Global Analysis of Factors Affecting the Outcome of Freshwater Fish Introductions

JENNIFER L. RUESINK

Department of Biology, University of Washington, Box 351800, Seattle, WA 98195-1800, U.S.A., email ruesink@u.washington.edu

Abstract: *As humans move species around the globe, biotic homogenization decreases diversity. It is therefore crucial to understand factors influencing invasion success at a global scale. I analyzed factors predicting establishment of freshwater fishes transferred internationally, based on 1424 cases of first introductions from one country to another as reported in FishBase, an encyclopedic database of finfish biology. I used multiple logistic regression to explore four classes of predictor variables: species traits, environmental traits, match between species and environment, and propagule pressure. The best regression model, selected by Akaike's information criterion, included four factors that explained variation in establishment of 789 cases for which complete information was available. Establishment was higher for fishes in families with small body size and for omnivores. Establishment rose with endemism of the recipient country's fish fauna. Species were more likely to establish when humans intended their establishment (384/506 = 76%) rather than when fish were cultivated or used with no explicit desire for naturalization (524/918 = 57%). Three factors proved unrelated to establishment: latitudinal difference between countries of origin and introduction, native species richness of the recipient country (adjusted for area), and date of first introduction. Classification-tree analysis correctly classified (success vs. failure) 60% of 789 cases, based on the same predictor variables as in multiple logistic regression. My significant results reinforce current ideas that invasion risk is high for rapidly reproducing, generalist species introduced into isolated environments. The success of intentional introductions implies that higher propagule pressure generates riskier invasions. Both models were tested by applying them to 445 cases not used for model development. With the regression model, invasion fate was correctly predicted for low-risk (only 40% established) and high-risk (90% established) introductions. With the classification tree, 67% were correctly classified. These analyses could be used to guide quantitative risk assessment of future international transfers of freshwater fishes. The overall high rate of establishment (64%) and strong influence of propagule pressure, however, suggest that few planned introductions of freshwater fishes have low establishment risk.*

Key Words: establishment, introduced species, invasion, risk assessment

Análisis Global de los Factores que Afectan las Repercusiones de las Introducciones Peces Dulceacuícolas

Resumen: *Conforme los humanos se mueven alrededor del planeta, la homogeneización biótica disminuye la biodiversidad. Por lo tanto es crucial entender los factores que influyen en el éxito de invasiones a una escala global. Analicé los factores que predicen el establecimiento de peces dulceacuícolas transferidos internacionalmente, con base en 1424 casos de primeras introducciones de un país a otro registrados en FishBase, una base de datos enciclopédica de biología de peces. Utilicé regresión logística múltiple para explorar cuatro casos de variables predictoras: características de especies, características ambientales, correspondencia entre especies y ambiente y presión de propágulos. El mejor modelo de regresión, seleccionado con el criterio de información de Akaike, incluyó cuatro factores que explicaron la variación en el establecimiento de 789 casos de los que se disponía de información completa. El establecimiento fue mayor para familias de peces con tamaño corporal pequeño y para omnívoros. El establecimiento incrementó con el endemismo de la ictiofauna del país recipiente. Las especies tenían mayor probabilidad de establecimiento cuando los humanos tenían la intención de hacerlo (384/506 = 76%) que cuando los peces eran cultivados o utilizados sin el*

Paper received April 1, 2004; revised manuscript accepted February 17, 2005.

Conservation Biology ***–***

DOI: 10.1111/j.1523-1739.2005.00289.x

deseo explícito de naturalización (524/918 = 57%). Tres factores no tuvieron relación con el establecimiento: diferencia latitudinal entre países de origen y de introducción, riqueza de especies nativas del país recipiente (ajustada para superficie) y fecha de primera introducción. El análisis de árboles de clasificación clasificó correctamente (éxito vs. fracaso) a 60% de 789 casos, con base en las mismas variables predictoras usadas para la regresión logística múltiple. Mis resultados significativos refuerzan la idea actual de que el riesgo de invasión es alto para especies generalistas, de reproducción acelerada introducidas en ambientes aislados. El éxito de introducciones intencionales implica que la mayor presión de propágulos genera invasiones más riesgosas. Ambos modelos fueron probados al aplicarlos a 445 casos no utilizados para el desarrollo del modelo. Con el modelo de regresión, el destino de la invasión fue predicho correctamente para introducciones de bajo riesgo (establecimiento de sólo 40%) y de alto riesgo (establecimiento de 90%). Con el árbol de clasificación, 67% fue clasificado correctamente. Estos análisis pudieran ser utilizados para guiar la evaluación cuantitativa del riesgo de futuras transferencias internacionales de peces dulceacuícolas. Sin embargo, la alta tasa general de establecimiento (64%) y la fuerte influencia de la presión de propágulos sugieren que pocas introducciones de peces dulceacuícolas planeadas tienen bajo riesgo de establecimiento.

Palabras Clave: especies introducidas, establecimiento, invasión, evaluación de riesgo

Introduction

Biological invasions reduce two components of biodiversity. The spread of species across the globe tends to make assemblages more similar, and this loss of distinction reduces beta diversity (Rahel 2002; Olden et al. 2004). Introduced species also endanger native species (Moyle & Williams 1990; Foin et al. 1998; Wilcove et al. 1998), a second component of biodiversity loss even though invasions initially raise local species richness. Countries worldwide recognize the ecological and economic costs of invasions (Pimentel 2002), and ecological theory is now applied in the development of risk assessments to restrict harmful invaders (Ruesink et al. 1995; Kolar & Lodge 2001). I examined the predictability of establishment of freshwater fishes at a global scale.

A modern theory of invasion success includes four components: (1) species traits, particularly life-history variables that allow populations to increase rapidly from small population sizes, tolerate harsh or variable conditions, or use a wide variety of resources (Lodge 1993); (2) traits of the locality of introduction, particularly disturbance, anthropogenic impacts, available resources, or so-called empty niches that determine invasibility (Davis et al. 2000); (3) an interaction between species and environment that accounts for habitat and climate match (Blackburn & Duncan 2001); and (4) propagule pressure (size and number of initial populations), which can overcome low probabilities of establishment that arise from demographic stochasticity, environmental stochasticity (windows of opportunity), or genetic problems (Lee 2002). Testing this theory requires information on both successful and failed introductions. Data sets that have been examined include horticultural imports (e.g., Rejmanek & Richardson 1996; Reichard & Hamilton 1997), biocontrol releases (e.g., Beirne 1975), and planned releases of birds, mammals, and fishes (e.g., Veltman et al. 1996; Forsyth et al. 2004).

The answers that emerge from statistical analyses of introduction success are somewhat idiosyncratic, revealing different factors as the best predictors. Why has it been so difficult to identify consistent factors that determine invasion risk? Analyses often refer to different phases of the invasion process (establishment, spread, impact), usually address only a subset of likely factors, and do not account for interactions among factors. Relative importance of these factors may also vary with the spatial scale of analysis and may be taxon specific. On the other hand, published analyses have not concluded that invasion is entirely unpredictable, and rarely do results run counter to ecological theory (Kolar & Lodge 2001). Indeed, pursuing quantitative assessments of invasion risk is essential for better prediction of establishment and improved decision making about planned introductions and other vectors.

Many opportunities for reducing global biotic homogenization occur at a national level. In the United States, for example, Executive Order 13112 discouraged federal activities that promote invasions and established the National Invasive Species Council (NISC). This council, among coordinating other activities, developed a national plan with a core component of preventing invasions, in part through "a fair, feasible, risk-based comprehensive screening system for evaluating first-time intentionally introduced non-native species" (NISC 2001). The results of such risk assessments could then be reflected in trade policies and customs inspections. Of course, national borders are often biogeographically irrelevant. Freshwater fish transfers within the United States have increased biotic similarity among states by 7% (Rahel 2000), and the release of Nile perch (*Lates niloticus*) in Tanzania allowed its spread to other countries bordering Lake Victoria (Welcomme 1988). Nevertheless, risk assessments to address international transfers represent one feasible method for reducing harmful invasions at large spatial scales.

My analysis joins a rapidly rising number of statistical explorations of invasion risk (Kolar & Lodge 2001). Although freshwater fishes have been examined for invasion risk, previous analyses were based within regions of the United States (Kolar & Lodge 2002; Marchetti et al. 2004). At the same time, introductions continue to occur as byproducts of trade (Wonham et al. 2000), escapes from aquaria or aquaculture (Semmens et al. 2004), and direct releases in attempts to develop new fisheries (McKinney 2001), among others. I used a database of 1424 intentional international transfers of freshwater fishes to assess quantitatively which factors may influence establishment (FishBase; Froese & Pauly 1998). Eight predictor variables were available in this database, and, although not necessarily the best or complete from a theoretical perspective, at least one variable addressed each of the four components of invasion risk, which provided for an unusual opportunity to compare their relative importance. Specifically, is establishment related to size, diet, or taxonomy of the invading species? Do chances change with diversity or endemism of the recipient assemblage? What is the role of habitat match, as indicated by latitudinal difference of transfer? Finally, does propagule pressure matter, particularly via date of and reason for introduction? The transfer database is particularly appropriate for these questions because it includes both successful and failed invasions. I used part of the database to develop two predictive models of invasion risk (multiple logistic regression, classification tree) and tested the models against additional cases of planned introductions.

Methods

Data Source

FishBase is a relational database that provides encyclopedic coverage of many aspects of finfish biology (contents can be viewed in part online, www.fishbase.org). A product of the International Center for Living Aquatic Resource Management, it was designed to provide worldwide access to basic information for identification and stock assessment purposes (Froese & Pauly 1998). The database includes multiple tables, organized by species, cases, country, or other management unit. A table of fish introductions was added in 1991. This table was initially based on international transfers of inland fishes compiled by Welcomme (1988) for the United Nations Food and Agriculture Organization and has since been supplemented by published data on marine systems and by responses to questionnaires sent to fish biologists in many countries. FishBase is the most complete record currently available for fish introductions worldwide.

The table of introductions in FishBase records the first known transfer of each fish species from one country to another, excluding aquarium fish that have not established. For each introduction, many of the following fields are known: date of introduction, source and recipient countries, reason for introduction, and whether the species established and caused ecological or economic change. Each entry has an associated reference and can thus be traced to its source. In addition, the table of introductions can be linked via queries in Access (Microsoft, Redmond, Washington) to other tables in FishBase, which include information on species size, habitat, food, and summaries of fish faunas in each country.

As published in 1998, the table of introductions in FishBase contained 2751 cases in total, but only 1424 cases were relevant to my analysis of intentional introductions of freshwater fishes. My assessment of data quality primarily occurred during selection of cases for analysis. All duplicate records (>100 cases) were eliminated. I eliminated introductions of marine species, maintaining species that used freshwater for at least part of their life cycle. Freshwater fishes introduced for unknown reasons (446 cases) or as byproducts (e.g., in ballast water) (153 cases) were not included in the analysis because failures were unlikely to be included. In addition, fishes introduced for "ornamental" reasons were dropped (202 cases) because aquarium fish were included in the database only if established in the wild, thus incurring a bias toward establishment. One hundred seventy-six cases had no information on establishment and were excluded, but those that had "probably" or "probably not" established were considered successful and failed, respectively.

Within FishBase, table entries are generally based on published studies. This attention to peer review means data are accurate but not necessarily collected in a consistent way or applicable to a species throughout its range. Nevertheless, I did not attempt to adjust any information provided in the tables, and thus most likely maintained noise in predictor variables. Body size, for example, generally refers to average size of adults, but may apply to just one sex, and is sometimes reported as standard length (snout to base of tail) instead of total length.

Altogether for this analysis, 1424 intentional transfers of freshwater fishes involved 200 species brought into 162 separate countries or regions. Although large, the data set was undoubtedly incomplete. Specifically, based on information provided by country, species richness of freshwater fishes was 12% higher because of inclusion of exotic species (SE = 11.0–13.6%, back transformed after $\ln[X + 0.001]$ transformation, $n = 186$). Cases of successful establishment in the table of introductions accounted for only 6% higher species richness (SE = 4.9–6.7%).

Predictor variables available in FishBase represent a small subset of all that have been proposed to influence invasion. I found at least one variable to represent each component of invasion risk, however: species traits, environment traits, species-environment match, and propagule pressure.

Species Traits

Reproductive rate and generalism have been emphasized as species traits promoting invasion (Kolar & Lodge 2001). Population growth rates for fishes are not widely known or reported in FishBase. They may, however, be inversely related to body size (Peters 1983; Savage et al. 2004), which was reported for all but 3 of 200 species (six cases; FishBase species table). Generalism has been measured in terms of native range size, temperature tolerance, and diet (Kolar & Lodge 2002; Marchetti et al. 2004), but only the last was available in FishBase. To achieve adequate sample sizes, I combined diets into five categories: herbivore (plants and phytoplankton), zooplanktivore, feeder on benthos, feeder on nekton (including fish), and omnivore (plants and animals). Adult diet was reported or implied (e.g., because a species was introduced for weed control) for 106 species (1238 cases; FishBase ecology table).

Interspecific comparisons can be compromised by phylogenetic nonindependence (Felsenstein 1985; Wolf et al. 1998). Species-specific variables such as body size and diet could be linked erroneously to invasion risk if taxonomically related species are similarly invasive for other reasons. The problem is particularly acute for this data set in which a single species can be represented by more than 80 separate introductions (e.g., common carp [*Cyprinus carpio carpio*]). Fish phylogenies are poorly resolved (Ruesink 2003), but it is possible to determine whether establishment varies among fish families (Blackburn & Duncan 2001; Kolar & Lodge 2002). This sort of analysis requires a comparison of within- and among-family variation in establishment. Consequently, I was able to examine only families with more than two introduced species for which all other predictor variables were known (Centrarchidae, Cichlidae, Cyprinidae, Ictaluridae, Lutjanidae, Poecilidae, Salmonidae), although intentional introductions of freshwater fishes are reported from a total of 46 families.

Environment Traits

The country-level organization of FishBase hampered the development of meaningful predictor variables related to the site of introduction. These variables should probably involve disturbance and biodiversity at a watershed scale because resources and consumers affect invasion success locally (Shea & Chesson 2002). Nevertheless, I explored native species richness and endemism for countries as proxy variables that could influence invasibility (FishBase COUNTREF table). I calculated endemism as the proportion of native taxa found only in that country (transformed to the arc-sine square root) (available for all but 3 of 162 countries [three cases]). Native richness, corrected for area, was included as the residual from an empirical species-area relationship (ln[richness] $= -0.2204 + 0.3639$ ln[area, km^2], $n = 153$, $F_{1,151} = 150.7$, $p < 0.001$) (available for all but eight countries [nine cases]).

Species-Environment Match

A species is unlikely to persist after introduction if it is poorly adapted to the new climate or habitat (Wolf et al. 1998; Duncan et al. 2001). Although habitat information is available for species in FishBase, the habitat at the site of introduction is not, so I was unable to assess habitat match. In other studies, climate match has been explored by comparing the latitude of the native range to the introduction latitude (Blackburn & Duncan 2001). Such information is reported much more coarsely in FishBase. Because the source and introduction site of each case were defined spatially by country, I used the latitude of each country's capital (COUNTREF table) to define the distance between where the species came from and where it was transplanted. Northern and southern hemispheres were not considered separately; that is, a fish moved from 60°N to 55°S was considered a transfer of just 5°. Latitudinal difference was calculated for 1083 cases; others were unavailable because the source country was unknown.

Propagule Pressure

FishBase does not include numbers and sizes of introduction attempts, so I developed two other predictor variables that I expected to be related to propagule pressure. First, some fishes have been introduced because people perceive them as desirable additions to native faunas, and these introductions have most likely been pursued with more vigor than have imports in which establishment is not a goal. I combined several reasons for intentional establishment (fisheries, angling, providing forage, biological control of weeds, snails, or phytoplankton) into a category called "releases," and other reasons for intentional import (but not intentional establishment; aquaculture, bait, research) into a category called "imports." I had already dropped species that reached a country as byproducts of other human activities from consideration because failed establishment was unlikely to be reported.

Second, earlier introductions have had more time for subsequent attempts. Time of first introduction was sometimes reported as a particular year and in other cases as a range or known to within a few decades. In all cases, I used the earliest possible year a fish was introduced, which could be determined for 1220 cases.

Statistical Analysis

I looked for nonrandom patterns of establishment across species by comparing observed establishment with the probability expected from a binomial distribution (Lockwood 1999; Ruesink 2003). This analysis has been suggested as a way to test for all-or-none patterns of establishment (Moulton 1993). If some species establish regardless of where or how they are introduced and others always fail to establish, then this all-or-none pattern suggests a strong role for species traits. Other components of introduction risk—environmental traits, the match between species and environment, and propagule pressure—would all tend to increase the variability in outcome of species introduced to multiple locations.

I carried out two statistical analyses from a suite of possible options that focus on predicting establishment. Multiple logistic regression incorporated all eight predictor variables (body size, diet, family, recipient country species richness and endemism, latitudinal distance of transfer, date and reason for introduction) and a binary outcome (Trexler & Travis 1993; Veltman et al. 1996). Family was included as a random effect; all others were fixed. Models with subsets of the eight predictors were compared using information statistics, rather than simply comparing models for lack of fit. Akaike's information criterion (AIC) also penalizes models with more parameters (Burnham & Anderson 1998). I particularly examined Δ_i, the difference between AIC for any particular model and the minimum AIC for the best, most parsimonious model. As a rule of thumb, $\Delta_i > 4$–7 suggests that a model does not have strong empirical support (Burnham & Anderson 1998).

Classification tree analysis differs from multiple logistic regression primarily because it does not assume linear relationships between predictor variables and invasion risk, and it provides a dichotomous key for risk assessment (Urban 2002). The tree was restricted to minimum group sizes of 20 (~2% of the training data set) and pruned to a point where the misclassification rate changed minimally with branch number. To avoid correlated variables I did not consider family as a predictor variable in this analysis, relying on multiple logistic regression to reveal phylogenetic nonindependence in species traits. Computer software for analyses included JMP 5.1 (SAS Institute, Cary, North Carolina) for logistic regression and S-Plus 6.0 (Insightful Corporation, Seattle, Washington) for the classification tree.

Both models were parameterized with a subset of 789 cases for which all information was available (training data set). After some variables were eliminated because of statistical insignificance, additional introduction cases were available to assess these models. These additional cases did not have complete information on all eight predictor variables, but the subset of statistically important predictor variables was known. I compared the predicted probability of establishment to actual introduction fate with this independent (test) data set.

Results

Of 1424 cases of freshwater fishes introduced intentionally to new countries, 63.8% established. The subset of cases in the training data set had a similarly high probability of establishment (542/789: 68.7%). Most species had patterns of establishment that were indistinguishable from random (Fig. 1). Only 22 of 200 species had probabilities of establishment that fell outside the 90% confidence interval expected from a binomial distribution. The exceptions occurred in widely introduced species, however, so species introduced to at least 30 countries tended to establish either more or less frequently than expected. In multiple logistic regression, a model including four of eight factors generated the lowest AIC value (AIC = 455.6, $r^2 = 0.12$, $p < 0.001$). Establishment was variable among families and among fishes with different diets. Releases generally had higher risk of establishment than imports, and establishment increased with endemism of the recipient country. These results suggest that establishment depends in part on phylogeny. Removing diet, endemism, or reason from the model led to large changes in AIC ($\Delta_i = 23$–45), whereas adding year, latitudinal difference, or species richness led to small changes in AIC ($\Delta_i < 2$), so models with one additional parameter were also well supported by data.

The predictive value of family membership was nearly replaced by body size ($\Delta_i = 7$) and resulted in a model that could be applied to fishes in families other than the

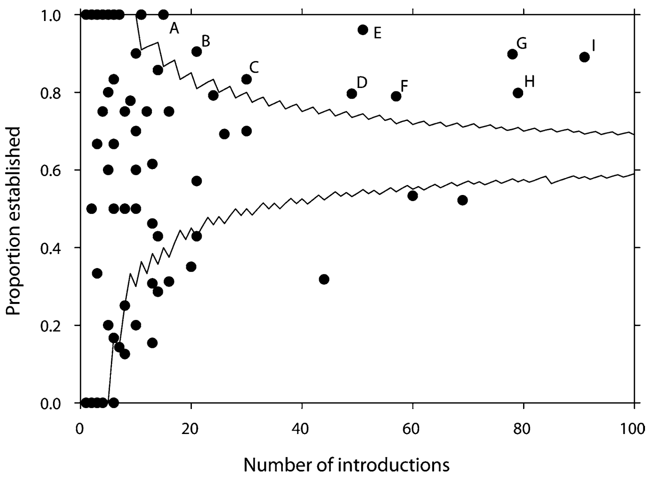

*Figure 1. Proportion of freshwater fish introductions that resulted in establishment for each of 200 species intentionally introduced to new countries. Lines show the upper and lower 90% confidence limits, represented by the nearest conservative integer values, around the average proportion established (63.8%) based on a binomial distribution. Species with particularly high rates of establishment include: A, black bullhead (*Ameiurus melas*); B, tilapia (*Oreochromis urolepis*); C, brown or sea trout (*Salmo trutta*); D, largemouth bass (*Micropterus salmoides*); E, mosquitofish (*Gambusia affinis*); F, tilapia (*Oreochromis niloticus*); G, tilapia (*Oreochromis mossambicus*); H, rainbow trout (*Oncorhynchus mykiss*); and I, common carp (*Cyprinus carpio*).*

seven in the training data set. The parameter estimates (±SE) in this model were intercept = 1.82 (0.24); diet (benthos) = 0.17 (0.17); diet (herbivore) = 0.00 (0.14); diet (nekton) = −0.84 (0.19); diet (omnivore) = 1.00 (0.21); reason (import) = −0.51 (0.10); endemism (transformed to the arc-sine square root) = 0.64 (0.34); and body size = −0.01 (0.00). Omnivores were more likely and nekton feeders less likely to establish. Imported fishes were less likely to establish than those released directly into the new environment. Establishment was higher for fishes with small adult body size and in countries with high endemism of native fishes.

These predictor variables also distinguished fish introductions by risk of establishment in a different statistical approach, classification-tree analysis (Fig. 2). Originally I included seven predictor variables, but in the resultant tree, latitudinal difference and native diversity were repeatedly invoked, indicating highly nonlinear relationships with establishment that were unlikely to inform risk assessment. Consequently I focused on the four predictor variables that emerged in the selected regression model. Body size appeared near the top of the tree and therefore explained much of the variation in establishment (Fig. 2). Reason for introduction appeared near the branch tips of the pruned tree, indicating lower predictive ability. At this level of complexity 40% (317/789) of the training data set was misclassified (Fig. 2). Regression-tree analysis successfully classified species that succeeded but was less accurate in classifying failed introductions because misclassifications primarily occurred when species established despite being sorted into a relatively low-risk (high failure) group. As in the results of the multiple logistic regression, fish were more likely to establish if body size was small, diet was not specialized, recipient country had high endemism, and release was with the intention to establish, rather than being imported (Fig. 2).

In terms of species traits, both body size and diet proved significantly related to establishment in multiple logistic regression, but body size in particular violated assumptions of phylogenetic independence. Likelihood of establishment declined with increasing size, but body size may simply indicate that families share other traits influencing establishment (Fig. 3). Omnivores were more likely and nekton feeders were less likely to establish than species in other trophic guilds. Examining all species in each diet category, weighted by number of cases, the likelihood of establishment was omnivores (82%) ≥ zooplanktivores (78%) = benthivores (66%) = herbivores (63%) ≥ nekton feeders (54%) ($F_{4,101} = 2.8$, $p = 0.03$).

Only one trait of the recipient assemblage was related to establishment. Establishment increased with a country's endemism (Fig. 4) but did not change with native fish species richness. Finally, one factor under human control was significantly related to establishment. Releases were more likely to lead to established populations (384/506 = 76% of full data set) than were imports (524/918 = 57%; Fig. 5). The single predictor variable representing the

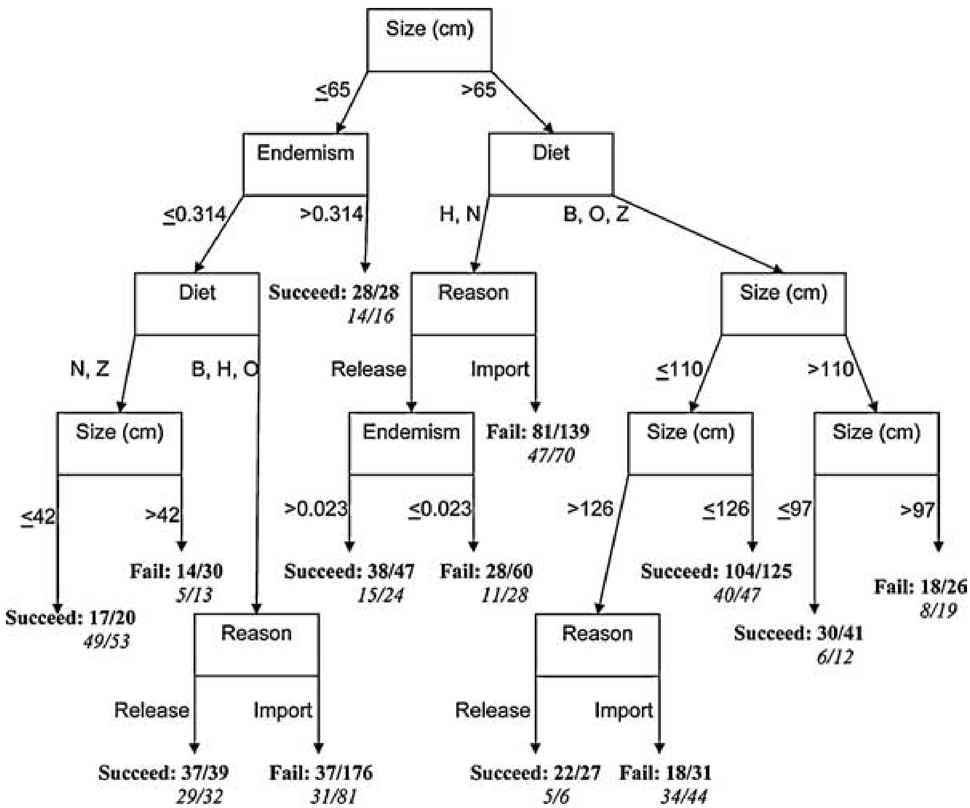

Figure 2. Classification tree used to predict introduction fate of freshwater fishes. Four variables are the predictors (body size, diet, reason for introduction, and endemism), and the tree is pruned to 13 branch tips based on minimal improvement in classification after this point. Proportion endemic was not transformed for this analysis. Diet codes: B, benthic feeder; H, herbivore; N, nekton feeder; O, omnivore; and Z, zooplankton feeder. Correct classifications are shown for the 789 cases used to develop the model (training data set, bold) and for 445 independent test cases (italic).

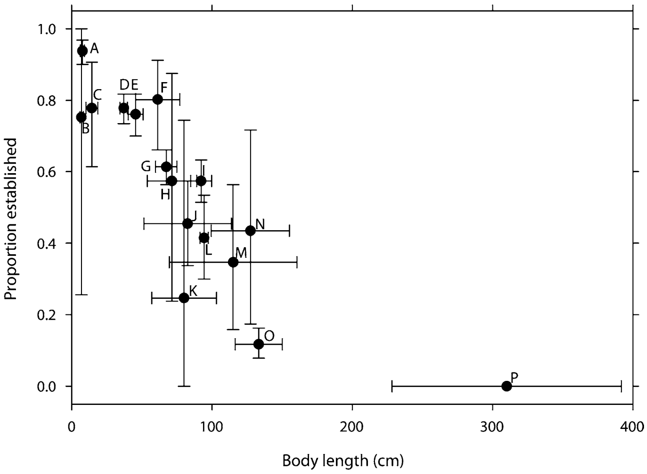

Figure 3. Proportion of freshwater fish introductions that resulted in establishment for taxa of different body sizes introduced worldwide. Each point represents one fish family with at least three introduced species. For establishment, family means and standard error bars were calculated from species' means transformed to the arc-sine square root, weighted by cases, and subsequently back transformed. For body size, means and standard error bars were calculated from all introduced species within the family. Families: A, Poecilidae; B, Aplocheilidae; C, Belontiidae; D, Cichlidae; E, Centrarchidae; F, Ictaluridae; G, Cyprinidae; H, Channidae; I, Salmonidae; J, Clariidae; K, Lutjanidae; L, Catostomidae; M,, Moronidae; N, Esocidae; O, Anguillidae; P, Acipenseridae. Thirty additional families with one or two introduced species are not shown.

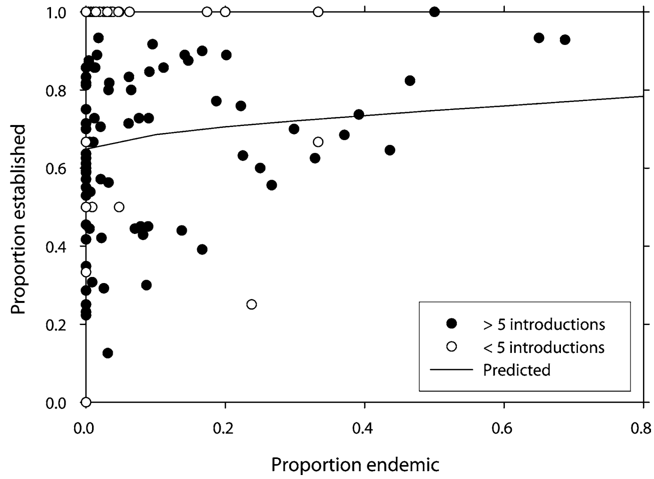

Figure 4. Proportion of freshwater fish introductions that resulted in establishment after introduction to countries with a range of endemism in their native fish faunas. Each point represents one country (total = 159), and countries with at least five introductions are distinguished from those with fewer than five. The line is establishment predicted from the multiple-logistic-regression model, given average values for all other predictor variables.

match between the colonist and its new environment, latitudinal proximity, was not related to establishment.

Of the 635 cases not used to develop models, 445 had information on the four significant predictor variables (test data set). The tree model successfully classified 67% (Fig. 2), and misclassifications primarily occurred because of successful establishment of species being classified as likely to fail. In multiple logistic regression, introductions with low scores were much less likely to establish than were those with higher scores (Fig. 6). Of the species with ≤40% probability of establishment, 40% established, whereas 90% established when they were predicted to have at least 80% probability of establishment.

Discussion

Testing Ecological Theory about Invasions

I used a database of successful and failed fish introductions to explore correlates of high-risk invaders. Four factors, including species traits, environmental traits, and propagule pressure, explained about 12% of the variation in establishment, based on multiple logistic regression. Body size was strongly conserved phylogenetically (among-family variation in body size exceeded within-family variation), and both body size and family membership were related to probability of establishment (Fig. 3). This correlation may indicate body size is a component of, or a proxy for, why families vary in invasion risk. The model predicting establishment was most parsimonious when family was included as a random factor, but it was also less useful because it could be applied to fishes in only seven families.

It has been suggested that traits that allow species to increase rapidly from small population sizes promote invasion (Kolar & Lodge 2001). The small size of successful fish invaders (Fig. 3) may be associated with high-*r* species because taxa of small body size often share a suite of life-history characteristics, including short lifespan and short generation time, although fecundity is generally lower (Marchetti et al. 2004). Generalists are also believed to be better invaders than specialists (Kolar & Lodge 2001), which is consistent with the high rates of establishment of omnivorous species in this analysis. Body size and diet together explained 5% of variation in establishment. At this international scale, however, predicting invasion based on species identity is difficult, primarily because species that depart from random probability of establishment are detectable only after numerous introduction attempts (Fig. 1).

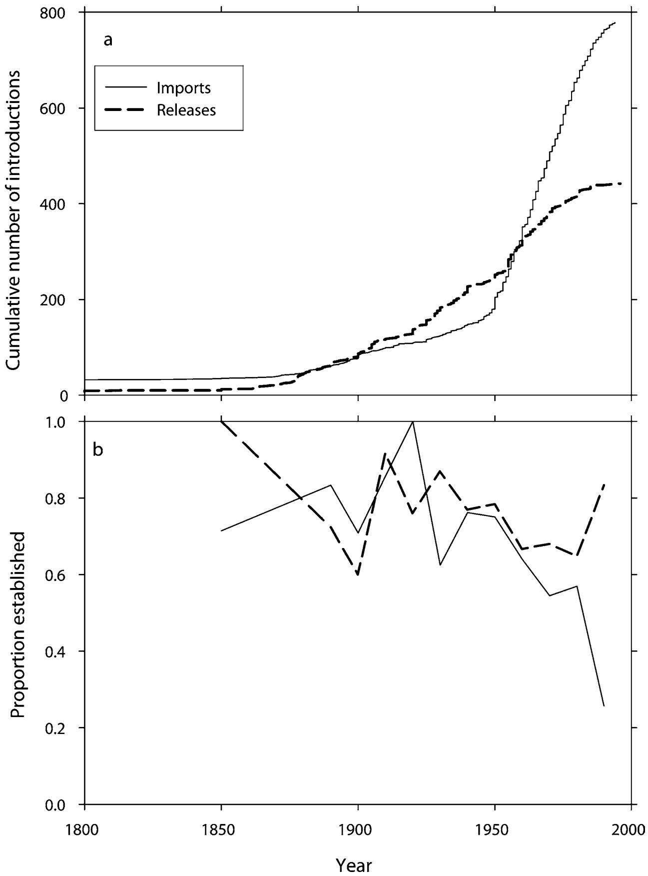

Figure 5. Time series of freshwater fish introductions and establishment, distinguishing species that were imported versus intentionally released: (a) cumulative number of introductions through time and (b) proportion established within time interval. Intervals are irregular but include approximately 50 attempts. Introductions of unknown time (total = 204) are not included.

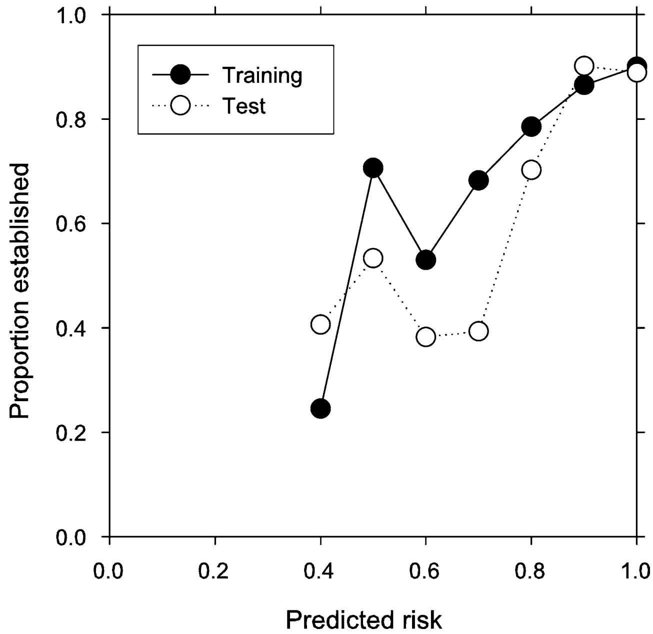

Figure 6. Comparison of actual with predicted introduction fate of freshwater fishes based on 789 cases used to parameterize the multiple-logistic-regression model (training data set) and 445 independent test cases.

Low diversity or high disturbance may contribute to an abundance of free resources, leaving an environment vulnerable to invasion (Davis et al. 2000; Shea & Chesson 2002). Of these factors, only native fish richness was available in FishBase, and when adjusted for country area it showed no relationship with establishment of new species. Thus, fish diversity did not appear to limit invasion at this international scale, which is consistent with positive relationships between native and non-native species richness across sites (Levine & D'Antonio 2002) and suggests that country-level diversity confers little resistance to invasion. In contrast, country-level endemism was positively associated with establishment (Fig. 4). Endemism indicates isolation as species evolve in restricted areas. Areas with high endemism include oceanic islands, the invasibility of which has been the subject of debate for decades (Elton 1958; Simberloff 1986). Endemism alone predicted just 1% of variability in establishment of freshwater fishes. The spatial scale of this analysis undoubtedly introduces error, however, because introduced fishes do not necessarily experience conditions associated with countries as a whole, especially in large countries. A more appropriate scale for judging how recipient assemblages or environmental conditions affect invasion would be based on watersheds.

Reason for introduction may influence the number of individuals or number of occasions when a species was introduced. When the intent is to establish a new species, humans may continue transferring individuals until establishment is successful. Thus propagule pressure could explain the discrepancy in establishment among species that were released to establish (76%) and those imported or cultivated (57%; Fig. 5). Another explanation for this pattern is that species intentionally released into the wild were better matched for habitat suitability than those that humans did not attempt to establish. This variable predicted >1% of variation in establishment of freshwater fishes, indicating that it was less predictive of establishment than species' traits but more predictive than environmental traits.

Species cannot persist in areas of unsuitable habitat or climate, so it was initially surprising that latitudinal difference had no relationship with establishment. The latitude of a country's capital, however, may be quite distant from the site of origin or release of a fish species. The lack of predictability associated with species-environment match most likely reflects a poor predictor variable rather than poor theory. It is also likely that fishes tend not to be introduced intentionally to places where their performance is expected to be poor.

Although year of introduction, species richness, and latitudinal difference were not included as factors in parsimonious models, the direction of their relationship with establishment was still possible to assess. In all cases this direction was consistent with ecological theory: later introductions were less likely to establish, species transferred across a larger latitudinal range were less likely to establish, and establishment was less likely in countries with higher native species richness. In the full data set, fish introductions carried out several decades ago had a higher likelihood of establishment (1950–1959: 163/212, 77%) than did more recent introductions (1990–1996: 6/26 = 23%); thus establishment seemed to lag behind arrival (Fig. 5). The time series also clearly showed a distinct history for worldwide fish imports versus releases. Imports accelerated after 1950, whereas releases have been carried out at a steady rate since before 1900.

Comparison with Other Taxa and Scales

The burgeoning literature quantifying invasion risk encourages comparison to determine whether or not different analyses provide consistent results. I selected three comparisons as a context for my analysis of international transfers of freshwater fishes: establishment of freshwater fishes at smaller scales, establishment of birds at a global scale, and impact of freshwater fishes based on FishBase.

At regional scales, establishment of freshwater fishes depends strongly on species traits. In California these traits include body size and generalism (large native range, physiological tolerance) (Marchetti et al. 2004), and in the Great Lakes traits include rapid individual growth and generalism (broad temperature and salinity tolerances [Kolar & Lodge 2002]). Environmental traits were not explored, either because there was little spatial variation in habitat or climate at these regional scales or because important environmental variables were difficult to quantify (e.g., disturbance; Moyle 1986; Marchetti et al. 2004). In California, propagule pressure also strongly influences establishment (Marchetti et al. 2004). These regional results are similar to patterns emerging from FishBase, although they tend to emphasize species traits rather than other components of invasion risk.

A recent analysis of bird introductions worldwide found that establishment was related to one species trait (generalism, as indicated by native range size) and to species-environment match (as indicated by the latitudinal difference from the midpoint of the range to the site of introduction) (Blackburn & Duncan 2001). Two environmental traits were included to represent biodiversity and isolation of the recipient area. Establishment varied significantly among biogeographic regions, but high-richness regions were not necessarily less invasible. Birds transferred to mainlands and islands had equal probabilities of establishment. So neither biodiversity nor isolation appeared to influence bird establishment, whereas fish were more likely to establish in areas of high endemism (Fig. 4). This comparison undoubtedly suffers from the use of slightly different environmental variables. The role of propagule pressure was not examined for birds at a global scale (Blackburn & Duncan 2001), although it has proved important in smaller-scale analyses (Veltman et al. 1996; Duncan 1997).

In addition to a score for establishment, FishBase also includes information on the ecological impacts of freshwater fishes, including changes in food availability, habitat structure, nutrient dynamics, or top-down trophodynamics. Of 1408 established cases, 22% had impacts and 5% had none; the remainder was unknown (Ruesink 2003). Because so few introductions have been categorized for impact, multiple logistic regression revealed few significant predictors. Only endemism mattered because the probability of impact increased with endemism (Ruesink 2003).

Application to Quantitative Risk Assessment

My analysis identified several factors associated with high-risk introductions of freshwater fishes. These factors left most variability in establishment unexplained (regression $r^2 = 0.12$, tree-based misclassification = 40%). Statistical approaches to invasion, such as classification trees and multiple logistic regression, simply describe factors associated with species that have invaded already. To be useful in a risk-assessment context, these models must also be predictive so that species of high risk can be identified before their introduction. Models performed well in predicting the introduction fate of the test cases: 40% of the low-risk introductions established, whereas 90% of the high-risk introductions established (Fig. 6). The multiple regression results were matched by the classification tree in terms of how different factors influenced establishment (Fig. 2). The tree primarily misclassified cases that were expected to be low risk but actually established, although the overall misclassification of the independent test data set was just 33%. As currently parameterized, these models successfully flag high-risk invaders. Small-sized omnivorous freshwater fish species introduced into countries of high endemism generally establish if their establishment is intended.

It is important to realize, however, that the variables I used do not represent complete or necessarily accurate components of risk (species traits, environment traits, species-environment match, propagule pressure), which may be why so much unexplained variation remains. Other variables would undoubtedly provide different risk assessments. My results support the notion that invasion is a multifactorial process. The imperfect data set with a restricted number of predictor variables still provided better-than-random assessments of relative risk for global introductions. In this analysis, species' traits emerged as relatively important, but FishBase did not include specific information about the place of introduction or how the transfer was carried out (number of times or individuals), so contributions of the recipient environment and propagule pressure are likely to be underestimated. If species' traits dominate invasion risk, then clearly conservation effort should be expended to develop ecologically informed screening protocols. To the extent that propagule pressure also contributes, however, effort should be directed at slowing the flux of living organisms worldwide, particularly for transfers not included in this analysis—by-products of travel and trade.

The major drawback of using this quantitative risk assessment in decision making stems from the fact that propagule pressure appears as a major predictor of establishment. Consequently it is difficult to say whether or not a particular species will establish in a particular country; rather, establishment simply becomes more likely as more are introduced. Additionally, many introduction decisions are ultimately made at much smaller scales. In these cases, regional analyses may be more successful at categorizing high and low risk species (Kolar & Lodge 2002; Marchetti et al. 2004). From this global analysis, however, emerges a critical conservation message. Although correctly predicting the fate of any particular introduction may be difficult, statistical patterns of factors related to establishment emerge when hundreds of introductions are examined simultaneously. Future attention should be paid to understanding factors that allow establishment in apparently low-risk cases. The overall high establishment (64% of 1424) of intentional introductions of freshwater fishes warns against continued imports and releases, which are rapidly contributing to global biotic homogenization.

Acknowledgments

The ideas for this paper were developed during a postdoctoral fellowship at the University of British Columbia. Many thanks to D. Pauly, L. Collado-Vides, and E. Buhle for inspiration and advice. Statistical analyses benefited from N. Mercaldo, M. Hussey, and M. Thornquist. The manuscript was greatly improved by P. Angermeier, E. Main, B. Scott, and three anonymous reviewers.

Literature Cited

Beirne, B. 1975. Biological control attempts by introductions against pest insects in the field in Canada. Canadian Entomologist **107:**225–236.

Blackburn, T. M., and R. P. Duncan. 2001. Determinants of establishment success in introduced birds. Nature **414:**195–197.

Burnham, K. P., and D. R. Anderson. 1998. Model selection and inference: a practical information-theoretic approach. Springer-Verlag, New York.

Davis, M. A., J. P. Grime, and K. Thompson. 2000. Fluctuating resources in plant communities: a general theory of invasibility. Journal of Ecology **88:**528–534.

Duncan, R. P. 1997. The role of competition and introduction effort in the success of passeriform birds introduced to New Zealand. The American Naturalist **149:**903–915.

Duncan, R. P., M. Bomford, D. M. Forsyth, and L. Conibear. 2001. High predictability in introduction outcomes and the geographical range size of introduced Australian birds: a role for climate. Journal of Animal Ecology **70:**621–632.

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

Felsenstein, J. 1985. Phylogenies and the comparative method. The American Naturalist **125:**1–15.

Foin, T. C., S. P. D. Riley, A. L. Pawley, D. R. Ayres, T. M. Carlsen, P. J. Hodum, and P. V. Switzer. 1998. Improving recovery planning for threatened and endangered species. BioScience **48:**177–184.

Forsyth, D. M., R. P. Duncan, M. Bomford, and G. Moore. 2004. Climatic suitability, life-history traits, introduction effort, and the establishment and spread of introduced mammals in Australia. Conservation Biology **18:**557–569.

Froese, R., and D. Pauly, editors. 1998. FishBase 98: concepts, design and data sources. International Center for Living Aquatic Resource Management, Manila.

Kolar, C. S., and D. M. Lodge. 2001. Progress in invasion biology: predicting invaders. Trends in Ecology & Evolution **16:**199–204.

Kolar, C. S., and D. M. Lodge. 2002. Ecological predictions and risk assessment for alien fishes in North America. Science **298:**1233–1236.

Lee, C. E. 2002. Evolutionary genetics of invasive species. Trends in Ecology & Evolution **17:**386–391.

Levine, J. M., and C. M. D'Antonio. 2002. Elton revisited: a review of evidence linking diversity and invasibility. Oikos **87:**15–26.

Lockwood, J. L. 1999. Using taxonomy to predict success among introduced avifauna: relative importance of transport and establishment. Conservation Biology **13:**560–567.

Lodge, D. M. 1993. Species invasions and deletions: community effects and responses to climate and habitat change. Pages 367–387 in P. M. Kareiva, J. G. Kingsolver, and R. B. Huey, editors. Biotic interactions and global change. Sinauer, Sunderland, Massachusetts.

Marchetti, M. P., P. B. Moyle, and R. Levine. 2004. Alien fishes in California watersheds: characteristics of successful and failed invaders. Ecological Applications **14:**587–596.

McKinney, C. L. 2001. Effects of human population, area, and time on non-native plant and fish diversity in the United States. Biological Conservation **100:**243–252.

Moulton, M. P. 1993. The all-or-none pattern in introduced Hawaiian passeriforms: the role of competition sustained. The American Naturalist **141:**105–119.

Moyle, P. B. 1986. Fish introductions into North America: patterns and ecological impact. Pages 27–43 in H. A. Mooney and J. A. Drake, editors. Ecology of biological invasions of North America and Hawaii. Springer-Verlag, New York.

Moyle, P. B., and J. E. Williams. 1990. Biodiversity loss in the temperate zone: decline of the native fish fauna of California. Conservation Biology **4:**275–284.

National Invasive Species Council (NISC). 2001. National management plan: meeting the invasive species challenge. January 18, 2001. NISC, Washington, D.C. Available from http://www.invasivespecies.gov/council/nmptoc.shtml (accessed October 2004).

Olden, J. D., N. L. Poff, M. R. Douglas, M. E. Douglas, and K. D. Fausch. 2004. Ecological and evolutionary consequences of biotic homogenization. Trends in Ecology & Evolution **19:**18–24.

Peters, R. H. 1983. The ecological implications of body size. University Press, Cambridge, United Kingdom.

Pimentel, D., editor. 2002. Biological invasions: economic and environmental costs of alien plant, animal, and microbe species. CRC Press, Boca Raton, Florida.

Rahel, F. J. 2000. Homogenization of fish faunas across the United States. Science **288:**854–856.

Rahel, F. J. 2002. Homogenization of freshwater faunas. Annual Review of Ecology & Systematics **33:**291–315.

Rejmanek, M., and D. M. Richardson. 1996. What attributes make some plant species more invasive? Ecology **77:**1655–1661.

Reichard, S. H., and C. W. Hamilton. 1997. Predicting invasions of woody plants introduced into North America. Conservation Biology **11:**193–203.

Ruesink, J. L. 2003. One fish, two fish, old fish, new fish: Which invasions matter? Pages 161–178 in P. Kareiva and S. A. Levin, editors. The importance of species: perspectives on expendability and triage. Princeton University Press, Princeton, New Jersey.

Ruesink, J. L., I. M. Parker, M. J. Groom, and P. M. Kareiva. 1995. Reducing the risks of nonindigenous species introductions. BioScience **45:**465–477.

Savage, V. M., J. F. Gillooly, J. H. Brown, G. B. West, and E. L. Charnov. 2004. Effects of body size and temperature on population size. The American Naturalist **163:**429–441.

Semmens, B. X., E. R. Buhle, A. K. Salomon, and C. V. Pattengill-Semmens. 2004. A hotspot of non-native marine fishes: evidence for the aquarium trade as an invasion pathway. Marine Ecology Progress Series **266:**239–244.

Shea, K., and P. Chesson. 2002. Community ecology as a framework for biological invasions. Trends in Ecology & Evolution **17:**170–176.

Simberloff, D. 1986. Introduced insects: a biogeographic and systematic perspective. Pages 3–26 in H. A. Mooney and J. A. Drake, editors. Ecology of biological invasions of North America and Hawaii. Spring-Verlag, New York.

Trexler, J. C., and J. Travis. 1993. Nontraditional regression analyses. Ecology **74:**1629–1637.

Urban, D. L. 2002. Classification and regression trees. Pages 222–232 in B. McCune and J. B. Grace, editors. Analysis of ecological communities. MjM Software Design, Gleneden Beach, Oregon.

Veltman, C. J., S. Nee, and M. J. Crawley. 1996. Correlates of introduction success in exotic New Zealand birds. The American Naturalist **147:**542–557.

Welcomme, R. L. 1988. International introductions of inland aquatic species. Fisheries technical paper 294. Food and Agriculture Organization, Rome.

Wilcove, D. S., D. Rothstein, J. Dubow, A. Phillips, and E. Losos. 1998. Quantifying threats to imperiled species in the United States. BioScience **48:**607–615.

Wolf, C. M., T. Garland, and B. Griffith. 1998. Predictors of avian and mammalian translocation success: reanalysis with phylogenetically independent contrasts. Biological Conservation **86:**243–255.

Wonham, M. J., J. T. Carlton, G. M. Ruiz, and L. D. Smith. 2000. Fish and ships: relating dispersal frequency to success in biological invasions. Marine Biology **136:**1111–1121.