

Traits associated with naturalization in *Anolis* lizards: comparison of morphological, distributional, anthropogenic, and phylogenetic models

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Abstract The worldwide spread of invasive species affects native biodiversity and causes economic loss, but also allows better understanding of historical biogeographic patterns. Prediction of likely invaders facilitates economic and conservation decisions and gives insight into characteristics that have allowed natural colonization over evolutionary time. However, it is not clear what types of characters best predict naturalization or even whether naturalization is predictable at all. Squamate reptiles have been understudied subjects for invasion biology. Lizards of the genus *Anolis* have been highly successful colonizers both recently and over evolutionary time. Nineteen of the approximately 350 described species of *Anolis* have established naturalized populations. We constructed models of naturalization using morphological, distributional, anthropogenic, and phylogenetic characters and compared these single character class models to each other and to a composite model incorporating all four classes. We show that (1) each class of variables significantly predicts invasion, (2) a composite model significantly outperforms each of the submodels, and (3) the final composite model displays extraordinary ability to objectively identify naturalized species of *Anolis*.

Keywords *Anolis* · Invasive species · Modeling · Naturalized · Randomization · Colonizers

Introduction

Invasive species provide important opportunities for the study of natural biogeographic processes. For example, our knowledge of the factors constraining range size, speciation, and community structure and assembly has been greatly enhanced by the study of recent biological invasions (Sax et al. 2007). Throughout evolutionary history, species have dispersed across biogeographic barriers to invade novel habitats. These natural invasions have shaped historical biodiversity patterns, just as recent invasions affect current patterns.

Many studies have sought to understand what characteristics allow some species to become successful invaders while other species, even closely related species, are unsuccessful (Mondor et al. 2007). Predicting and explaining invasiveness has been a challenging task as there are many factors both environmental and intrinsic that can affect a species' ability to invade or become naturalized. Although we occasionally refer to invasion (i.e., the spread of an established non-native species) or invaders in this paper we actually analyze naturalization (i.e., the establishment of a species outside its native range) (Richardson et al. 2000). Invasion warrants discussion

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as a greater concern than naturalization, but naturalization is easier to assess and thus more amenable to analysis, and is a necessary early stage of invasion.

Many studies have focused on morphological or other intrinsic characteristics of invaders and some have studied environmental, natural history, or phylogenetic factors (e.g. Rejmanek and Richardson 1996; Goodwin et al. 1999; Alcaraz et al. 2005; Allen 2006; Strauss et al. 2006). To our knowledge, no studies have attempted to predict naturalization by incorporating morphological, distributional, anthropogenic, and phylogenetic characters in a composite model. It is not clear which of these classes of variables best predicts naturalization or even whether naturalization is consistently predictable at all (Enserink 1999). The poor predictive ability of many naturalization models may be partially attributable to the homogeneity of variable types analyzed. Here we use a model comprised of multiple character classes in an attempt to improve predictive ability, and we compare submodels to assess the relative predictive ability of different classes of traits.

Most predictive invasion papers have focused on plants (Williamson and Fitter 1996; Lake and Leishman 2003) or birds (e.g. O'Connor 1986; Allen 2006; Hayes and Barry 2008). Few studies have focused on the prediction of naturalization in squamate reptiles.

Previously it has been shown that similarity of climate between native and introduced ranges as well as previous introduction success are significant predictors of introduction success (Bomford et al. 2009). Lizards of the genus *Anolis* are an excellent clade for studying invasion biology. One species, *Anolis sagrei*, is already a model organism for invasion biology having invaded a minimum of 7 countries (Kraus 2009) and been subject to ecological and genetic studies of invasion (Campbell and Echternacht 2003; Kolbe et al. 2004; Kolbe et al. 2007a, b; and Kolbe et al. 2008). Members of the genus *Anolis* have been highly successful colonizers. Williams (1969) hypothesized a minimum of 62 colonization events that gave rise to the current diversity of *Anolis* in the Caribbean, and 19 of approximately 350 species of *Anolis* are known to be naturalized (Lever 2003).

This study seeks to understand the factors that facilitate naturalization in the genus *Anolis*. We use a dataset of 235 species scored for morphological, distributional, anthropogenic, and phylogenetic factors to ask the following questions.

1. Are individual traits of morphological, distributional, phylogenetic, and anthropogenic factors non-randomly distributed among naturalized relative to non-naturalized species?
2. Do models employing morphological, distributional, phylogenetic, or anthropogenic variables adequately explain naturalization ability?
3. Which class, or combination of classes of the four sets of variables best explains or predicts naturalization ability?
4. Can we accurately predict naturalization of species of *Anolis*?

Materials and methods

Data

Our dataset is comprised of 235 anole species including all 19 known naturalized species. An additional five species of *Anolis* occasionally have been considered naturalized: *A. baleatus*, *A. bimaculatus*, *A. lucius*, *A. maynardi* (Kraus 2009), and *A. angusticeps*. We did not consider *A. lucius* and *A. maynardi* to be naturalized because the supposed naturalized populations are geographically proximal (i.e., *A. lucius* within 70 km of mainland Cuba on Archipelago de los Canarreos; *A. maynardi* within 20 km of Little Cayman Island on Cayman Brac) to native populations (Schwartz and Henderson 1991) and we know of no evidence to indicate these colonizations were not natural. We did not consider *A. bimaculatus* to be naturalized because we believe reports of this species as naturalized actually refer to populations assigned to *A. leachi*, which was formerly a subspecies of *A. bimaculatus*. We did not consider *A. baleatus* to be naturalized because its previously naturalized population apparently is no longer extant (Lever 2003). A 2007 web report by the Ministry of the Environment of Japan (<http://www.env.go.jp/>) discussed changing the national status of *A. angusticeps* from “Uncategorized Alien Species” to “Invasive Alien Species,” but we could obtain no further information on this case. Pending published confirmation of naturalization in this species, we currently do not consider *A. angusticeps* to be naturalized.

We used four classes of variables.

Morphological (seven variables)

We measured body length (snout to vent), head length, (from anterior edge of ear to tip of snout), and femoral length (from ventral midline to knee) of 235 species of *Anolis* ($n = 1\text{--}15$ male specimens per species). We recorded maximum male and female snout to vent length and calculated the median number of head scales across the snout between the second canthals from personal observation of 235 species of *Anolis*, Williams et al. (1995), and original species descriptions. We obtained median number of lamellae under the fourth toe and relative tail length (tail length/body length) mainly from Williams et al. (1995), supplemented by personal observations. All variables were natural-log transformed before analyses. Maximum male snout to vent length was used as a measure of body size. Sexual size dimorphism was measured as maximum female snout to vent length divided by maximum male snout to vent length. Head length, lamellae number and femur length were found to be strongly correlated with snout to vent length and so regression residuals were used in analyses. Mean head length and femur length were regressed against mean snout to vent length measured for the same specimens of each species. Median lamellae number was regressed against maximum male snout to vent length.

Distributional (four variables)

Range size (km²) was determined using the compute polygon function in Google Earth ProTM for each species using published range maps (Schwartz and Henderson 1991; Avila-Pires 1995; Johnson et al. 2001; Savage 2002; Kohler 2008, and unpublished notes from Ernest Williams). Minimum elevation estimates were determined from published sources, personal observations, and georeferenced range maps (Schwartz and Henderson 1991; Avila-Pires 1995; Johnson et al. 2001; Savage 2002; Kohler 2008, and unpublished notes from Ernest Williams). Species were coded for solitary status (present on islands with no sympatric congeners) based on Williams et al. (1995) and Losos and de Queiroz (1997). Species were classified into seven categories based on native range. The categories are North America, Puerto Rico, Jamaica, Hispaniola, Cuba, Central America, South America, and the Lesser Antilles. Table 1

shows acronyms for analyzed traits used throughout the remainder of the paper.

Phylogenetic (one variable)

We performed a parsimony analysis of data from Nicholson et al. (2005) (mitochondrial DNA, nuclear ITS DNA), 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 1,267 parsimony-informative characters scored to 52 characters for some species scored only for external morphology. This analysis resulted in 1,344 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 3 months of computer time).

In order to obtain branch lengths to measure phylogenetic distances between species, we performed a separate analysis of the mitochondrial dataset of Nicholson et al. (2005). We used the Akaike Information Criterion (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 to one of the optimal topologies obtained above with the constraint that only clocklike branchlengths were accepted and species that were not scored for mtDNA excluded. 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 used the branch lengths to measure the phylogenetic distance of each species to its closest naturalized relative.

Anthropogenic (one variable)

We coded 235 *Anolis* species for proximity to container ship ports. A species was assigned zero if its minimum elevation range is above sea-level or if its range is completely inland. A code of one indicates that a species is found on a coast away from a port or near a small port. A code of two was assigned to species with a distributional range that encompassed a large port. Port size was categorized based on the level

Table 1 Abbreviations used for traits analyzed in this paper

Abbreviation	Explanation	Category
SVL	Body length (snout to vent length)	Morphological
SSD	Sexual size dimorphism (maximum female SVL/maximum male SVL)	Morphological
HL	Head length	Morphological
FL	Femur length	Morphological
HS	Head scales (number of scales across the head between the second canthals)	Morphological
LM	Number of lamellae under the fourth toe	Morphological
TL	Relative tail length (tail length/SVL)	Morphological
RS	Range size	Distributional
EL	Minimum elevation	Distributional
SOL	Solitary status (present on islands with no sympatric congeners)	Distributional
NR	Geographic region of a species native range	Distributional
NA	Species with a native range in North America	Distributional
PR	Species with a native range in Puerto Rico	Distributional
J	Species with a native range in Jamaica	Distributional
H	Species with a native range in Hispanola	Distributional
CUBA	Species with a native range in Cuba	Distributional
CA	Species with a native range in Central America	Distributional
SA	Species with a native range in South America	Distributional
LA	Species with a native range in the Lesser Antilles	Distributional
PHY	Phylogenetic distance to closest naturalized relative	Phylogenetic
POR	Whether range encompasses a port	Anthropogenic

of annual container traffic. A port with annual traffic < 2,000 twenty foot equivalency units (TEU's) was categorized as small whereas a port with annual container traffic of > 2,000 TEU's was considered large. We obtained data for 2006 from the American Association of Port Authorities website (AAPA 2006) which provides containership data for ports throughout the Western Hemisphere.

Univariate tests for nonrandom distribution of traits among naturalized species

We calculated mean values for the 19 naturalized species for each of the seven morphological, four distributional, one anthropogenic and one phylogenetic traits. We compared these mean values to means for 1,000 equiprobable random samples of 19 species from the pool of 235. By comparing the mean values for each trait for the 19 invasive species to this null distribution, a *P* value was calculated. Randomizations were done using the program R (R Development Team Core 2008). The resulting *P* values were

corrected using a Step-up false discovery rate approach (Garcia 2004) to minimize the risk of type I errors (wrongly rejecting null hypotheses). This is a more liberal approach than a Bonferroni correction, as it does not assume all comparisons are non-significant.

Modeling naturalization

We analyzed the predictive ability of the four classes of variables separately and in a single model using logistic regression with naturalization (naturalized:1, not:0) as the dependent variable. We analyzed models incorporating all (referred to as FULL; 19 parameters, see below), morphological (MORPH; seven parameters), distributional (DIST; 11 parameters, including geography as a composite variable of seven parameters and a range × geography interaction), anthropogenic (ANTH; one parameter), and phylogenetic (PHYLO; one parameter) variables. The interaction of range with geography was modeled by multiplying a species range size by its presence

(multiplied by 1) or absence (multiplied by 0) on a large landmass (Greater Antillean or mainland) by range size. We checked variables for colinearity by treating each independent variable as a dependent variable and regressing the remaining variables against the tested variable in multiple regression. One pair of parameters was found to be problematic: EL and POR were correlated. We still analyzed each of these parameters in its own submodel (Distributional and Anthropogenic, respectively) but omitted EL from analyses including all parameters, i.e. analyses of model FULL.

We first reduced each model using a backwards-stepwise procedure. For each of the reduced models (FULL and four submodels) we started with a maximally parameterized model and then removed individual parameters sequentially according to which parameter caused the smallest decrease in likelihood. We stopped this procedure when removal of any remaining parameter caused a significant decrease in likelihood according to a likelihood ratio test. The seven parameters describing geography were treated jointly in this procedure (Sokal and Rohlf 1995). That is, if any one of the geographic parameters was significant then all seven were retained in the model during that step. The statistical bases of stepwise model selection procedures such as this one have been criticized (e.g., Whittingham et al. 2006). Like other authors (Hallstan et al. 2010 and Fenesi and Botta-Dukát 2010 and Marco et al. 2010), we continue to use such approaches due to the lack of an objective and rigorous alternative method for reducing overparameterized models.

We compared submodels to each other and to the full model using the Akaike Information Criterion (AIC), which favors models with the lowest score of $2k - 2\ln(\text{likelihood})$, where $k = \#$ of parameters.

We assessed predictive ability of all models using R^2 values and classification tables. We consider the reduced FULL model to be the best overall predictor of invasive ability.

Results

Univariate randomization tests

Seven variables were found to be significantly associated with naturalized species, including three

morphological variables (SVL, SSD, HS), two distributional variables (EL, NR), and each of the phylogenetic and anthropogenic variables (Table 3).

Modeling naturalization

Modeling results are summarized in Table 4.

Six parameters dropped out during stepwise regression of the model based on morphological parameters, leaving a final model including one parameter:

$$N_{MORPH} = -8.30(SSD) - 4.10 \quad (1)$$

The final model of distributional parameters employed eight of the original eleven parameters including the composite geographic parameter:

$$\begin{aligned} N_{DIST} = & -69.74 + 33.96(NA) - 8.98(SA) \\ & + 29.81(PR) + 32.04(J) + 25.71(HISP) \\ & + 22.44(CUBA) + 69.45(LA) \\ & + 4.01(R * G) \end{aligned} \quad (2)$$

The Phylogenetic and Anthropogenic models each significantly predicted naturalization:

$$N_{PHYL} = -0.28 - 5.00(PHY) \quad (3)$$

$$N_{ANTH} = -3.63 + 0.99(POR) \quad (4)$$

The final Full model includes Distributional and Morphological variables:

$$\begin{aligned} N_{FULL} = & -128.62 + 31.98(NA) + 43.14(PR) \\ & + 45.63(J) + 34.17(H) + 28.50(CUBA) \\ & + 114.93(LA) + 7.45(R * G) \\ & + 3.02(SVL) \end{aligned} \quad (5)$$

We present a ranking of *Anolis* species according to their fit to the model, i.e. their naturalization ability (Table 2).

Discussion

Role of morphological variables

We were able to identify three morphological characters significantly correlated with naturalization ability in *Anolis*. Maximum male SVL of naturalized species was found to be significantly large. Snout to vent length correlates with head length with larger

Table 2 Species naturalization rank based on the reduced full model

Species	Score	Rank	Species	Score	Rank	Species	Score	Rank
<i>carolinensis</i>	165.0	1	<i>tropidogaster</i>	123.5	81	<i>anchicayae</i>	89.5	161
<i>cybotes</i>	147.3	2	<i>monticola</i>	123.2	82	<i>pachypus</i>	89.4	162
<i>richardi</i>	146.0	3	<i>pentaprion</i>	122.9	83	<i>macrolepis</i>	88.5	163
<i>griseus</i>	145.9	4	<i>nebulosus</i>	122.8	84	<i>antoni</i>	88.4	164
<i>chlorocyanus</i>	145.8	5	<i>capito</i>	122.8	85	<i>liogaster</i>	88.4	165
<i>semilineatus</i>	145.7	6	<i>meridionalis</i>	122.2	86	<i>jacare</i>	86.6	166
<i>garmani</i>	145.7	7	<i>bremeri</i>	121.0	87	<i>anisolepis</i>	86.3	167
<i>equestris</i>	145.6	8	<i>vermiculatus</i>	120.9	88	<i>cristifer</i>	85.8	168
<i>bimaculatus</i>	145.6	9	<i>etheridgei</i>	120.9	89	<i>altae</i>	85.8	169
<i>ferreus</i>	145.5	10	<i>tropidonotus</i>	120.9	90	<i>tropidolepis</i>	84.7	170
<i>leachi</i>	145.3	11	<i>alumina</i>	120.8	91	<i>tolimensis</i>	84.6	171
<i>sagrei</i>	145.3	12	<i>rodriguezi</i>	120.0	92	<i>apollinaris</i>	83.2	172
<i>oculatus</i>	144.8	13	<i>websteri</i>	119.9	93	<i>smintus</i>	83.0	173
<i>valencienni</i>	144.8	14	<i>bahorucoensis</i>	119.4	94	<i>aequatorialis</i>	82.7	174
<i>luciae</i>	144.7	15	<i>jubar</i>	119.3	95	<i>breedlovei</i>	81.9	175
<i>roquet</i>	144.5	16	<i>paternus</i>	119.1	96	<i>mariarum</i>	81.8	176
<i>cristatellus</i>	144.5	17	<i>singularis</i>	118.9	97	<i>kemptoni</i>	80.9	177
<i>marmoratus</i>	144.4	18	<i>mestrei</i>	118.8	98	<i>nicefori</i>	79.6	178
<i>extremus</i>	144.4	19	<i>frenatus</i>	118.5	99	<i>fraseri</i>	78.8	179
<i>lividus</i>	144.4	20	<i>limifrons</i>	118.0	100	<i>boettgeri</i>	78.7	180
<i>porcatus</i>	144.3	21	<i>cyanopleurus</i>	117.5	101	<i>fungosus</i>	78.3	181
<i>nubilis</i>	144.3	22	<i>baracoae</i>	117.2	102	<i>ventrimaculatus</i>	78.1	182
<i>aeneus</i>	144.2	23	<i>cupreus</i>	115.6	103	<i>omiltemanus</i>	77.8	183
<i>trinitatus</i>	144.0	24	<i>transversalis</i>	114.8	104	<i>reconditus</i>	75.7	184
<i>grahami</i>	144.0	25	<i>poncencis</i>	113.1	105	<i>roosevelti</i>	74.6	185
<i>lineatus</i>	144.0	26	<i>insignis</i>	112.8	106	<i>conspersus</i>	74.6	186
<i>homolechis</i>	144.0	27	<i>cupeyalensis</i>	112.1	107	<i>ernestwilliamsi</i>	72.6	187
<i>chamaeleonides</i>	144.0	28	<i>longitibialis</i>	111.8	108	<i>maculigula</i>	72.2	188
<i>gingivinus</i>	144.0	29	<i>vittigerus</i>	111.5	109	<i>cooki</i>	72.2	189
<i>lineatopus</i>	143.9	30	<i>fowleri</i>	111.5	110	<i>acutus</i>	72.0	190
<i>bonairensis</i>	143.9	31	<i>petersi</i>	111.0	111	<i>fitchi</i>	71.6	191
<i>sabanus</i>	143.8	32	<i>uniformis</i>	111.0	112	<i>desechensis</i>	71.5	192
<i>olssoni</i>	143.7	33	<i>caudalis</i>	110.9	113	<i>peraccae</i>	71.3	193
<i>allogus</i>	143.7	34	<i>insolitus</i>	110.8	114	<i>ruizi</i>	70.0	194
<i>wattsi</i>	143.3	35	<i>brasiliensis</i>	110.1	115	<i>nigropunctatus</i>	68.0	195
<i>angusticeps</i>	143.2	36	<i>rubribarbus</i>	109.8	116	<i>solitarius</i>	64.6	196
<i>gundlachi</i>	143.2	37	<i>spectrum</i>	109.8	117	<i>eugenegrahami</i>	63.2	197
<i>stratulus</i>	143.2	38	<i>poecilopus</i>	109.7	118	<i>monensis</i>	62.5	198
<i>opalinus</i>	143.1	39	<i>marcanoi</i>	109.7	119	<i>altavelensis</i>	62.2	199
<i>distichus</i>	143.0	40	<i>humilis</i>	109.6	120	<i>marron</i>	62.1	200
<i>pulchellus</i>	143.0	41	<i>scypheus</i>	108.5	121	<i>placidus</i>	61.9	201
<i>ricordi</i>	142.9	42	<i>crassulus</i>	108.5	122	<i>rimarum</i>	61.8	202
<i>pogus</i>	142.9	43	<i>shrevei</i>	108.0	123	<i>sheplani</i>	61.5	203
<i>schwartzi</i>	142.8	44	<i>quadriocellifer</i>	107.9	124	<i>koopmani</i>	61.4	204

Table 2 continued

Species	Score	Rank	Species	Score	Rank	Species	Score	Rank
<i>lucius</i>	142.5	45	<i>barkeri</i>	107.5	125	<i>guamuhaya</i>	60.0	205
<i>krugi</i>	142.4	46	<i>barbatus</i>	106.9	126	<i>longiceps</i>	58.0	206
<i>baleatus</i>	142.3	47	<i>carpenteri</i>	106.6	127	<i>brunneus</i>	57.7	207
<i>ophiolepis</i>	142.3	48	<i>auratus</i>	106.3	128	<i>scriptus</i>	57.7	208
<i>alutaceus</i>	142.2	49	<i>rejectus</i>	105.8	129	<i>maynardi</i>	57.7	209
<i>allisoni</i>	139.5	50	<i>strahmi</i>	105.7	130	<i>luteosignifer</i>	56.7	210
<i>pumilus</i>	136.3	51	<i>trachyderma</i>	105.0	131	<i>clivicola</i>	56.4	211
<i>cuvieri</i>	136.3	52	<i>rupinae</i>	104.9	132	<i>guazuma</i>	56.3	212
<i>evermanni</i>	136.2	53	<i>lionotus</i>	104.8	133	<i>vanidicus</i>	55.7	213
<i>aliniger</i>	135.9	54	<i>nitens</i>	104.1	134	<i>concolor</i>	29.4	214
<i>coelestinus</i>	135.5	55	<i>squamulatus</i>	103.8	135	<i>gadovi</i>	29.4	215
<i>argillaceus</i>	134.6	56	<i>laeviventris</i>	101.5	136	<i>taylori</i>	29.3	216
<i>argenteolus</i>	134.3	57	<i>ahli</i>	101.2	137	<i>nelsoni</i>	29.0	217
<i>brevirostris</i>	133.7	58	<i>bartschi</i>	100.2	138	<i>cuprinus</i>	28.9	218
<i>luteogularis</i>	133.7	59	<i>quercorum</i>	100.2	139	<i>vociferans</i>	28.3	219
<i>isolepis</i>	133.4	60	<i>heterodermus</i>	99.8	140	<i>villai</i>	28.2	220
<i>christophei</i>	133.3	61	<i>polylepis</i>	98.1	141	<i>parvicirculatus</i>	28.2	221
<i>barbouri</i>	132.6	62	<i>microtus</i>	98.1	142	<i>magnaphallus</i>	28.1	222
<i>porcus</i>	131.5	63	<i>chrysolepis</i>	97.3	143	<i>megapholidotus</i>	28.1	223
<i>occultus</i>	131.0	64	<i>bombiceps</i>	96.3	144	<i>pinchoti</i>	28.1	224
<i>biporcatus</i>	129.6	65	<i>woodi</i>	95.8	145	<i>fortunensis</i>	27.8	225
<i>centralis</i>	129.6	66	<i>maculiventris</i>	95.7	146	<i>townsendi</i>	27.8	226
<i>punctatus</i>	129.4	67	<i>latifrons</i>	95.6	147	<i>agassizi</i>	14.6	227
<i>armouri</i>	129.3	68	<i>chloris</i>	95.5	148	<i>soinii</i>	13.3	228
<i>fuscoauratus</i>	128.2	69	<i>fasciatus</i>	95.1	149	<i>gemmosus</i>	12.7	229
<i>whitemani</i>	128.1	70	<i>subocularis</i>	95.0	150	<i>williamsmittermeierorum</i>	12.7	230
<i>smallwoodi</i>	126.8	71	<i>aquaticus</i>	94.8	151	<i>lynchi</i>	12.5	231
<i>ortonii</i>	126.5	72	<i>festae</i>	94.3	152	<i>cuscoensis</i>	12.3	232
<i>sericeus</i>	126.1	73	<i>bitectus</i>	94.1	153	<i>menta</i>	12.2	233
<i>lemurinus</i>	125.9	74	<i>granuliceps</i>	93.8	154	<i>new sp.1</i>	12.2	234
<i>smaragdinus</i>	125.8	75	<i>lyra</i>	93.0	155	<i>medemi</i>	11.9	235
<i>loysianus</i>	125.5	76	<i>dollfusianus</i>	93.0	156			
<i>hendersoni</i>	124.4	77	<i>dunni</i>	90.9	157			
<i>noblei</i>	124.3	78	<i>notopholis</i>	90.8	158			
<i>barahonae</i>	124.2	79	<i>huilae</i>	90.5	159			
<i>dolichocephalus</i>	124.2	80	<i>gracilipes</i>	90.4	160			

Currently naturalized species are denoted by boldface type

species able to consume a wider range of prey sizes (Schoener and Gorman 1968), which may allow them easier access to a greater diversity of new habitats. Larger species also may better tolerate dispersal, as smaller species are likely to be more susceptible to desiccation, starvation, and predation.

The mean number of scales across the snout at the second canthal (HS) was significantly fewer in number among naturalized species, indicating larger scale size. Malhotra and Thorpe (1991) suggest that scale size may play a role in desiccation tolerance, a character that may directly benefit a species in long-distance

Table 3 Results of univariate analyses

Characters of naturalized species	<i>P</i> value	Explanation
SVL	0.001*	Naturalized <i>Anolis</i> possess greater SVL
SSD	0.001*	Naturalized <i>Anolis</i> possess greater SSD
HL	0.057	
FL	0.533	
HS	0.008*	Naturalized <i>Anolis</i> possess fewer scales across the snout
LM	0.034	
TL	0.820	
RS	0.620	
SOL	0.120	
ME	0.001*	Naturalized <i>Anolis</i> are native to lower elevations
NR	0.001*	Naturalized <i>Anolis</i> are native to few geographic areas
PHY	0.001*	Naturalized <i>Anolis</i> are clustered on the phylogeny
POR	0.003*	Naturalized <i>Anolis</i> are more likely to have a range encompassing a port

* Indicates significance using Step-up false discovery rate approach

dispersal. Larger scales may play a role in reducing interscale water loss (Horton 1972). Brown and Thorpe (1991) showed this to be the case in an island lizard *Chalcides sexlineatus*, with higher scale counts in mesic areas and the lowest number in the most arid regions.

Sexual size dimorphism was shown to be greater in naturalized species. Schoener (1969) suggested that increased SSD allows solitary species to partition available resources among sexes, a benefit that may also be useful in establishment in a new environment. Colonizing species may become established more easily if males and females are not competing intraspecifically for resources that may be extremely limited in the initial colonizing environment.

These morphological traits may be significant individually, as discussed above, or they may be indicative of a generalized morphological type that is conducive to colonization (or a phylogenetic trend; see below). This latter inference is supported by the preponderance of Trunk-Crown and Trunk-Ground ecomorphs among naturalized species (these are two of the six specialized ecological/morphological types identified by Williams 1983 and Losos et al. 2006, designations for each species were obtained from Losos 2009). All of the naturalized species analyzed here that have been categorized ecomorphologically are either Trunk-Crown or Trunk-Ground ($P = 0.0033$; $n = 102$; Mann–Whitney U Test comparing

naturalized versus non-naturalized species with all species grouped as either Trunk-Crown/Trunk-Ground or Other).

Role of distribution

Naturalized species are disproportionately found at lower elevations (Table 3). All 19 naturalized species have a minimum elevational occurrence of sea level. The explanation for this occurrence may be anthropogenic (see below) or natural. That is, species that are able to live in lowland (i.e., coastal) areas may be more suited to invade new habitats that are more likely to be lowland rather than higher elevation due to accessibility for dispersing waifs.

Geography plays a role in species' naturalization ability (Table 3). A disproportionate number of naturalized species have native ranges in the Lesser Antilles. Nine of 19 (47%) naturalized species are from the Lesser Antilles whereas only 22/235 (9%) of all anoles in our dataset are native to the Lesser Antilles. This region may be an arena where invasion attempts are so frequent due to proximity to potential source islands that current species are likely to have evolved to be superlative colonizers (Poe et al., in review). Surviving Lesser Antillean species are adept at colonization, repellance of attempted invaders, and establishment in a homogeneous (due to small geographic size) and climatically capricious (due to

Table 4 Comparison of models

Model type	Number of parameters total/reduced	Likelihood	P value	R ²	Classification ability		
					% Naturalized correct	% All correct	AIC
Phylogenetic	1/1	-55.99	<0.0001	0.152	0	91.91	113.98
Morphological	7/1	-53.39	<0.0001	0.191	10.53	92.34	108.786
Distributional	11/8*	-30.10	<0.0001	0.544	15.79	92.77	76.203
Anthropogenic	1/1	-60.59	0.001	0.082	0	91.91	123.18
Full	20/9*	-26.216	<0.0001	0.603	47.37	93.62	70.432

Parameter counts marked with (*) consider geography to include seven parameters (see text)

hurricanes and resulting effects) area. All of these traits would be useful in modern colonization.

Role of anthropogenic factors

Naturalized species were more likely to have a range encompassing a major port than non-naturalized species, suggesting that human action may play a role in the introduction of naturalized *Anolis*. This result is congruent with the conclusion of Zabin et al. (2007) who suggested that vessel traffic played a key role in the spread of the invasive barnacle *Chthamalus proteus* to Hawaii. Jeschke and Strayer (2006) showed that association with humans is generally a strong determinant of invasion success in North American and European vertebrates (fish, mammals, and birds).

Role of phylogeny

The phylogenetic distribution of invasive species has been shown to be nonrandom in plants (Pyšek 1998; Richardson and Rejmánek 2004), Iberian fish (Alcaraz et al. 2005) and birds (Lockwood 1999; Blackburn and Duncan 2001). Closely related species tend to be similar in traits (Felsenstein 1985), including morphology and life history traits that may be conducive to naturalization. Clearly, some clades of *Anolis* such as the South American Phenacosaur and Cuban Chamaeleolis lack the great naturalization capacity of clades such as the *bimaculatus* and *roquet* series.

The nonrandom phylogenetic distribution of naturalized anoles suggests that phylogeny is a composite predictor of naturalization. Like other biological traits, each of the traits analyzed in this paper is nonindependent of phylogeny. Thus, our above discussions of the potential invasive value of

morphological, distributional, and anthropogenic factors in isolation are necessarily speculative—at least some and potentially most of the nonrandomly distributed traits (Table 3) may have little to do with invasion and rather may simply be phylogenetically (or otherwise) correlated with invasive traits. We allowed phylogeny to compete with other parameters for explanatory power via the PHY parameter in order to assess which parameters are most valuable for predicting naturalization (Jiang et al. 2010). This approach does not address the separate question of which parameters are causal and which are correlative.

Comparison of models

Each of the submodels adequately explains the data in the sense that each class of variables includes at least one significant predictor of naturalization. However there is great variability in relative explanatory status of the models according to the AIC (Table 4). Among submodels, Distribution is the clear favorite for predicting naturalization. This result is likely due to the evolutionarily selective environment shaping evolution in ways that are not tracked by the other variables in our analyses. As discussed above, the small-island and/or solitary environments may be conducive to invasion. If an analysis is restricted to a particular class of variables, it seems that distributional variables are preferable to predict naturalization, at least in this case.

The final composite model includes both distributional and morphological parameters and has a better AIC than all submodels. This result demonstrates the value of analyzing multiple character classes in predicting invasion. Many previous attempts to predict invasion have been based on a single class

of variables, often morphological (to assess inherent tendency for invasion) (Rejmanek and Richardson 1996) or phylogenetic (as a composite measure of invasiveness) (Strauss et al. 2006). Our results show that naturalization success in *Anolis* is correlated with each class of variables, but not well predicted by any of them individually. When multiple classes of variables are analyzed together, better predictive ability is evident. Although the performance of some classes of characters might be improved by inclusion of additional parameters (e.g., one can imagine other ways to code for human influence), the superior performance of the composite model is not merely due to its greater number of parameters. The AIC results, which account for number of parameters, clearly favor the composite model (Table 4) and comparisons involving more extensively parameterized submodels are still significantly worse than composite models according to the AIC and likelihood ratio tests (results not shown).

The composite model

The predictive model in this study is a useful tool for identifying the most likely future invasive species in the genus *Anolis*. Identification of likely invaders is the first step in making informed conservation and economic management decisions. This information may also help drive policy decisions seeking to mitigate the economic damages incurred by these species and their concurrent spread once naturalized.

Our final model displays extraordinary ability to objectively identify naturalized species of *Anolis*. Based on only geography, a single morphological character (SVL), and an interaction term (see above), all 19 invasive *Anolis* are among the top 40 (of 235) predicted invaders. The most likely future invaders include any large species that are widespread in large landmasses or present in the Lesser Antilles. *Anolis griseus*, a large Lesser Antillean species, *A. semilineatus*, a widespread Hispaniolan form, and *A. bimaculatus*, a large Lesser Antillean species whose sometime subspecies (*A. [bimaculatus] leachi*) has already become naturalized, are predicted to be among the next to become naturalized (Table 2). The final verdict on the utility of our model will be made over the next several years when we will be able to document whether the expected colonizers fulfill their destiny.

Conclusions

Prediction or explanation of which species are able to become naturalized is a challenging task, and no single class of variables has been shown to display special predictive ability across taxa. We studied morphological, distributional, phylogenetic, and anthropogenic models and found that each displays statistically significant predictivity of naturalization in *Anolis* lizards. However, a composite model outperforms these submodels and ranks all nineteen naturalized species among the top 40 predicted invaders. Future predictive studies may benefit from using a diversity of variable classes rather than focusing on single-variable class models.

Squamate reptiles have been understudied subjects in invasion biology. *Anolis* lizards are a model system for research in evolution and ecology, and two species of *Anolis* (*A. sagrei*, *A. carolinensis*) are well-studied invaders (e.g., Campbell and Echternacht 2003; Kolbe et al. 2004). We have shown that naturalization in *Anolis* lizards may be predicted using a simple logistic model. Perhaps naturalization of reptile species is as predictable as naturalization in more obvious invaders such as vagile birds, hermaphroditic plants and oceanic barnacles. Future studies should assess the naturalization capabilities of still less likely reptile invaders such as crocodylians and snakes.

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