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Criag R. Allen
*University of Nebraska-Lincoln*, callen3@unl.edu

Kristine T. Nemec
*University of Nebraska-Lincoln*, kristine.nemec@huskers.unl.edu

Donald A. Wardwell
*University of Nebraska-Lincoln*

Justin D. Hoffman
*University of Nebraska-Lincoln*, jhoffman@mcneese.edu

Mathew L. Brust
*University of Nebraska-Lincoln*, mbrust@csc.edu

*See next page for additional authors*

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## RESEARCH PAPER

# Predictors of regional establishment success and spread of introduced non-indigenous vertebrates

Craig R. Allen[1], Kristine T. Nemec[2]*, Donald A. Wardwell[2], Justin D. Hoffman[4]†, Mathew Brust[3], Karie L. Decker[2], Daniel Fogell[4], Jennifer Hogue[4], Aaron Lotz[2], Thaddeus Miller[2], Marcy Pummill[4], Luis E. Ramirez-Yañez[4] and Daniel R. Uden[2]

[1]*US Geological Survey-Nebraska Cooperative Fish and Wildlife Research Unit, 423 Hardin Hall, University of Nebraska–Lincoln, Lincoln, NE 68583, USA,* [2]*Nebraska Cooperative Fish and Wildlife Research Unit, 422 Hardin Hall, University of Nebraska–Lincoln, Lincoln, NE 68583, USA,* [3]*Department of Entomology, University of Nebraska–Lincoln, Lincoln, NE 68583, USA,* [4]*School of Natural Resources, University of Nebraska–Lincoln, Lincoln, NE 68583, USA*

## ABSTRACT

**Aim** To provide the first analysis of predictors of both establishment and spread, both within and across taxa, for all vertebrate taxa within a region. We used Florida, USA, as our study system because it has a well-documented history of introduction and invasion, and is a hotspot for biological invasions.

**Location** Florida, USA.

**Methods** We analysed non-indigenous species (NIS) data from peninsular Florida – which included both successful and unsuccessful introductions from all vertebrate classes – to determine the best predictors of both establishment and spread for fish (65 species), herpetofauna (63 species), birds (71 species) and mammals (25 species). We used 10 variables proposed to be associated with the establishment and spread of NIS: body mass, geographic origin, reproductive rate, diet generalism, native-range size, latitude of native range, number of NIS present at date of introduction, presence of NIS congeners, morphological proximity to other NIS (in terms of body mass) and propagule pressure. A multimodel selection process was used with an information-theoretic approach to determine the best fit models for predicting establishment and spread of NIS. We selected a priori plausible predictive models for establishment and spread.

**Results** Large native-range size and small body mass best predicted establishment of non-indigenous herpetofauna. The presence of NIS congeners had the largest positive effect on the establishment of non-indigenous fish. For mammals, the number of NIS present at the time of introduction best explained establishment. No single model best explained bird establishment. For all taxa but birds, the number of NIS present at time of introduction was included in at least one of the best-supported models for explaining spread.

**Main conclusions** Our analyses suggest that predictors of establishment and spread differ across vertebrate taxa at the scale studied. Most predictive variables can be interpreted as measures of competitive interactions among species.

*Correspondence: Kristine T. Nemec, Nebraska Fish and Wildlife Cooperative Research Unit, 422 Hardin Hall, University of Nebraska–Lincoln, Lincoln, NE 68583, USA. E-mail: kristine.nemec@huskers.unl.edu †Present address: Department of Biological and Health Sciences, McNeese State University, Lake Charles, LA 70609, USA.

## INTRODUCTION

Humans have facilitated biological invasions by accidentally or intentionally transporting animals, plants and microorganisms into new areas (Mack *et al.*, 2000; Cox, 2004). During the past century, the number of human-assisted invasions has increased by orders of magnitude, and invasive species have become globally widespread, coinciding with increases in the speed and volume of human transportation as well as anthropogenic transformation of native habitats (Mack *et al.*, 2000; Ruiz & Carlton, 2003). Non-indigenous species (NIS) may negatively affect native species by disrupting food webs, modifying habitats and competing with native species (Manchester & Bullock, 2000; Kats & Ferrer, 2003; Pimentel *et al.*, 2005). As a result, biodiversity may decline and some native species may become extinct (Clavero *et al.*, 2009).

The invasion process consists of four stages (Blackburn *et al.*, 2011a). A species must first be transported outside of its native range, it must then be released or escape, it must reproduce and establish a viable population and finally it must spread beyond the original point of introduction (transport, introduction, establishment and spread). Ecologists have made considerable efforts to determine why some NIS become established, while others fail to do so. Identifying a limited number of variables that explain establishment success and spread in NIS can potentially increase the effectiveness of management of NIS (Simberloff, 2009). The objective of this study is to provide the first analysis of predictors of both establishment and spread, both within and across taxa, for all vertebrate taxa within a region.

Several variables have been associated with the establishment of NIS, including body size (Allen *et al.*, 1999; Cassey, 2001; Kolar & Lodge, 2001; Hayes & Barry, 2008), migratory behaviour (Kolar & Lodge, 2001; Cassey *et al.*, 2004a; Hayes & Barry, 2008), phylogeny (Lockwood, 1999; Cassey, 2001), geographic origin and range size (Blackburn & Duncan, 2001; Duncan *et al.*, 2001; Kolar & Lodge, 2001; Hayes & Barry, 2008), behavioural and ecological flexibility (Sol *et al.*, 2005, 2008) and abiotic factors (Moyle & Light, 1996; Blackburn & Duncan, 2001). Many studies suggest that predictor variables differ across species and communities (e.g. Forys & Allen, 1999; Miller *et al.*, 2002; Allen, 2006). Only propagule pressure (the number of introduced individuals from a species and the frequency of introduction events; Lockwood *et al.*, 2005), climatically suitable habitat and history of establishment success or invasive success (spreading once established) have consistently proven to be significant predictors of establishment (Duncan *et al.*, 2001; Forsyth & Duncan, 2001; Kolar & Lodge, 2001; Cassey *et al.*, 2004b; Lockwood *et al.*, 2005; Hayes & Barry, 2008; Bomford *et al.*, 2009; Aikio *et al.*, 2012), although we cannot know how many analyses with non-significant results were never published.

Once established, some NIS fail to spread beyond the introduction site, whereas others spread aggressively over broad and heterogeneous geographic areas. Determining which species are likely to spread may also be crucial to controlling invasions. However, the few studies focusing on this part of the invasion process have suggested that different factors affect spread. For example, Holway (1998) suggested that abiotic suitability of the invaded community governs the rate of spread in Argentine ants. Duncan *et al.* (2001) and Forsyth *et al.* (2004) attributed the spread of introduced birds and mammals in Australia to small body size, high reproductive rate, large native range size and large area of climatically suitable habitat.

For vertebrates in general, few studies have included analyses of establishment success or spread among multiple taxa (Allen *et al.*, 1999; Forys & Allen, 1999; Duncan *et al.*, 2001; Forsyth & Duncan, 2001; Forsyth *et al.*, 2004; Jeschke & Strayer, 2005; Arim *et al.*, 2006) and none have focused on all vertebrate classes within a given region. In order to fill this gap in knowledge of the invasion process, we used a study system of introductions of NIS in peninsular Florida, including unsuccessful introductions, from all vertebrate taxa (fish, herpetofauna, birds and mammals) to determine the best predictors of the third and fourth stages of the invasion process: establishment and spread. Florida provides a unique study system because it is a highly invaded, continental community with a non-indigenous fauna that has been well-documented (Semmens *et al.*, 2004; Stohlgren *et al.*, 2006; Blackburn & Cassey, 2007; Krysko *et al.*, 2011). Florida has at least 111 established non-native species, or about 6% of the total number of native vertebrates (S. Hardin, Florida Fish and Wildlife Commission, Tallahassee, Florida, pers. comm.). We analysed data for NIS from peninsular Florida to determine the best predictors of both establishment and spread, using 10 variables proposed to be associated with the establishment and spread of NIS: body mass, geographic origin, reproductive rate, diet generalism, native-range size, latitude of native range, number of NIS present at date of introduction (NSP), presence of NIS congeners, morphological proximity to other NIS (in terms of body mass) and propagule pressure.

## METHODS

### Data on NIS

We compiled lists of species introduced, intentionally or inadvertently, into peninsular Florida for each vertebrate taxon. We included species with known propagules of at least five individuals, species known to have bred in peninsular Florida and/or species observed for at least five consecutive years in the wild. We defined peninsular Florida as all counties east of the Apalachicola River. Appendices S1–S4 in the Supporting Information include the NIS lists for fish, herpetofauna, birds and mammals and the sources of introduction, spread, establishment and life-history information for each taxon. Species introduced after the year 2000, or with numerical estimates of propagule sizes of fewer than five individuals, were not included. These restrictions account for time lags that may occur after an initial introduction and for minimum population sizes necessary for potential reproduction and establishment.

### Variables

Non-indigenous vertebrates known to be reproducing in Florida were designated as successfully established. We measured spread

for each established species by determining the number of counties in which they were present (see Appendices S1–S4). Spread values ranged from 1 to 57, the total number of counties in peninsular Florida.

Data were collected for 10 variables proposed to be associated with the establishment and spread of NIS: body mass ($\log_{10}$), geographic origin, reproductive rate, diet generalism, native range size, latitude of native range, NSP, presence of NIS congeners, morphological proximity (in terms of body mass) to other NIS and propagule pressure.

### Body mass

The mean body masses of birds and mammals were obtained from published sources (see Appendices S3 and S4). In cases where only ranges of body mass were available, the median value was used. Male and female body masses were averaged.

Most estimates of herpetofauna body mass were acquired from published sources (see Appendix S2). However, some body masses (*Anolis extremus*, *Anolis ferreus*, *Anolis porcatus*, *Basiliscus plumifrons* and *Cnemidophorus motaguae*) were estimated from snout–vent lengths using regressions of known weights and the snout–vent lengths of closely related and similarly sized species. In some cases, only adult male body mass data were available.

We used maximum mass in lieu of mean mass for most fish species, because this information was more readily available (Froese & Pauly, 2006). For some species, body masses were not available and were calculated from the maximum lengths (Froese & Pauly, 2006) of morphologically and behaviourally similar congeners using the von Bertalanffy growth equation (Wootton, 1998):

$$W_t = W_\infty \{1 - \exp[K(t - t_0)]\}^3.$$

In cases where an appropriate congener was not available, a morphologically and behaviourally similar species from the same family was used for comparison (see Appendix S1).

### Geographic origin

Geographic origin refers to a species' native continent. We collected origin data and combined some of the continents into single categories to maintain relatively equal numbers of observations in each category (see Appendices S1–S4). The categories used were Africa, Eurasia (Europe and Asia), North America, South America and Australia.

### Reproductive rate

We measured reproductive rate as the average number of young or eggs produced annually. Reproductive rates were gathered from published sources for herpetofauna, birds and mammals (see Appendices S2–S4). Fish reproduction data were gathered mostly from FishBase (Thorpe *et al.*, 2003; Froese & Pauly, 2006). Because fish typically produce substantially more eggs or young per year than terrestrial vertebrates, we adjusted the fish reproduction data by two orders of magnitude for all analyses. In cases where reproduction data were not available, we estimated the rate with congeners or confamiliars.

### Diet generalism

The variable diet generalism quantified the types of food items in a species' diet. We gathered the data from published sources for fish, herpetofauna, birds and mammals (see Appendices S1–S4). Congeners and confamiliars were used to estimate the number of diet categories of species for which we were unable to find published data. We used the Saunders & Ingram (1995) diet classification to determine generalism in birds and mammals. We created diet classifications a priori for herpetofauna and fish because the food groups consumed by these taxa are different from those of birds and mammals.

Herpetofauna diets were classified into 12 categories: (1) vegetation; (2) fruit; (3) nectar; (4) arthropods; (5) molluscs; (6) mammals; (7) birds; (8) reptiles; (9) amphibians; (10) fish; (11) bird/reptile eggs; and (12) insect eggs. Fish diets were classified into 11 categories: (1) detritus; (2) phytoplankton; (3) zooplankton; (4) finfish; (5) insects; (6) crustaceans; (7) worms; (8) plant matter; (9) molluscs; (10) terrestrial/surface insects; and (11) terrestrial vertebrates.

### Native range size, latitude of native range

We acquired native ranges of NIS for fish, herpetofauna, birds and mammals (see Appendices S1–S4). For some feral or cosmopolitan mammal species [i.e. feral dog (*Canis familiaris*), feral cat (*Felis catus*), feral goat (*Capra hircus*), Norway rat (*Rattus norvegicus*), black rat (*Rattus rattus*) and house mouse (*Mus musculus*)], maps depicting their native range prior to domestication or introduction were not available. In those cases, we used general descriptions of native ranges to produce estimates. We redrew the geographic range of each species on a 21.6 cm × 27.9 cm map of the globe which was overlaid with a 1-cm$^2$ grid. We counted the numbers of cells occupied to obtain an estimate of native range size. We determined the latitude of each species from the centre of their native range and measured as degrees from the equator.

### NSP, morphological proximity to other NIS and presence of NIS congeners

We sorted lists of introduced species chronologically to determine the number of NIS present at date of introduction (NSP), morphological proximity to other NIS and the presence of NIS congeners at the time of introduction. NSP is a count of the number of established within-taxon NIS present at the time of a species' introduction. For example, the first introduced bird species has a NSP of 0, while a bird species introduced in 1955 has an NSP equal to the number of established birds introduced prior to 1955. Species introduced in the same year received the same NSP value, because we could not determine which species

was introduced first. Morphological proximity is the difference between a NIS and its closest NIS neighbour (in terms of $\log_{10}$-transformed body mass). Nearest neighbours included only previously introduced and established NIS. Presence of congeners is a binomial variable, in which non-indigenous members of the same genus were either present or absent. Congeners were considered present when an established NIS had been introduced the same year before the species in question.

*Propagule pressure*

We created numerical estimates of propagule pressure for fish and birds by consulting the US Geological Survey Nonindigenous Aquatic Species Database and references therein (USGS, 2005) for fish and a variety of references as listed in Appendix S3 for birds. Propagule pressure may be defined as the composite measure of the number of invasive individuals released into a region to which they are not native (Lockwood *et al.*, 2005). For each species for which population estimates were available, the total number of individuals that had been recorded in peninsular Florida from date of introduction until 2001 was used as the estimate for propagule pressure. There was not enough numerical information on propagule pressure for herpetofauna and mammals to include these species in the data analysis.

## Data analysis

We used a multimodel selection process, with an information-theoretic approach for the analyses to determine the best fit models for predicting establishment and the subsequent spread of non-indigenous fishes, herpetofauna, birds and mammals. Multimodel inference should be useful in analysing establishment and spread of NIS because these phenomena are complex, multiple hypotheses are plausible and predictors can be tested in combination (Stephens *et al.*, 2005). We selected a priori plausible predictive models for establishment and spread (Table 1) including a null model which predicts that establishment and spread are random with respect to all variables. These models were based on a literature review suggesting the importance of the 10 variables described above. We took a parsimonious approach and kept our models as simple as possible. All models were compared with one another using the corrected Akaike information criterion ($AIC_c$) which considers both model fit and complexity. We used $AIC_c$ rather than AIC because $n/K$ was less than 40 (Burnham & Anderson, 2002). The model with the lowest $AIC_c$ value is considered the 'best' fit model (Burnham & Anderson, 2002). Models that have a difference of less than two between their AIC values are the best-supported models (denoted by $\Delta AIC_c$) (Burnham & Anderson, 2002). Additionally, we calculated model weights ($\omega$) for each model, which indicate the weight of evidence for a model compared with the rest of the models (Burnham & Anderson, 2002). Model average estimates (MAE) and associated standard errors (SE) were calculated for each variable in all $AIC_c$ analyses using equations from Burnham & Anderson (2002). This allowed us to determine the importance of each variable to predict establishment and spread of NIS.

We performed a logistic regression analysis in R to determine which models were the best predictors of establishment (R Development Core Team, 2012). Logistic regression was appropriate for this analysis because establishment is a binary variable. To analyse the spread of NIS, we fit linear models in R (R Development Core Team, 2012). $R^2$ values are reported for the establishment and spread models (Nagelkerke's $R^2$, the output of the R program for logistic regression, is reported for establishment models). We included propagule pressure for models involving birds and fish, the two taxa for which we had sufficient propagule information for data analysis. Including propagule pressure provided more information about a parameter with the potential to explain establishment or spread, but also resulted in lowering our degrees of freedom for the bird and fish models.

## RESULTS

### Numbers of introduced species

Most documented introductions of vertebrate species into peninsular Florida before 2001 were birds, followed by fish, herpetofauna and mammals (Fig. 1, Appendices S1–S4). Many bird and fish species belonged to families popular in the pet trade. Twenty-nine (41%) of the introduced bird species were from the family Psittacidae (true parrots), which are popular pets in Florida, and 44 (68%) of the introduced fish belonged to the four families that make up most of the popular aquarium fish sold in pet supply stores (Cichlidae, Cyprinidae, Poeciliidae and Characidae; Duggan *et al.*, 2006).

### Establishment

Herpetofauna had the highest proportion of introduced species becoming established (78.8%), followed by birds, mammals and fish (Fig. 1, Appendices S1–S4). The confidence set, or the set of best models for explaining establishment with $\Delta AIC_c$ of two or less, for herpetofauna consisted of one model (Table 2). The best fit model indicated that herpetofauna with a smaller body mass and larger native range were more likely to establish. For mammals, the number of species present at the time of introduction was the only model in the confidence set, and success decreased with an increase in NSP (Table 2). For fish, data supported two models, which included the parameters presence of congeners and Eurasia as the geographic origin (Table 2). Species with congeners present were more likely to be successful, and those originating from Eurasia were less likely to be successful. The confidence set of supported models for bird introduction success was large, and model weights were all < 0.14 (Table 2). For birds, diet generalism and native range size appeared in more than one supported model. When all taxa were combined into a single analysis predicting success, models containing diet generalism and native range size had the most support (Table 2).

### Spread

Our results did not support the 'tens' rule (Williamson, 1996), which states that approximately 10% of introductions will be

**Table 1** Models used in corrected Akaike information criterion ($AIC_c$) analyses to determine best fits of establishment and spread of non-indigenous vertebrates (fish, herpetofauna, birds, mammals, and a combined all-taxa analysis) in Florida. Shaded cells indicate the parameters included within each model.

| Parameter | Models | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 | 21 | 22 | 23 | 24 | 25 | 26 | 27 | 28 | 29 | 30 | 31 |
| NULL | ■ | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| ALL (all of the parameters below) | | ■ | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| Africa geographic origin | | | | ■ | ■ | ■ | | | | | | | | | | | | | | | | | | | | | ■ | | | | |
| Australia geographic origin† | | | ■ | ■ | ■ | ■ | | | | | | | | | | | | | | | | | | | | | | ■ | | | |
| Eurasia geographic origin | | | ■ | ■ | ■ | ■ | | | | | | | | | | | | | | | | | | | | | | | ■ | | |
| North America geographic origin | | | ■ | ■ | ■ | ■ | | | | | | | | | | | | | | | | | | | | | | | | ■ | |
| South America geographic origin | | | ■ | ■ | | | | | | | | | | | | | | | | | | | | | | | | | | | ■ |
| Presence of NIS congeners (Cong) | | | | ■ | | | ■ | ■ | ■ | ■ | ■ | ■ | | | | | | | | | | | ■ | | | | | | | | |
| Diet generalism (General) | | | | ■ | | | ■ | ■ | | | | | | | | | | | | | | | | ■ | | | | | | | |
| Latitude of native range (Lat) | | | | | | | | | | | | | | ■ | ■ | | | | | | | | | ■ | | | | | | | |
| Body mass (Mass) | | | | | | | | | | | | ■ | ■ | | | | | | | | ■ | | | | ■ | | | | | | |
| Morphological proximity to other NIS (Morph) | | | | ■ | | | | | | ■ | ■ | | | | | | | ■ | | | | | | | | | | | | | |
| Number of NIS present at date of introduction (NSP) | | | ■ | | | | | | | | | | | | ■ | ■ | | | | | | | | | | | | | | | |
| Propagule size (Prop)* | | | | | | | | | | | | | | | | ■ | | | | | | | | | | ■ | | | | | |
| Reproductive rate (Repro) | | | | | | ■ | | | | | | | | | | | | | | | | | | | | | ■ | | | | |
| Native range size (Range) | | | ■ | | | | | ■ | ■ | | ■ | | | | | | | | ■ | | | | ■ | | | | | | | | |

NIS, non-indigenous species.

*Included only for fish, bird and all-taxa establishment and spread models.

†Included only for bird and all-taxa establishment and spread models.
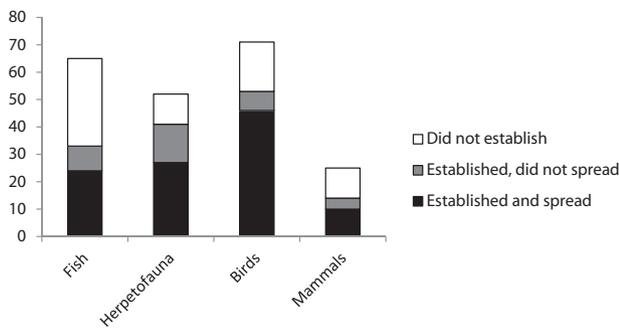
**Figure 1** Number of species belonging to each taxon that were introduced in peninsular Florida before 2001, further divided into the number of species that did not establish, established but did not spread, and established and spread beyond their county of introduction.

successful and 10% of successful introductions will be invasive. Other studies have also rejected this hypothesis for vertebrates, finding higher levels of establishment and spread than 10% (e.g. Jeschke & Strayer, 2005; White *et al.*, 2008; Kraus, 2009). We found that when a species had the potential to establish, that is when at least five individuals were introduced, 51–79% of introductions within a taxon established, and that 66–87% of established species within a taxon spread beyond the county into which they were introduced, with the highest proportion recorded for birds (Fig. 1, Appendices S1–S4). NSP, either alone or in combination with other variables, was predictive of spread for fish, herpetofauna and mammals, with species introduced when the number of NIS was lower being more likely to spread (Table 3).

For fish, four models were supported, NIS from Africa, NSP, latitude of native range, and the null model; NSP and latitude had a negative impact on spread (Table 3). The spread of non-indigenous herpetofauna was best explained by two models that

**Table 2** Best models for explaining establishment of non-indigenous vertebrates with ΔAICc of 2.000 or less. Models are ranked by their associated corrected Akaike information criterion (AIC$_c$) values, and include the number of parameters ($K$), differences in AIC$_c$ between each model and the highest ranked model (ΔAIC$_c$), AIC$_c$ weights (ω) and parameter estimates [model averaged estimate (MAE) ± standard error; average estimates where the parameter is included in more than one model in the confidence set].

| Model | $K$ | AIC$_c$ | ΔAIC$_c$ | ω | $R^2$ |
|---|---|---|---|---|---|
| (a) Fish | | | | | |
| Cong | 2 | 61.58 | 0.00 | 0.23 | 0.1381 |
| Eurasia | 2 | 63.45 | 1.87 | 0.09 | 0.0889 |
| MAE | Intercept 0.45 ± 0.44; Cong 2.03 ± 1.01; Eurasia −1.30 ± 0.74 | | | | |
| (b) Herpetofauna (does not include propagule information – insufficient sample size) | | | | | |
| Mass + Range | 3 | 78.21 | 0.00 | 0.49 | 0.1969 |
| MAE | Intercept 1.06 ± 0.53; Mass −0.58 ± 0.27; Range 0.030 ± 0.013 | | | | |
| (c) Birds | | | | | |
| General + Range | 3 | 59.12 | 0.00 | 0.13 | 0.1452 |
| General | 2 | 59.75 | 0.63 | 0.10 | 0.0678 |
| Null | 1 | 59.98 | 0.86 | 0.09 | < 0.0000 |
| Range | 2 | 60.72 | 1.60 | 0.06 | 0.0407 |
| NSP | 2 | 60.83 | 1.71 | 0.06 | 0.0378 |
| Australia | 2 | 60.95 | 1.83 | 0.05 | 0.0344 |
| South America | 2 | 61.05 | 1.93 | 0.05 | 0.0315 |
| MAE | Intercept 1.50 ± 0.96; General −0.60 ± 0.36; Range 0.0046 ± 0.0036; NSP 0.025 ± 0.022; Australia 15.55 ± 1696.73; South America −0.68 ± 0.66 | | | | |
| (d) Mammals (does not include propagule information – insufficient sample size) | | | | | |
| NSP | 2 | 30.03 | 0.00 | 0.63 | 0.3347 |
| MAE | Intercept 1.23 ± 0.23; NSP −0.58 ± 0.018 | | | | |
| (e) All taxa | | | | | |
| General + Range | 3 | 150.21 | 0.000 | 0.33 | 0.1079 |
| General | 2 | 151.70 | 1.490 | 0.16 | 0.0687 |
| MAE | Intercept 1.40 ± 0.51; General −0.33 ± 0.14; Range 0.0043 ± 0.0026 | | | | |

Australia, Australian geographic origin; Cong, presence of non-indigenous species congeners; Eurasia, Eurasian geographic origin; General, diet generalism; Mass, body mass; NSP, number of non-indigenous species present at date of introduction; Range, native range size; South America, South American geographic origin.

**Table 3** Best models for explaining spread of non-indigenous vertebrates with ΔAIC$_c$ of 2.000 or less. Models are ranked by their associated corrected Akaike information criterion (AIC$_c$) values, and include the number of parameters ($K$), differences in AIC$_c$ between each model and the highest ranked model (ΔAIC$_c$), AIC$_c$ weights (ω) and parameter estimates (model averaged estimate (MAE) ± standard error; average estimates where the parameter is included in more than one model in the confidence set).

| Model | $K$ | AIC$_c$ | ΔAIC$_c$ | ω | $R^2$ |
|---|---|---|---|---|---|
| (a)  Fish | | | | | |
| Africa | 3 | 284.67 | 0.00 | 0.15 | 0.043 |
| NSP | 3 | 285.25 | 0.57 | 0.11 | 0.031 |
| Null | 2 | 285.51 | 0.84 | 0.10 | 0.000 |
| Lat | 3 | 285.75 | 1.08 | 0.09 | 0.021 |
| MAE | Intercept 3.77 ± 1.32; Africa 3.22 ± 1.83; NSP −0.10 ± 0.066; Lat −0.072 ± 0.051 | | | | |
| (b)  Herpetofauna (does not include propagule information – insufficient sample size) | | | | | |
| Mass + Morph | 4 | 431.21 | 0.00 | 0.60 | 0.223 |
| Morph + NSP + Mass + Cong | 6 | 432.52 | 1.31 | 0.31 | 0.240 |
| MAE | Intercept 8.97 ± 2.45; Mass −3.24 ± 0.89; Morph 12.86 ± 4.41; NSP −0.16 ± 0.098; Cong −0.53 ± 2.01 | | | | |
| (c)  Birds | | | | | |
| Prop + Repro + Mass | 5 | 437.38 | 0.00 | 0.46 | 0.229 |
| Repro | 3 | 439.29 | 1.91 | 0.18 | 0.156 |
| MAE | Intercept 9.86 ± 8.42; Prop 0.0088 ± 0.0041; Repro 1.64 ± 0.50; Mass −4.76 ± 3.30; | | | | |
| (d)  Mammals (does not include propagule information – insufficient sample size) | | | | | |
| NSP + Morph + Cong | 5 | 219.62 | 0.00 | 0.48 | 0.483 |
| MAE | Intercept 18.71 ± 12.91; NSP −1.39 ± 0.87; Morph 28.79 ± 13.25; Cong 28.04 ± 10.84 | | | | |
| (e)  All taxa | | | | | |
| General + Range | 4 | 945.13 | 0.00 | 0.26 | 0.0795 |
| Lat + Range + Eurasia + Africa + South America+ North America + Australia | 8 | 946.02 | 0.89 | 0.17 | 0.109 |
| Mass + Range | 4 | 946.68 | 1.55 | 0.12 | 0.0673 |
| Range | 3 | 946.73 | 1.60 | 0.12 | 0.0580 |
| MAE | Intercept 12.66 ± 9.81; General −1.59 ± 0.83; Range 0.032 ± 0.012; Lat 0.16 ± 0.14; Eurasia −29.88 ± 9.49; Africa −25.77 ± 9.86; South America −23.41 ± 9.45; North America −26.82 ± 9.62; Australia cannot estimate due to small sample size | | | | |

Africa, African geographic origin; Australia, Australian geographic origin; Cong, presence of non-indigenous species congeners; Eurasia, Eurasian geographic origin; General, diet generalism; Lat, latitude of native range; Mass, body mass; Morph, morphological proximity to other non-indigenous species; North America, North American geographic origin; NSP, number of non-indigenous species present at date of introduction; Prop, propagule size; Range, native range size; Repro, reproductive rate; South America, South American geographic origin.

included the parameters body mass, morphological proximity to other NIS, presence of congeners and NSP; all parameters except for morphological proximity had a negative impact on spread (Table 3). Two models including propagule pressure, body mass and reproduction rate were supported for the spread of birds; reproductive output and propagule pressure were positively associated with spread, and body mass size was negatively associated with spread (Table 3). The confidence set for mammals included one model with three variables, NSP, morphological proximity to other NIS and presence of NIS congeners (Table 3). Morphological proximity and presence of NIS congeners were positively associated with spread of mammals while NSP was negatively associated with spread.

When all taxa are combined and analysed four models were supported, containing the variables diet generalism, native range size, each of the five countries of geographic origin, and body mass (Table 3). Native range size was the only variable present in each of the models.

## DISCUSSION

Despite the number of plausible invasion-success hypotheses proposed by ecologists, the use of multimodel selection in testing predictors of establishment has been limited. We believe this approach has great promise for sifting amongst the broad number of competing hypotheses that have been generated in

the young field of invasion biology. For both introduction success and spread, supported models tended to be different for the different taxa analysed. While the combined taxa analysis for establishment reflected the two top models supported for birds, the combined taxa analysis for spread did not clearly reflect the best models for any one individual taxon.

No single variable emerged as being important for explaining introduction success across taxa. Interestingly, the presence of congeners has a positive effect on success for fish and the spread of mammals, but a negative effect on the spread of herpetofauna. Other studies have reported both positive and negative relationships between presence of congeners and establishment. For example, similar results were found by Tingley *et al.* (2011) for amphibian species world-wide, with the probability of successful establishment increasing when congeneric species were present at an introduction site. In contrast, a meta-analysis of fish invasions in 12 regions throughout the world found the presence of native congeners was not a significant predictor of establishment (Ricciardi & Mottiar, 2006). It is possible that NIS may share more life-history traits with established NIS congeners than with native congeners, explaining the strong relationship that was found in our study for fish.

Two parameters, large native-range size and small body mass, explained success of herpetofauna. Species having larger native ranges were more likely to be successful. Duncan *et al.* (2001) found that larger native ranges of birds increase the likelihood of introduction success in Australia. Species with larger native ranges may be more generalist in their habitat use and resource acquisition than species with smaller ranges, enabling them to adapt more readily to new environments (Brown, 1995). Species with larger native ranges may also be more likely to be introduced than species with smaller ranges (Blackburn & Duncan, 2001; Jeschke & Strayer, 2006). Additionally, body mass was included with native range size in the best model for explaining establishment of herpetofauna, with species of smaller body masses being more likely to establish. Small habitat patches, such as those that occur in urban environments, can support greater numbers of small herpetofauna species compared to large species, making it more likely that smaller species can successfully reproduce and establish (Rodda & Tyrrell, 2008).

The seven best-supported models for introduction success of birds in peninsular Florida included the null model. This suggests that none of the variables or models included in our analysis was an especially important predictor of introduction success for non-indigenous birds in peninsular Florida. Allen (2006) examined non-native birds in south Florida and determined that many of the same variables that we employed in our analysis were not significant predictors of introduction success. The only significant predictors of success were distance to nearest neighbour (in terms of body mass) and distance to body-mass aggregation edge. Our work and that of Allen (2006) are consistent in rejecting many variables as predictors of non-native bird establishment in Florida. We did not include distance to body-mass aggregation edge in our analysis, and our measurement of morphological proximity is only determined for NIS, while Allen (2006) includes morphological proximity to native birds. These differences may

explain the disparity in the selection of the null model in our study and the results of Allen (2006).

For introduced mammals, the number of non-indigenous species present (NSP) at the time of introduction was the only supported model for introduction success in peninsular Florida. The earliest species introduced, when fewer other non-native species are present, were more likely to be successful. This suggests a priority effect as documented in other taxa at other locations (Moulton, 1993). Early mammal introductions into Florida, such as the feral pig (*Sus scrofa*), feral cat and house mouse, have been highly successful. Most of the species introduced prior to the 20th century have subsequently spread to the entire state. These early invaders may appear to be more successful because they consist of obvious species that have had more time to be documented, or NIS arriving in Florida may have first occupied niches that had not been filled by other NIS. However, as mammal introductions increased over time, the mammal community may have become saturated.

A combination of factors was responsible for spread within individual taxa, but one variable, NSP, was supported in the confidence sets for all taxa except birds. Species introduced when fewer NIS were present spread more, possibly because of less competition with other aggressive species. NSP may be interpreted as a priority effect, whereby species introduced earlier interacted with fewer species and experienced less competition, and therefore spread into a unsaturated community more successfully (Moulton, 1993).

While propagule pressure has consistently been found to be a significant predictor of establishment in other studies, in our study propagule pressure only appeared once in a best-supported model, the best model explaining spread of birds, along with high reproduction rate and small body mass size. Larger propagule pressure was associated with a greater likelihood of spread. Other studies have found a positive relationship between propagule pressure and establishment of birds (Duncan *et al.*, 2001; Forsyth & Duncan, 2001; Blackburn *et al.*, 2011b). However, the universality of propagule pressure as a factor in establishment has been questioned by Moulton *et al.* (2011) who argued that it has largely arisen from studies on a taxon within a single region, New Zealand birds. The relationship between propagule pressure for other taxa such as fish and stages of the invasion process has received comparatively little attention (García-Berthou, 2007). Our results could largely be attributed to several bird species that had a large propagule size (> 100) and became widespread in peninsular Florida, occurring in all 57 counties, including the budgerigar (*Melopsittacus undulatus*) and common starling (*Sturnus vulgaris*). Because there are no native Florida members of the families to which the budgerigar (family Psittacidae) and common starling (family Sturnidae) belong, lack of competition with confamiliars may have enhanced the spread of these species.

## CONCLUSIONS

Research evaluating the factors that predict both establishment and subsequent spread of NIS is limited, and that research has

been restricted to birds and mammals in Australia (Duncan *et al.*, 2001; Forsyth *et al.*, 2004). In those studies, climatically suitable habitat, propagule pressure and previous successful introductions outside of Australia predicted establishment in both birds and mammals. Spread for both groups was predicted by climatically suitable habitat, large native range size and variables associated with increased growth rates (e.g. smaller body mass). Non-herbivorous mammals were also more likely to spread (Forsyth *et al.*, 2004). Our results differ in that explanatory variables best predicting both establishment and spread differed within each taxon, although the variables were consistently associated with factors reflecting competitive interactions. Other studies have found the factors influencing establishment to differ among both taxa and regions (Kolar & Lodge, 2002; Hayes & Barry, 2008). Differing results may be obtained because stages of the invasion process may be affected not only by the biological characteristics of species within a taxon but also by the physical characteristics of the ecosystem to which a species is introduced (Bomford *et al.*, 2009; Lapointe & Light, 2012) and the spatial scale at which a study is conducted (Blanchet *et al.*, 2009). Establishment and spread of invasive species may therefore differ among regions because of differences in the spatial scale of the region studied and regional differences in climate, geology and native vegetation (Moulton *et al.*, 2011). The relative level of human density and infrastructure associated with human development may also play a role in affecting invasion establishment and spread and deserves further attention (Strubbe & Matthysen, 2009; Florance *et al.*, 2011). The Florida landscape contains a higher density of people and urban development than larger regions which have been studied, such as Australia and New Zealand, which may affect the factors that lead to greater establishment and success in the species introduced into Florida. For example, small body size is advantageous for colonizing and reproducing in the small habitat patches characteristic of urban habitats, and in our study small body size was found to be important for establishment of herpetofauna in Florida. Because of the potential for regional differences in invasion processes, additional research should be conducted on a wider variety of taxa in regions such as Africa and Asia that have been subjected to relatively little invasion research (Pyšek *et al.*, 2008) before determining whether it is appropriate to draw broad conclusions about the factors that influence establishment and spread in vertebrate taxa.

There are limitations on which variables were included in our analyses. For example, introduction effort plays an important role in the establishment of most non-indigenous species (Duncan *et al.*, 2001; Forsyth & Duncan, 2001; Kolar & Lodge, 2001; Cassey *et al.*, 2004b); however, it was impossible to provide accurate measures of introduction effort for all species in each taxon. We were able to estimate introduction effort, or propagule pressure, for 73% of the fish species and 72% of the bird species in our data set but did not have estimates for enough herpetofauna or mammal species to analyse propagule pressure for these taxa. Also, we assumed the number of counties containing NIS was an accurate measure of spread. However, this does not account for species that may have been introduced on

multiple occasions or at multiple locations. Introduction data are limited, especially for unsuccessful and inadvertent introductions, so we were unable to incorporate multiple attempts or release points in our analysis.

Future research should focus on these complex interactions and should implement analytical methods designed to simultaneously consider multiple plausible hypotheses. Attempts should be made to sift among the varying influences of intrinsic traits, community characteristics and ecosystem structures that affect invasion success. Similarly, research should include multiple taxa, systems and relationships between indigenous and non-indigenous species. Establishment and spread should be jointly investigated using the same study communities; few studies (Duncan *et al.*, 2001; Forsyth *et al.*, 2004) have taken this approach. Insight gained from these types of analyses may prove invaluable to community ecology and invasion biology. Discovering the role that competitive interactions among species have in invasions should be formally addressed in order to help improve NIS management, potentially saving governments billions of dollars and preserving biodiversity.

## ACKNOWLEDGEMENTS

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## SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's web-site.

**Appendix S1** Fish introduced into peninsular Florida before 2001.
**Appendix S2** Herpetofauna introduced into peninsular Florida before 2001.
**Appendix S3** Birds introduced into peninsular Florida before 2001.
**Appendix S4** Mammals introduced into peninsular Florida before 2001.

### BIOSKETCH

**Craig Allen** received his PhD in wildlife ecology and conservation from the University of Florida in 1997. His research focuses on the relationships between invasions, extinctions and landscape change, and upon understanding resilience in complex systems of people and nature.

Author contributions: C.R.A. conceived the ideas; M.B., K.L.D., D.F., J.D.H., J.H., A.L., T.M., M.P., L.E.R.-Y. and D.A.W. collected the data; C.R.A., D.R.U. and D.A.W. analysed the data; and C.R.A. and K.T.N. led the writing.

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