used the Maximum Clade Credibility tree from Poe et al. (2017), pruned to include only the 336 species analysed here. To assess robustness of phylogenetic comparative results, we also analysed an additional 100 trees from the Bayesian postburnin sample of Poe et al. (2017).

2.2 | Analyses

We calculated mean values for SVL, HLL, HDL and HDS for each assemblage. We are interested in testing whether nonnative assemblages are representative of native assemblages or, to put it another way, whether native and nonnative assemblages are significantly similar. Thus, we used equivalence testing (Anderson & Hauck, 1983) to compare groups. We employ the “two one-sided tests” (TOST; Schuirmann, 1987) approach to test whether native and nonnative assemblages are surprisingly similar in mean trait values, given some hypothesized effect size. Specifically, we employ the two-group unpaired mean-equivalence t test with unequal variances, as implemented in STATA (Statacorp 2011) by Dinno (2015). We use t tests rather than a nonparametric equivalent because most of our studied distributions may be at least roughly interpreted as Normal (e.g., Figure 1) and our trials with nonparametric equivalence testing produced strange results (e.g., distributions with the same mean to two decimal places were not considered equivalent).

Selection of a hypothesized effect size for TOST, like selection of an acceptable Type I error (i.e., p -value), is a subjective endeavour. Use of a small enough null effect size will guarantee nonequivalence, and use of a large enough value will predetermine equivalence. Given the historical use of equivalence testing in pharmaceutical and then social science studies, hypothesized effect sizes traditionally have been based on acceptable levels of drug efficacy relative to some standard (e.g., a currently favoured but expensive alternative drug), feasibility concerns regarding number of human subjects, or replication of some previous study (Lakens, 2017; Rogers, Howard, & Vessey, 1993; Walker & Nowacki, 2010). To be statistically valid, a hypothesized effect size must be chosen a priori, but there are no guidelines for evolutionary or ecological studies. Presumably, researchers would prefer some value deemed ecologically significant. Here we use a hypothesized effect size of one standard deviation of the pooled (i.e., native plus nonnative assemblages) sample for each trait because this value seems to produce biologically reasonable effect thresholds and to be conservative given our goal of testing equivalence. For example, our sample of *Anolis* assemblages displays a range of mean relative limb lengths of 0.235 to 0.318 (mean 0.275, standard deviation 0.018), with means for individual *Anolis* species ranging from 0.161 to 0.380. Using the standard deviation of 0.018 as a hypothesized effect size roughly codifies a supposition that, for example, nonnative assemblages with mean relative limb lengths of 0.25 are equivalent to native assemblages with mean relative limb length of 0.26, but nonequivalent to native assemblages with mean

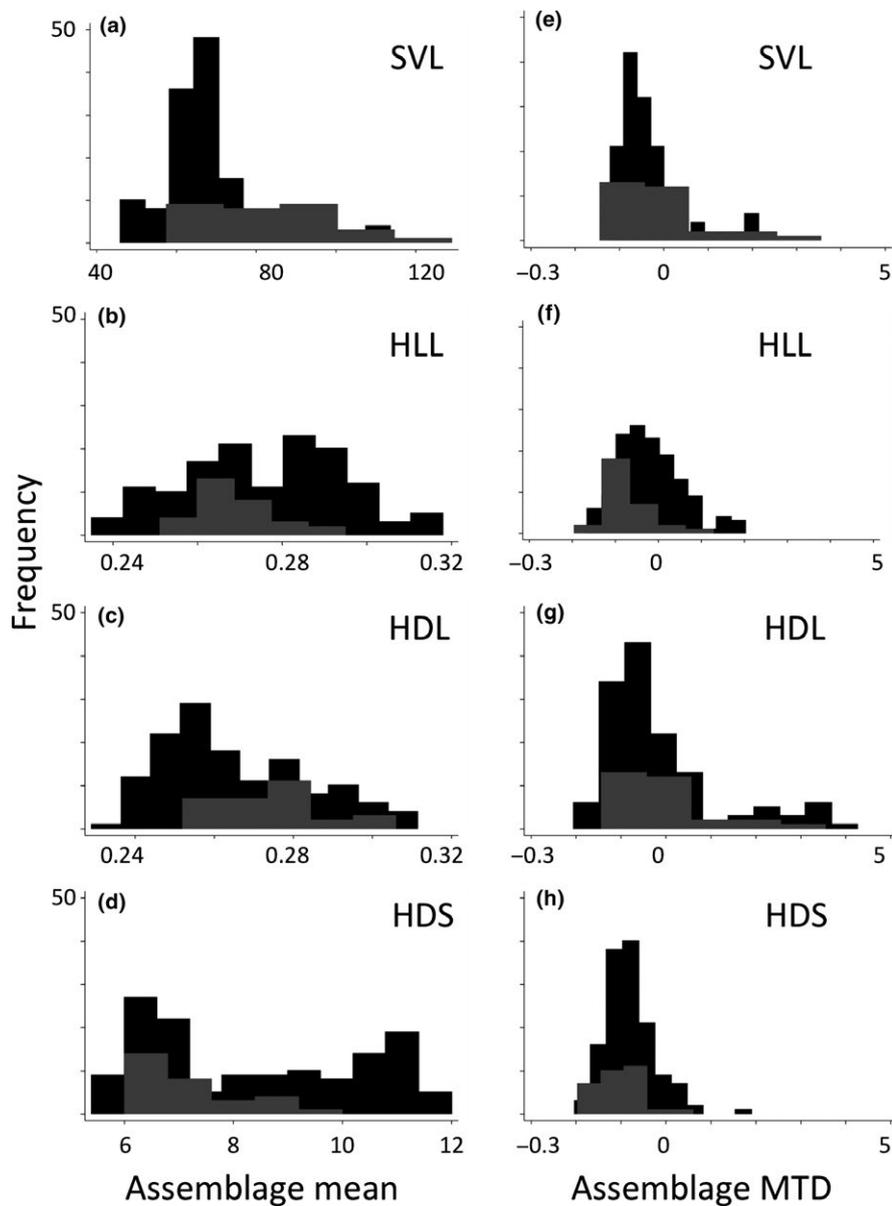


FIGURE 1 Comparison of distributions of mean (a–d) and variance (e–h; MTD) of trait values for native (black) and nonnative (grey) assemblages for four morphological traits for *Anolis*: body length (SVL), relative hindlimb length (HLL), relative head length (HDL) and head scale size (HDS)

relative limb length of 0.27. Any statistical cut-off is arbitrary, but we suspect that most ecologists would not find a difference of 0.01 limb length units to be ecologically significant in this case.

We used Phylocom (Webb, Ackerly, & Kembel, 2008) to measure the morphological and phylogenetic structure of native and nonnative assemblages. We used the mean trait distance (MTD) metric in Comtrait, which measures the dispersion of a trait within an assemblage as the mean pairwise trait distance between species in that assemblage. The significance of this value is calculated with randomization, via comparison with within-assemblage distances for 9,999 samples of the same size as the original (e.g., a value for a five-species assemblage is compared to values for equiprobable samples of five species from the analysed tree[s] including all species). We applied this test to each morphological trait for each assemblage.

We compared the mean p -value of each distribution for MTD (native and nonnative) to 0.5 using a one-sample t test. This comparison

tests whether each kind of anole assemblage (native, nonnative) tends to be overdispersed (i.e., species in an assemblage tend to be morphologically different, e.g., $p > 0.95$) or underdispersed (i.e., species in an assemblage tend to be morphologically similar, e.g., $p < 0.05$), under the assumption that if there were no trends towards over- or underdispersion among assemblages, then the distribution of p -values would be centred around 0.5.

We used the same equivalence testing approach as above to test whether trait dispersion is significantly similar between native and nonnative assemblages. We hypothesized an effect size of one standard deviation of the pooled (native and nonnative) scaled MTD (i.e., “SESMTD” in Phylocom) values for TOST analyses of each trait.

We tested for phylogenetic over- or underdispersion of *Anolis* assemblages using the mean phylogenetic distance (MPD) metric in Phylocom. This metric is the mean pairwise phylogenetic branch length distance among members of an assemblage. Significance is calculated with randomization as above. We compared distributions

of *p*-values for MPD of native and nonnative assemblages to 0.5 using a one-sample *t* test as above. We tested equivalence of native and nonnative assemblage dispersion using TOST analyses and a hypothesized effect size of one pooled standard deviation.

The above analyses ask the question: “Can distributions of native and nonnative assemblages be shown to be similar based on measured characteristics of each assemblage?” As an alternative perspective on the native–nonnative distinction, we performed logistic regression. That is, we also ask the subtly different question: “Can the nonnative status of an assemblage be predicted by characteristics of that assemblage?” We analysed the dependent variable native/nonnative with respect to candidate models of logistic regression incorporating predictor variables of dispersion (i.e., MPD) and central tendency (i.e., assemblage means) for the four morphological traits, and geography (mainland vs. island). We also analysed assemblages under zero-inflated Poisson regression using the same independent variables but a dependent variable of fraction of naturalized assemblage denizens (we checked the suitability of the Poisson–count–distribution by also coding naturalized assemblages with integers corresponding to per cent of nonnative species). We allowed all included variables in each tested model to function as potential “inflation” variables. Regression analyses were performed in STATA (StataCorp, 2011).

3 | RESULTS

Table 1 shows the results of equivalence tests of means. Nonnative assemblages were found to be significantly similar to native assemblages in mean trait values for HLL, HDS and HDL. Nonnative assemblages were not equivalent to native assemblages in SVL. In fact, nonnative assemblages include significantly larger species ($p < 0.0001$, two-sided *t* test). Results were consistent between full (i.e., 30 nonnative assemblages) and reduced (i.e., 23 nonnative assemblages with >50% nonnative species) datasets.

Table 2 shows the results of equivalence tests of trait dispersion. Nonnative assemblages were found to be significantly similar to native assemblages in trait dispersion (MTD) for all four tested traits. Results were consistent between full (i.e., 30 nonnative assemblages) and reduced (i.e., 23 nonnative assemblages with >50% nonnative species) datasets. We note that FL and SVL would be rendered nonsignificant under multiple test corrections that result in more stringent Type I error rates than 0.05. Some traits were found to be significantly clustered in native (SVL, HDL, HDS) and nonnative (HLL, HDS) assemblages; that is, assemblages tend to be clusters of morphologically similar species for these traits. No trait was found to be significantly overdispersed in either group.

TABLE 1 Results of equivalence analyses of mean trait values within assemblages, native vs. nonnative assemblages

	$P(\bar{x}_{\text{Nat}} - \bar{x}_{\text{Nonnat}} > d)$	$P(\bar{x}_{\text{Nonnat}} - \bar{x}_{\text{Nat}} > d)$	Mean, native assemblages	Mean, nonnative assemblages
SVL	<0.0001/<0.0001	0.7504/0.6090	67.63	84.16
HLL	<0.0001/<0.0001	<0.0001/<0.0001	0.28	0.27
HDL	<0.0001/<0.0001	0.0009/0.0018	0.27	0.27
HDS	0.0050/0.0035	<0.0001/<0.0001	8.40	7.19

Notes. HDL: Head length; HDS: head scale size; HLL: Hindlimb length; SVL: snout vent length. Probability (*p*) values refer to two one-sided *t* tests with hypothesized effect size *d* of one standard deviation. If both one-sided tests are significant (e.g., $p < 0.05$), then the hypothesis of a difference as large as the hypothesized effect size is rejected. According to this interpretation, all traits except SVL are equivalent between native and nonnative assemblages. Mean SVL is in millimetres; mean HLL and HDL are in units of SVL; and mean HDS is a count (see text). Values to the left of the slash show results from the full dataset; values to the right show results from reduced dataset including only those nonnative assemblages with >50% nonnative species content.

TABLE 2 Results of equivalence analyses of trait dispersion (MTD) within assemblages, native vs. nonnative assemblages

	$P(\bar{x}_{\text{Nat}} - \bar{x}_{\text{Nonnat}} > d)$	$P(\bar{x}_{\text{Nonnat}} - \bar{x}_{\text{Nat}} > d)$	Mean, native assemblages	Mean, nonnative assemblages	$P(p_{\text{Nat}} = 0.5)$	$P(p_{\text{Nonnat}} = 0.5)$
SVL	<0.0001/<0.0001	0.0373/0.0135	-0.35	0.04	<0.0001	0.7796
HLL	0.0166/0.0566	<0.0001/<0.0001	-0.17	-0.65	0.0553	<0.0001
HDL	<0.0001/<0.0001	<0.0001/<0.0001	-0.15	-0.03	0.0004	0.7445
HDS	0.0008/0.0008	<0.0001/<0.0001	-0.81	-1.02	<0.0001	<0.0001

Notes. HDS: head scale size; HLL: Hindlimb length; SVL: snout vent length. Probability ($P[\bar{x}_1 - \bar{x}_2 > d]$) values refer to two one-sided *t* tests with hypothesized effect size *d* of one standard deviation. If both one-sided tests are significant (e.g., $p < 0.05$), then the hypothesis of a difference as large as the hypothesized effect size is rejected. Means are standardized trait dispersion (MTD) values; negative values indicate underdispersion (i.e., clustering), and positive values indicate overdispersion (i.e., dissimilar species). According to this interpretation, all traits exhibit equivalent degrees of dispersion between native and nonnative assemblages. Probability ($P[p = 0.5]$) values refer to *t* test of whether distribution of *p*-values for dispersion is centred around 0.5. If significant (e.g., $p < 0.05$), then the hypothesis of no trend towards over- or underdispersion is rejected. Values to the left of the slash show results from the full dataset; values to the right show results from reduced dataset including only those nonnative assemblages with >50% nonnative species content.

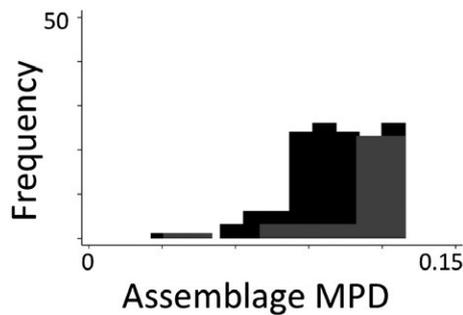


FIGURE 2 Comparison of distributions of phylogenetic dispersion for native (black) and nonnative (grey) assemblages. Larger values indicate greater phylogenetic clustering; that is, assemblages tend to be composed of close relatives

Native and nonnative assemblages were found to be equivalent in phylogenetic dispersion (TOST: $p < 0.0001/p < 0.0001$; mean, $MPD_{\text{native}} = 0.10$; mean, $MPD_{\text{nonnative}} = 0.11$; Figure 2). Native assemblages tend to be composed of close relatives ($p < 0.0001$), whereas p -values for clustering of nonnative assemblages were not significantly different from 0.5 ($p = 0.1573$). There was very little variation in MPD results across the 100 sampled postburnin trees (average standard deviation in MPD across assemblages = 0.009; Supporting Information Appendix S2).

Logistic model results are summarized in Table 3. A model including morphological dispersion (i.e., MTDs) alone was unable to predict nonnativeness of assemblages (1/30 nonnative assemblages identified as nonnative). A model including mean trait values for assemblages fared slightly better (9/30 nonnative assemblages identified correctly), as did composite models (8/30 or 13/30 correct). However, no analysed model displayed much practical utility. In general, models performed roughly as well as a hypothetical uninformative model that predicts all assemblages to be native (i.e., correct for 137/167 assemblages, 82%).

Zero-inflated model results are summarized in Table 3. All tested models are nonsignificant. That is, they are unsuccessful at predicting the fraction of nonnative content in assemblages.

4 | DISCUSSION

4.1 | Ecological interpretation

The significantly similar morphological patterns between native and nonnative assemblages may indicate that some similar community assembly/interaction processes are operating in these systems. Such an inference is by no means straightforward, as it is well-established that multiple processes may result in similar patterns of clustering (e.g., Cadotte & Tucker, 2017; Mayfield & Levine, 2010). However, the shared recent evolutionary history of the members of these systems may make an inference of similar process more palatable in this case. That is, the shared morphological/biogeographical/ecological history among members of the *Anolis* clade, and associated similarity of native and nonnative *Anolis* assemblages, seems more given to shared processes than would be two sets of assemblages from distantly related clades (comparison of lizard assemblages and bacterial assemblages, for example). Thus, it seems informative to consider the possibility of shared processes of assembly while being cognizant of the above caveats.

The standard explanation for phenotypic clustering in an assemblage, as observed in both native and nonnative assemblages, is “environmental filtering,” wherein characteristics of the environment are deemed to exclude species that lack some clustered trait(s) (e.g., Swenson et al., 2012; Weiher, Clarke, & Keddy, 1998). The soundness of this interpretation has been questioned by work demonstrating that patterns of clustering may be due to other processes such as competition (Mayfield & Levine, 2010). We note that the nonnative assemblages meet some of the criteria for filtering discussed by Kraft et al. (2015): Their constituent species became established from diverse areas (at least spatially), and they exist locally in the absence of other assemblage members (see Lever, 2003).

These aspects are harder to assess in the native case, for which biogeographical effects should be stronger and competition has long been identified as the overriding structural driver, at least in Caribbean *Anolis* assemblages (Losos, 1994). Note, for example, the

TABLE 3 Morphological, phylogenetic and geographical assemblage composition does not predict nonnative composition

Model	Logistic model			Zero-inflated model	
	ln L	Nonnative assemblages classified as nonnative	Native assemblages classified as native	Overall model accuracy	Ln L/P
Mean _{SVL} + Mean _{HDL} + Mean _{HLL} + Mean _{HDS}	-62.4	9/30	130/137	83.2%	-38.95/0.31
MTD _{SVL} + MTD _{HDL} + MTD _{HLL} + MTD _{HDS}	-71.4	1/30	135/137	81.4%	-45.48/1.00
Mean _{SVL} + Mean _{HDL} + Mean _{HLL} + Mean _{HDS} + MTD _{SVL} + MTD _{HDL} + MTD _{HLL} + MTD _{HDS}	-54.3	8/30	129/137	82.0%	-34.61/0.23
Mean _{SVL} + Mean _{HDL} + Mean _{HLL} + Mean _{HDS} + MTD _{SVL} + MTD _{HDL} + MTD _{HLL} + MTD _{HDS} + MI	-53.8	13/30	131/137	86.2%	-35.81/0.29

Notes. Ln-likelihoods and classification accuracy of logistic regression models for predicting inclusion of nonnative species in an assemblage, and ln-likelihoods and overall model significance (p -value = P) for zero-inflated Poisson model predicting fraction of nonnative species in an assemblage. Variable *MTD* measures dispersion of morphological traits within an assemblage. Variable *Mean* is mean morphological trait value within an assemblage. Variable *MI* scores whether an assemblage is found on mainland or island environments.

partitioning of habitat performed by different “ecomorphs” among *Anolis* communities of the Greater Antilles (e.g., Williams, 1983). If filtering is a shared process structuring native and nonnative assemblages, it seems likely to be operating in concert with competition, at least in native assemblages of the Caribbean.

The differences in mean SVL of nonnative assemblages relative to native assemblages likely reflects the youth of nonnative assemblages (see below). Latella et al. (2011) found large body size (among other characteristics) to be a significant predictor of naturalization. Nonnative assemblages by definition include some nonnative species, so it is not surprising that nonnative assemblages include larger species. Large body size may aid colonization by reducing desiccation and starvation, allowing consumption of a wider range of prey sizes, enabling dominance over smaller competitors and avoidance of predators, and/or reducing intersexual competition by allowing increased sexual size dimorphism (Calder, 1984; Peters, 1983).

The phylogenetic similarity between native and nonnative assemblages (Figure 2) likely reflects a combination of ecological filtering and biogeography. Phylogenetic clustering, which is strongest in native assemblages, reflects both geography and trait effects. Close phylogenetic relationship begets possession of similar traits, and some of these traits may restrict admission to a particular locality/assemblage through competition or habitat filtering (Kraft et al., 2015). Native assemblages are formed from geographically proximal species, which are likely to be close relatives. Nonnative assemblages are not so restricted, but nevertheless only certain geographically (and thus phylogenetically) restricted species have been able to become invaders (Latella et al., 2011). In particular, outside of the island-sourced mainland species *Anolis carolinensis*, only island species such as *A. sagrei* and *A. distichus* have become invaders. The geographical proximity (and thus phylogenetic nearness) of species in the source pools of native assemblages, and the geographical restriction (i.e., island forms) of nonnative forms, couples with possible habitat filtering (i.e., restriction of assemblage membership to similar species, which tend to be close relatives) to result in strong patterns of phylogenetic clustering in native assemblages and weaker but comparable phylogenetic clustering in nonnative forms. An upshot of the comparable trait-based signal and lesser geographical effect in native and nonnative assemblages is the slightly weaker phylogenetic clustering in nonnative relative to native assemblages observed here (Figure 2).

Caveatly, we note that we have examined only one clade of lizards and a tiny subset of potentially varying characteristics between native and nonnative assemblages. Aspects of behaviour and ecological malleability, as well as morphological traits we have not examined, may yet be found to distinguish native and nonnative assemblages of *Anolis* or other species. Žagar, Carretero, Vrezec, Drašler, and Kaliontzopoulou (2017) demonstrated differences in bite force and climbing speed in two morphologically similar sympatric lizard species. Future work should address whether communities at different stages of succession, including “invaded” communities that harbour nonnative species, differ in the kinds of traits that allow coexistence.

4.2 | Implications for the status of nonnative species

A prerequisite for prejudice should be the ability to distinguish the group against which the bias is directed (e.g., Simpson & Yinger, 1985). In the case of nonnative assemblages, our results show that this distinction is not straightforward. When judged by contemporary appearance alone, nonnative assemblages appear strongly to mirror native assemblages in morphological structure (Figure 1; Table 2) and most mean trait values (Figure 1; Table 1). With regard to these characteristics, Sagoff’s question is answered in the negative: A naïve observer would be unable to identify a particular assemblage or group of assemblages as native or nonnative based on morphological means or structure of its constituent species.

But nonnative assemblages tend to include larger species than native assemblages, so native and nonnative assemblages actually are distinguishable (Figure 1; Table 1). Does this result mean that Sagoff was mistaken, native and nonnative assemblages are different? This conclusion of fundamental difference between native and nonnative assemblages should be entertained as a possibility, given the results presented here.

However, we suggest that an alternative, more precise conclusion is more explanatory. We submit that perhaps “invaded” assemblages do not resemble natural assemblages in general, but rather that they resemble *young* natural assemblages (see Meiners, Rye, & Klass, 2007). That is, invaded assemblages and early-stage “natural” assemblages should be similar to each other and distinguishable from late-stage “natural” assemblages. This alternative is testable, although unfortunately not straightforwardly so with the current dataset. Testing this idea would require at least approximate dating of the formation of natural assemblages, which might be possible in some cases. For example, a lower bound on island assemblage age could be calculated based on island emergence.

Fortunately, there is evidence that bears on the idea of invaded assemblages as early-stage natural assemblages in the vast literature on succession (e.g., Bazaaz, 1996; Clements, 1916; Connell & Slatyer, 1977; Glenn-Lewin, Peet, & Veblen, 1992), including studies that address succession in the context of nonnative species (Davis, 2009; Meiners et al., 2007; Prach & Walker, 2011). For example, Meiners et al. (2007) found no difference in population dynamics of native and nonnative plants among those species common during early succession (i.e., ruderal forms) within a community. Later stages of their studied community differed from early stages in typical major ways (i.e., more woody plants, fewer short-lived herbaceous species in later stages). Taken together, these results are compatible with the idea of invaded communities being similar to early-stage natural communities but different from late-stage communities. Comparative studies of multiple communities are needed to supplement these single-community studies and address this issue generally.

The similarity of native and nonnative assemblages documented here contributes to the growing literature suggesting that there is nothing special about nonnative species and assemblages. Rates, distances and means of dispersal for species seem undeniably greater due to human transport (Simberloff, 2011),

and “invadable” environments are likely to be more common now due to humans’ agricultural activity and urban development. As in many other groups, *Anolis* lizards have been documented to invade only highly disturbed environments (Lever, 2003). Once selection biases such as a focus on “harmful” species are taken into account, the effects and behaviours of nonnative species may be indistinguishable from those of native species (Meiners et al., 2007; Vilá & Weiner, 2004).

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AUTHORS’ CONTRIBUTIONS

S.P. conceived the study, performed some of the analyses, wrote the manuscript and collected some of the data. I.M.L. collected some of the data and performed some of the analyses.

DATA ACCESSIBILITY

Data used in this article are available in Dryad Digital Repository (<https://doi.org/10.5061/dryad.2p03rn2>) and at stevenpoe.net (Poe & Latella, 2018).

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