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Evaluating establishment success of non-native fishes introduced to inland aquatic habitats of tropical Pacific islands

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Abstract. An information-theoretic approach was used to evaluate non-native freshwater fish species introduced to insular habitats of Hawaii and Guam comparing successful establishments *vs.* failures. Since the late 1800s, as many as 81 non-native freshwater fish species have been recorded as introduced to Hawaii and Guam (combined) and 50 (62%) of these are documented as having one or more established populations. We examined eleven independent variables to investigate establishment success by creating 21 *a priori* logistic regression models ranked using Akaike's Information Criterion adjusted for small sample size. An additional eight post-hoc models were included that comprised the best *a priori* model and various combinations of individual variables. The best overall model of establishment probability included effects of taxonomic affinity (family membership), prior establishment success on other tropical islands, and hypoxia tolerance. Establishment success in Hawaii and Guam was highest for those species established on many other islands, and according to our best model air-breathing fishes were more likely to become established. Six fish families, each with from three to 18 species introduced to Pacific islands, were highly successful at establishment: Cichlidae (16 established of 18 species introduced), Poeciliidae (seven of eight), Cyprinidae (four of seven), Centrarchidae (four of four), Clariidae (three of three), and Loricariidae (three of four). Those that successfully established include both small and moderately large-bodied taxa, while representing a diverse array of other morphological and life-history traits. Pathways and motives associated with fish introductions in the Pacific have been linked to desires to develop aquaculture, enhance wild stocks of food, sport, and bait fishes, for use as biological control agents, or are linked to the ornamental fish trade. We found that many established species were introduced via multiple pathways (up to eight) and our analyses suggest that the combination of prior establishment success on other tropical islands and presence of non-native fishes in multiple pathways was indicative of high propagule pressure. Our study results and conclusions on Pacific tropical island introductions are in general agreement with previous studies on non-native freshwater fishes in other regions of the world and similar to observations in continental ecosystems and temperate zones.

Key words: nonindigenous fishes, Hawaii, Guam, Micronesia, prior establishment success, hypoxia tolerance, air breathing

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Introduction

A major focus of invasion biology is the screening and profiling of species for the purpose of identifying non-native taxa predisposed to becoming successful invaders (Kolar 2004, Marchetti et al. 2004a, b, Howeth et al. 2016, Meyers et al. 2020). The process typically involves gathering information on a species' biological attributes and determining which traits, if any, are advantageous to establishment in a novel ecosystem. Such assessments require detailed knowledge of the ecology and life history of an organism in its native range, although information about a species' introduction history is equally important. Mechanisms or conditions that promote the invasion process, such as existence of transport pathways, climate match, and propagule pressure are also commonly part of many such analyses. Consequently, predicting the identity or range of potential invaders commonly involves selection, categorization, analysis, and assessment of an array of variables (Andersen et al. 2004, Copp et al. 2009, Keller et al. 2011, Howeth et al. 2016, Lodge et al. 2016, Davidson et al. 2017).

Terms and concepts in invasion biology are not widely standardized; consequently, there exist nuanced and, in some cases, marked differences in the way different authors have defined or used them (Fuller et al. 1999, Davis & Thompson 2000, Colautti & MacIsaac 2004, Copp et al. 2005a, b). Herein, the term "establishment" refers to a non-native species that has been introduced with human assistance outside of its natural range and has successfully attained a self-sustaining population in the wild. Establishment is one stage in the invasion process, a sequence commonly described as having four stages: transport, introduction, establishment, and spread (Blackburn et al. 2011). In general, successful establishment suggests the population persists, is relatively stable or increasing, and that the possibility of its eradication by natural causes or by humans is unlikely. Establishment failure occurs when a species is unable to overcome barriers in the transition from introduction to establishment.

Non-native species that successfully colonize novel areas are often considered to have certain advantageous characteristics, many not mutually exclusive. In particular, successful invaders are frequently described as those that are: widespread and abundant in their native range, habitat or ecological generalists, behaviourally flexible, highly tolerant to abiotic stressors, capable of rapid dispersal, exploitative of disturbed habitats, more often classified as r-selected rather than k-selected and, affiliated in some way to humans (Ehrlich 1986, 1989, Lodge 1993, Ricciardi & Rasmussen 1998, Kolar & Lodge 2002, Alcaraz et al. 2005). Admittedly, many studies have found that some or many of the above listed traits and descriptors are not necessarily the best predictors of establishment or invasion success, and that differences may depend on the phylogenetic group, the geographic region, and the invasion process stage examined (Kolar & Lodge 2001, Ruesink 2005, García-Berthou 2007, Gozlan et al. 2010).

To better understand the complex relationship between invasion success and species characteristics, investigators increasingly apply quantitative modelling approaches to the problem (Kolar & Lodge 2001, 2002, Kolar 2004, Marchetti et al. 2004a, Moyle & Marchetti 2006, Howeth et al. 2016). Comparisons of the results of studies, whether quantitative or qualitative, is challenging because of differences among studies in the variables selected for examination, the organisms and spatial scales evaluated, and the specific analytical, statistical, and interpretive methods used (García-Berthou 2007). Factors associated with failed introductions may be equally as important as those leading to successful establishment. However, there are often few data available on failed introductions and suggested reasons behind known failures may be subject to biased interpretation (Kolar & Lodge 2001, García-Berthou et al. 2005, Hayes & Barry 2008).

Although investigations at the global or continental scale are valuable, such broad studies may be limited in their extrapolative or predictive ability (Gido & Brown 1999, Ruesink 2005). Consequently, studies focused at regional scales can be more informative in assessing establishment success and invasion risk (Moyle & Marchetti 2006). García-Berthou (2007) reviewed 12 different quantitative studies on the characteristics of invasive fishes. Among other findings, he concluded that there was a lack of comparative studies at multiple scales while also noting the absence or shortage of research in the tropics and other areas outside northern temperate regions.

The aim of the current study was to identify and assess factors contributing to establishment

Fig. 1. Map of the Pacific Ocean showing the locations of the Hawaiian Islands and Guam. The number of established non-native fish species is included (in parentheses is the number of established species as a percent of all known non-native fishes introduced to inland fresh waters of each of the two study sites). Many of the larger small tropical islands are shown in red, but thousands of other Pacific islands are too small to display.

success of non-native freshwater fish species introduced to Hawaii and Guam. Both are oceanic islands or island groups located in the tropics. Applying a frequentist approach, our analysis focus was on the initial stage of the invasion process with establishment as the outcome. To aid our investigation, we also examined data on fish introductions and establishment for other tropical islands in the Pacific and at a global scale. Our research found records documenting as many as 46 non-native, freshwater fish species to be established in inland and estuarine waters of Hawaii; in contrast, only about 13 species are known to be established on Guam (Brock 1960, Maciolek 1984, Eldredge 1994, Fuller et al. 1999, Yamamoto & Tagawa 2000, Mundy 2005). Inclusion of Hawaii, rather than Guam alone (our original intent), provided necessary and sufficient data for improving the power of our modelling approach and ultimately allowed development of a quantitative model useful for analytical purposes.

The combination of Hawaii and Guam data also permitted us to more adequately evaluate a wider range of species traits and other factors potentially associated with successful establishment.

Study Area

Guam and the Hawaiian Islands both represent small areas of extreme geographic isolation, each situated in remote regions of the Pacific Ocean far from continental land masses (Fig. 1). The island of Guam (13.4443° N, 144.7937° E) is part of the Mariana Islands within Micronesia of the western Pacific Ocean. Guam is the western-most territory of the United States with a land mass of 547 km^2 and the largest island in Micronesia. Non-native freshwater fishes are present in a variety of streams, reservoirs, ditches, and ponds on the island. The Hawaiian Islands (19.8968° N, 155.5828° W) are an archipelago of eight major islands and multiple small islets and atolls remotely situated near the

Table 1. Model variables pertaining to establishment success of non-native fishes introduced to inland waters of the Hawaiian Islands and Guam.

Parameter	Description	States
Dependent variable	Status on Hawaii and/or Guam	0 – introduced but not established; 1 – established
Independent variable	Taxonomic affinity	
	1. Family	34 different fish families
Independent variable	Distributional attributes and history of introductions	
	2. History (prior invasion success; number of tropical islands/island groups where taxon was introduced and became established)	0-43
Independent variable	Propagule pressure	
	3. Pathway	1 – raised in aquaculture facilities/ponds; 2 – in aquarium trade; 3 – stocked as ornamental; 4 – biological control; 5 – stocked as food fish; 6 – stocked as recreational game fish for sport, commercial, or subsistence fishing; 7 – stocked as prey base; 8 – used as bait; 9 – present in live food markets; 10 – ballast water; 11 – contaminant with stocking of another species; 12 – ceremonial release
Independent variable	Life-history attributes	
	4. Body size (maximum adult length)	1 – small (< 10 cm); 2 – medium (10-29 cm); 3 – large (30-100 cm); 4 – very large (> 100 cm)
	5. Adult trophic category	1 – detritivore/algivore; 2 – herbivore; 3 – planktivore; 4 – omnivore; 5 – invertivore; 6 – invertivore/piscivore; 7 – piscivore/top predator
	6. Reproductive guild (level of parental care, fecundity, and egg size)	1 – non-guarders, high fecundity, small egg; 2 – guarder, medium fecundity and egg size; 3 – bearer, low fecundity and large egg size[a]
	7. Spawning habitat	1 – lotic; 2 – lentic; 3 – coastal/estuarine[b]; 4 – lotic and lentic; 5 – lotic, lentic and coastal/estuarine
Independent variable	Physiological tolerance	
	8. Climate profile (climate regions included in native geographic distribution)	1 – temperate; 2 – subtropical; 3 – tropical; 4 – temperate/subtropical; 5 – subtropical/tropical
	9. Salinity tolerance	1 – intolerant to salinity < 1 ppm (stenohaline); 2 – moderately tolerant > 1 and < 10 ppm; 3 – very tolerant > 10 ppm (euryhaline)
	10. Hypoxia tolerance	1 – intolerant of low dissolved oxygen; 2 – moderately tolerant; 3 – tolerant, air breathing
	11. Environmental tolerance	3-12 (summation of scores for variables 8-10)

[a] Includes live-bearing species (e.g. *Poecilia*), species that carry eggs externally (e.g. *Oryzias*, *Ancistrus*), and species that brood eggs internally in their orobranchial cavity (e.g. *Oreochromis*, *Melanochromis*).

[b] Includes species that spawn offshore or on reefs (e.g. *Anguilla marmorata*).

centre of the Pacific Ocean (Juvik & Juvik 1998; Fig. 1). Its nearest major landmass is North America about 5,000 km to the east. The islands are a state of the United States and have a combined land area of about 16,640 km^2. Non-native freshwater fishes have been introduced to at least seven of the major islands of Hawaii, the greatest number occurring on the island of Oahu (Maciolek 1984, USGS 2021). Non-native fishes are found in most inland aquatic habitats of Hawaii, including various streams, reservoirs, natural and artificial wetlands and lagoons, Hawaiian fishponds (ancient aquaculture structures) and farm ponds, ditches, and natural anchialine pools, as well as various estuarine sites (Yamamoto & Tagawa 2000, Mundy 2005).

Material and Methods

Non-native fishes included in estimation of establishment success

Information on Pacific Island fish introductions and establishment status used in this study were gathered from many sources. Included were data assembled from an in-depth review of published and unpublished literature, consultation with numerous experts and local authorities, search of museum records and specimens, and examination of records in the U.S. Geological Survey's Nonindigenous Aquatic Species (NAS) database (USGS 2021). A few of the more useful sources of information on non-native fishes in the Pacific region are works that contain review and summary data (e.g., Maciolek 1984, Devick 1991, Eldredge 1994, 2000, Fuller et al. 1999, Yamamoto & Tagawa 2000, Mundy 2005). In addition, we relied heavily on our own original field observations including fish specimens collected by us during surveys conducted in Hawaii, Guam, Pohnpei, Saipan, the Republic of Palau, and the Galapagos.

Guam was treated as analogous to a Hawaiian island in the context of evaluating establishment success of non-native fishes among islands of the broad study area of the tropical Pacific. Thus, data for both regions (81 taxa, both introduced and established) were combined for analysis, which was required to obtain model convergence. An established species was defined as any taxon known to have one or more self-sustaining wild populations in Hawaii, Guam, or both. Species include those that are restricted to fresh water in their native distribution (most species in our data matrix), species that occur in both fresh and brackish waters (e.g. mangrove goby *Mugilogobius cavifrons*) and highly euryhaline species that inhabit fresh, brackish, and marine waters (e.g. Gulf killifish *Fundulus grandis* and Mozambique tilapia *Oreochromis mossambicus*).

Positive identification of non-native fish species is a challenge, especially given the taxonomic instability of certain groups and growing recognition of cryptic forms. During our assignment of fish names, we relied heavily on recent taxonomic revisions and occasionally consulted with taxonomic experts. In the current study, 14 species identifications were questionable, representing taxa that were originally reported as genus only, belong to unresolved taxonomic complexes, or are commonly misidentified cryptic species. For these taxa, variables used in the analysis were scored based on species most likely to have been introduced as evidenced from other introductions (Maciolek 1984, Fuller et al. 1999, Eldredge 2000, Mundy 2005, USGS 2021), or putative related species presumed to share similar life-history, ecological, and physiological attributes. The species and status of all taxa in our data set are summarized in Table S1.

Variables

Ten independent variables were selected *a priori* to evaluate establishment success: 1) family; 2) number of tropical islands or tropical island groups where a species was introduced and became established, excluding Hawaii and Guam (Table S2); 3) pathway of introduction or human use; 4) maximum body length; 5) adult trophic category; 6) reproductive guild; 7) spawning habitat; 8) climate in a species' native range; 9) salinity tolerance, and; 10) hypoxia tolerance (Table 1). An additional independent variable (11), designated environmental tolerance, was established *a posteriori* and represented a composite of variables 8-10. These variables were scored based on published literature, technical data summarized in FishBase (Froese & Pauly 2021), closely related or similar species in cases where data were unavailable, and personal knowledge of the authors. Detailed descriptions and rationale for selection of variables are provided in Appendix S1.

Model set

The data matrix used in our model of establishment success is provided in Table S3. Establishment success was a binary response variable scored as 1 for non-native fish species with one or more self-sustaining, reproducing populations in the wild in Hawaii or Guam, and 0 for non-native fish species

Table 2. Set of competing models of establishment success for non-native fishes introduced into inland waters of Hawaii and Guam and the hypotheses that each model represents. The first 21 models were defined *a priori*. Models 22-28 were *a posteriori* variation of the *a priori* model with the most support. Model 29 was an *a posteriori* version of the best model among models 1-28 in which the number of hypoxia tolerance scores were reduced from 3 to 2.

Model No.	Model name	Hypothesis	Reference
1	Family + history + pathways + length + diet + reproductive guild + spawning habitat + environmental tolerance	Our most general model	Present study
2	Family + history + pathways + length + diet + reproductive guild + environmental tolerance	Best model of Marchetti et al. 2004a	Marchetti et al. 2004a
3	Family + pathways + length + diet + reproductive guild + environmental tolerance	Invasive species characteristics	Kolar & Lodge 2001
4	Family + history + pathways + length + reproductive guild + environmental tolerance	Expert opinion model	Marchetti et al. 2004a
5	Family + history + pathways + diet + spawning habitat + environmental tolerance	Human interest and habitat generalist	Present study
6	Family + history + pathways + reproductive guild + environmental tolerance	Best model in a different study	Marchetti et al. 2004b
7	Family + length + diet + reproductive guild + spawning habitat	Life history	Present study
8	Family + pathways + diet + environmental tolerance	Invasive species characteristics	Moyle & Light 1996a, b
9	Family + diet + reproductive guild + environmental tolerance	Best model 1 of Kolar & Lodge 2002	Kolar & Lodge 2002
10	Family + history + reproductive guild + environmental tolerance	Best model 2 of Kolar & Lodge 2002	Kolar & Lodge 2002
11	Family + pathways + reproductive guild + spawning habitat + environmental tolerance	Propagule pressure, population growth and habitat	Williamson & Fitter 1996a, b
12	Family + diet + spawning habitat + environmental tolerance	Habitat generalist	Present study
13	Family + diet + environmental tolerance	Ecological characteristics or novel environments	Marchetti et al. 2004a
14	Family + length + reproductive guild	Life history or high population growth	Marchetti et al. 2004a
15	Family + history + pathways	Human interest	Marchetti et al. 2004a
16	Family + pathways + diet	Best model in a different study	Ruesink 2005
17	Family + history + spawning habitat	Prior establishment success and spawning habitat	Present study
18	Family + history + length	Best model in a different study	Ribeiro et al. 2008
19	Family + history	Taxonomic affinity + Prior establishment success	Bomford et al. 2010

Table 2. continued

Model No.	Model name	Hypothesis	Reference
20	Family + pathways	Propagule pressure	Blackburn et al. 2009
21	Family	Taxonomic effect only	Present study
22	Family + history + climate profile	Best *a priori* model + climate profile	Bomford et al. 2010
23	Family + history + hypoxia tolerance	Best *a priori* model + hypoxia tolerance	Present study
24	Family + history + salinity tolerance	Best *a priori* model + salinity tolerance	Present study
25	Family + history + climate profile + hypoxia tolerance	Best *a priori* model + climate profile + hypoxia tolerance	Present study
26	Family + history + climate profile + salinity tolerance	Best *a priori* model + climate profile + salinity tolerance	Present study
27	Family + history + hypoxia tolerance + salinity tolerance	Best *a priori* model + hypoxia tolerance + salinity tolerance	Present study
28	Family + history + climate profile + hypoxia tolerance + salinity tolerance	Best *a priori* model + climate profile + hypoxia tolerance + salinity tolerance	Present study
29	Family + history + hypoxia tolerance	Best *a priori* model + hypoxia with number of hypoxia scores reduced from 3 to 2 (hypoxia scores of 1 and 2 lumped *vs.* 3)	Present study

introduced but not known to be established in those two areas. Introduction records and establishment success were based on published or online sources (Maciolek 1984, Eldredge 1994, 2000, Fuller et al. 1999, Mundy 2005, USGS 2021). Logistic regression was used for our analysis because of the binary nature of our response variable (Agresti 2013, 2018). This approach is common in studies of establishment success of non-native species (Marchetti et al. 2004a, b, Ruesink 2005, Ribeiro et al. 2008, Bomford et al. 2009, 2010, Fujisaki et al. 2009).

We created a set of 21 competing *a priori* logistic regression models each representing a different hypothesis regarding establishment success (Table 2). This model set included the most general model that contained as many of the ten independent variables as possible while still achieving convergence. The most general model included the composite environmental tolerance variable. The remaining 20 models in the set each included a unique subset of the independent variables in the most general model. Most of the competing models were formulated by reviewing the literature. Not all previously published models could be reproduced exactly using our variable set. In such cases we approximated published models as closely as possible with the variables in our dataset. A few additional competing models were added based on consideration of our unique dataset.

Each of the 21 *a priori* models in our model set were ranked using Akaike's Information Criterion (AIC_c) adjusted for small sample size (Burnham & Anderson 2002, Symonds & Moussalli 2011). AIC_c balances model precision and bias; the best model has the lowest AIC_c. We calculated Akaike weights (w_i) to evaluate support for each model and for individual variables. These Akaike weights sum to 1.0 and indicate relative support for a given model. Climate, salinity tolerance, and hypoxia tolerance were added to the best model in an exploratory post-hoc fashion by creating seven additional models to represent every possible combination of these three variables. An additional *a posteriori* model was added that reduced the number of hypoxia tolerance scores from three to two (hypoxia intolerant and moderately tolerant combined *vs.* air breathing).

Model approach

To specify differences in establishment among species, the probability of establishment on the logit scale was formulated as a linear combination of random and fixed covariates. Model parameters were estimated using the "lmer" function for linear mixed models (Gelman & Hill 2006, Gałecki & Burzykowski 2013, West et al. 2015) in R (R Core Team 2020). Each of the 21 *a priori* competing models included a random family effect. When no random effect is supported by the data the "lmer" function estimates a constant intercept with a variance of zero, essentially removing the random family effect from the model. Twenty-one families were represented by a single species; inclusion of families with only one species in our model is not a problem when using a random family effect (Gelman & Hill 2006, Gelman et al. 2020).

After identifying the best model, we assessed fit of that model by estimating its error rate. Error rate is the proportion of observations in the data set for which the fitted value > 0.5 and species status in the study area = 0 or fitted value < 0.5 and status = 1. We compared the error rate of the best model to the error rate of the null model. The null model is simply the proportion of observations in the data set for which species status = 1. Error rate of the null model is 1 minus the proportion of observations in the data set with a species status = 1. Ideally the error rate of the best model is low and substantially lower than the error rate of the null model.

We also assessed fit of the most general model by creating 1,000 simulated data sets based on that model using the "sim" function in the R package "arm" (Gelman & Hill 2006, Gelman et al. 2020). We used proportion of observations in the data set with a species status = 0 as our test statistic and compared the value of that test statistic to the same proportion for each of the 1,000 simulated data sets. A two-sided *P*-value was used to estimate whether the test statistic differed significantly from values obtained via simulation. Results of the model fitting procedure are summarized in Appendix S2 and Fig. S1 and S2.

Results

Of the 81 non-native fish taxa included in this analysis, 50 (62%) became established in Hawaii, Guam, or to both places, and 31 (38%) failed to become established. Fifteen taxa were introduced to both Hawaii and Guam. Number of known established species for Hawaii is 46 and for Guam is 13. Ten taxa became established in both the Hawaiian Islands and Guam. The non-native fishes in our analysis represent 33 families and 64 genera (Table S1). The family Cichlidae was represented by the most species (18), followed by Poeciliidae (8), Cyprinidae (7), Centrarchidae (4), Loricariidae (4), and Salmonidae (4). All other families were represented by one to three species introduced. Numbers of non-native fish taxa introduced and established in inland waters of the Hawaiian Islands, Guam, other tropical Pacific islands or island groups, and all tropical islands globally are summarized in Table 3.

Just over one-half (41 species) of the non-native fishes introduced to Hawaii or Guam are also established globally on other tropical islands/island groups. Excluding Hawaii and Guam, number of islands/groups on which a species became established ranged from 0 to 43 (mean = 3.2). Of the 81 species in our data set, 46 (58%) were introduced to other tropical Pacific islands where they did not become established, and 39 (49%) were introduced to other tropical islands globally but did not become established. Eight species became established on one or more tropical Pacific islands/groups, and 12 species on tropical islands/groups globally, but not in the Hawaiian Islands or Guam.

Table 3. Summary of the numbers of introduced and established non-native fish taxa in inland waters of the Hawaiian Islands and Guam. Values in last two columns represent number of taxa in common with those introduced (established or not) on Hawaiian Islands, Guam, or both. Additional non-native fish species never introduced to Guam or Hawaii but established on other tropical islands are excluded.

Island or island group	Number of taxa introduced	Number of taxa established (percentage of total introduced)	Number of taxa established on other tropical Pacific islands	Number of taxa established on other tropical islands globally
Hawaii	70	46 (66%)	31	37
Guam	25	13 (52%)	15	18
Hawaii plus Guam	81	50 (62%)	35	41

The following numbers and percentages pertain to species introduced to tropical islands/island groups globally. Thirteen species (16%) became established on only one other tropical island/group, and 24 (30%) became established on from 2-12 tropical islands/groups. A few species are widely established among different tropical islands/groups. The most broadly distributed include the Mozambique tilapia, recorded as established on at least 43 other tropical islands/groups, and three different members of the family Poeciliidae: the guppy *Poecilia reticulata* established on 30 other tropical islands/groups; the mosquitofish *Gambusia* spp. – *Gambusia affinis* and *Gambusia holbrooki* identifications are often commingled (Courtenay & Meffe 1989, Fuller et al. 1999) – established on 23 other tropical islands/groups; and the green swordtail *Xiphophorus hellerii* established on 15 other tropical islands/groups. All four of these taxa are also established in Hawaii and Guam. Twenty-two of 23 species introduced into Hawaii or Guam and established on at least three other tropical islands/groups became established in Hawaii or Guam. The giant goramy *Osphronemus goramy* was established on seven other tropical islands/groups, but did not become established after being introduced into Hawaii (Brock 1960, Mundy 2005).

All 81 non-native fishes introduced to Hawaii, Guam, or both places were scored for each of the 13 pathway categories (Fig. S3). Sixty-three of the 81 fish taxa were recorded as being in the aquaculture industry pathway and of these 63% became established. Numbers of species and percentage of these established for the other pathways were: 57 (68%) present in the aquarium trade; seven (86%) stocked as ornamentals; 22 (64%) used as agents for biological control; 20 (55%) stocked or transported as fish for human consumption; 20 (60%) stocked as sport or game fish; six (100%) stocked as forage for other fish; 11 (73%) used as bait; 23 (61%) present in live food markets; two (100%) transported in ballast water; five (20%) occurring as unintentional contaminants with, or in place of, other species, and; one (100%) known to be associated with ceremonial release. No species was scored as having been introduced for conservation purposes. Although rock flagtail *Kuhlia rupestris* has been stocked in Australia to restore populations (Hutchison et al. 2002), in this study it was not scored as such because its introduction to Hawaii, where it failed to establish, was likely for sport fishing (Brock 1960). The total number of pathways any single species scored ranged from one to eight (mean = 2.98). The common carp *Cyprinus carpio*

Table 4. Best models of establishment success of non-native fishes introduced to inland waters of Hawaii and Guam. Only models with Akaike weight ≥ 0.01 are included. Asterisks designate *a priori* models. Model 29 was excluded from comparison since that post-hoc model was two steps removed from being *a priori*.

Model number	Model	Number of parameters in model	Log-likelihood	AIC$_c$	Δ AIC$_c$	Akaike weight
23	Family + history + hypoxia tolerance	5	–39.2382	89.28725	0	0.587
27	Family + history + hypoxia tolerance + salinity tolerance	7	–38.7221	92.9998	3.712554	0.092
19*	Family + history	3	–43.4619	93.23956	3.952312	0.081
25	Family + history + climate profile + hypoxia tolerance	7	–38.9803	93.51617	4.228921	0.071
10*	Family + history + reproductive guild + environmental tolerance	6	–40.7468	94.64419	5.356942	0.040
15*	Family + history + pathways	4	–43.1532	94.83976	5.552514	0.037
18*	Family + history + length	6	–40.8552	94.86112	5.573872	0.036
24	Family + history + salinity	5	–42.7962	96.40313	7.115879	0.017
6*	Family + history + pathways + reproductive guild + environmental tolerance	7	–40.6548	96.86508	7.577831	0.013
22	Family + history + climate profile	5	–43.2218	97.25438	7.967138	0.011
28	Family + history + climate profile + hypoxia tolerance + salinity tolerance	9	–38.6093	97.79007	8.502822	0.008

and Mozambique tilapia were associated with the greatest number of different pathways, each with the maximum of eight categories.

Models of establishment success of non-native fish species introduced to Hawaii and Guam were compared using an information-theoretic approach. The best *a priori* model (19), which was the third best model overall, included an effect of taxonomic affinity (family) and prior establishment success (history) on tropical islands/island groups excluding Hawaii and Guam (Table 4). The best overall model of establishment probability, which was a post-hoc model (23), included a random family effect with a non-zero standard deviation (SD = 2.61), an effect of prior establishment success on tropical islands/island groups, and an effect of hypoxia tolerance (Table 4). This model with the lowest AIC_c and highest Akaike weight had substantial support (Akaike weight = 0.59, evidence ratio = w_{25}/w_{27} = 6.4). No other model had an Akaike weight > 0.1 and the second, third and fourth best models were only minor variations of our best model. Effect of prior establishment success in our best model had a positive slope, as expected ($\hat{\beta}_{\text{history}} = 0.45$, $\hat{SE} = 0.19$), suggesting establishment probability in Hawaii and Guam was higher for species established on a large number of islands/island groups excluding Hawaii and Guam. According to our best model air-breathing fishes were most likely to become established ($\hat{\beta}_{\text{hypoxia 3}} = 2.36$, $\hat{SE} = 1.71$). Fourteen air-breathing species were included in our study; of these, 11 (79%) are established in Hawaii or on Guam, but only the snakehead *Channa* spp. is common to both (Table S1).

Point estimates for the random family effect in our best model ranged from –3.48 to 3.76 (Table S4). Of the nine families represented by two species or more, Cichlidae (3.76), Centrarchidae (2.54), and Poeciliidae (2.11) had the highest point estimates, representing relatively high establishment probability among the families represented in our data set. Osphronemidae (–3.48), Salmonidae (–1.76), and Anguillidae (–0.88) had the lowest point estimates, indicating relatively low establishment probability. These establishment probabilities at the family level are relative to each other since they are drawn from a common distribution.

We plotted probability of establishment based on our best model using the mean of fixed plus random family intercept (Kinney & Dunson 2007) that incorporated the history variable as the x-axis (Fig. 2). The mean estimated establishment probability was 0.37 among all 13 species with a hypoxia score of one and not established on other

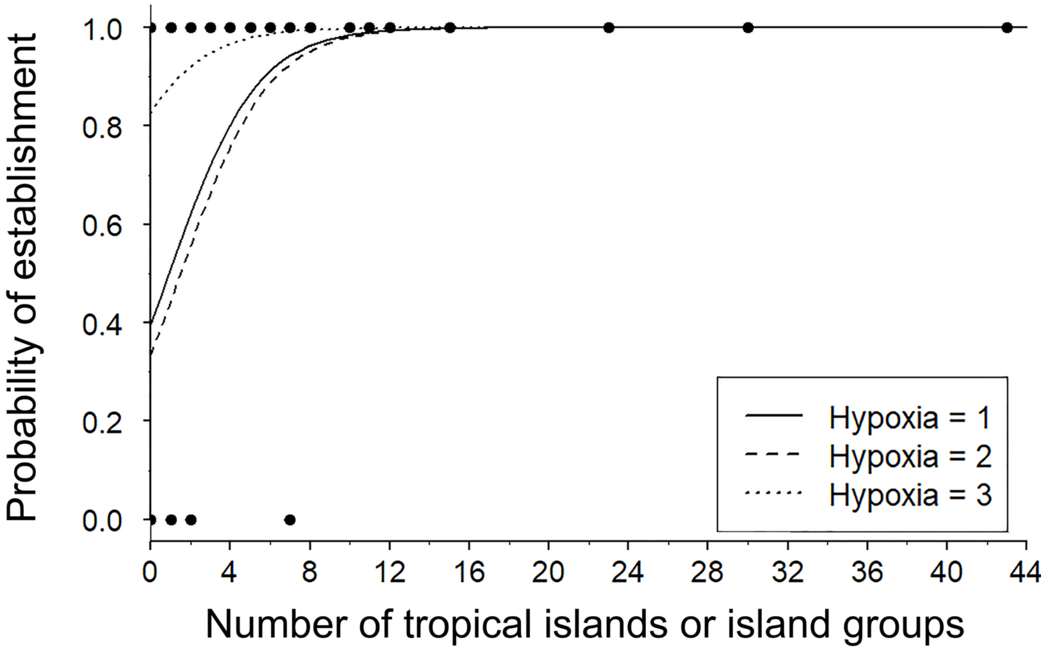

Fig. 2. Probability of establishment of non-native fishes introduced to inland waters of Hawaii and Guam as a function of number of tropical islands/island groups on which a species is established, excluding Hawaii and Guam, and hypoxia tolerance. Logit-scale plots based on mean of fixed plus random family intercept. Hypoxia tolerance score: 1 – intolerant of low dissolved oxygen, 2 – moderately tolerant, 3 – are air-breathers. Closed circles represent number of tropical islands or island groups on which a species is known to be established; many circles represent more than one species.

islands/island groups, using estimated family intercepts (estimated probability was 0.44 using a fixed intercept). Mean estimated probability of establishment was > 0.30 for species with a hypoxia score of one if established on two or more islands/island groups using random family intercepts (estimated probability > 0.66 using fixed intercept), but only three species were in this category in the data set (the brown trout *Salmo trutta*, the channel catfish *Ictalurus punctatus*, and the rainbow trout *Oncorhynchus mykiss*). Species with a hypoxia tolerance score of two had only a 0.06 probability of becoming established if they were not established on any other island/island group using a fixed intercept. However, when using random family effects, the mean estimated probability was 0.39 for the 19 species of this group. The probability rose to > 0.49 for species with a hypoxia score of two and established on six or more islands/island groups using a fixed intercept (mean estimated probability > 0.92 using a random intercept). For eight species established on ≥ 10 islands/island groups, all with a hypoxia score of two, mean estimated probability of establishment was 0.86 using the fixed intercept (0.99 using random family intercepts). Species with a hypoxia tolerance score of three (air breathers) had an 0.89 estimated probability of becoming established if not established on any other island/island group, also using a fixed intercept; the mean estimated probability for the seven species of this group was marginally lower, 0.84, when using random family intercepts. For air-breathing species established on ≥ 3 islands/island groups, the estimated probability was 0.97 using a random family intercept and reached ≥ 0.99 for those on ≥ 6 islands/island groups.

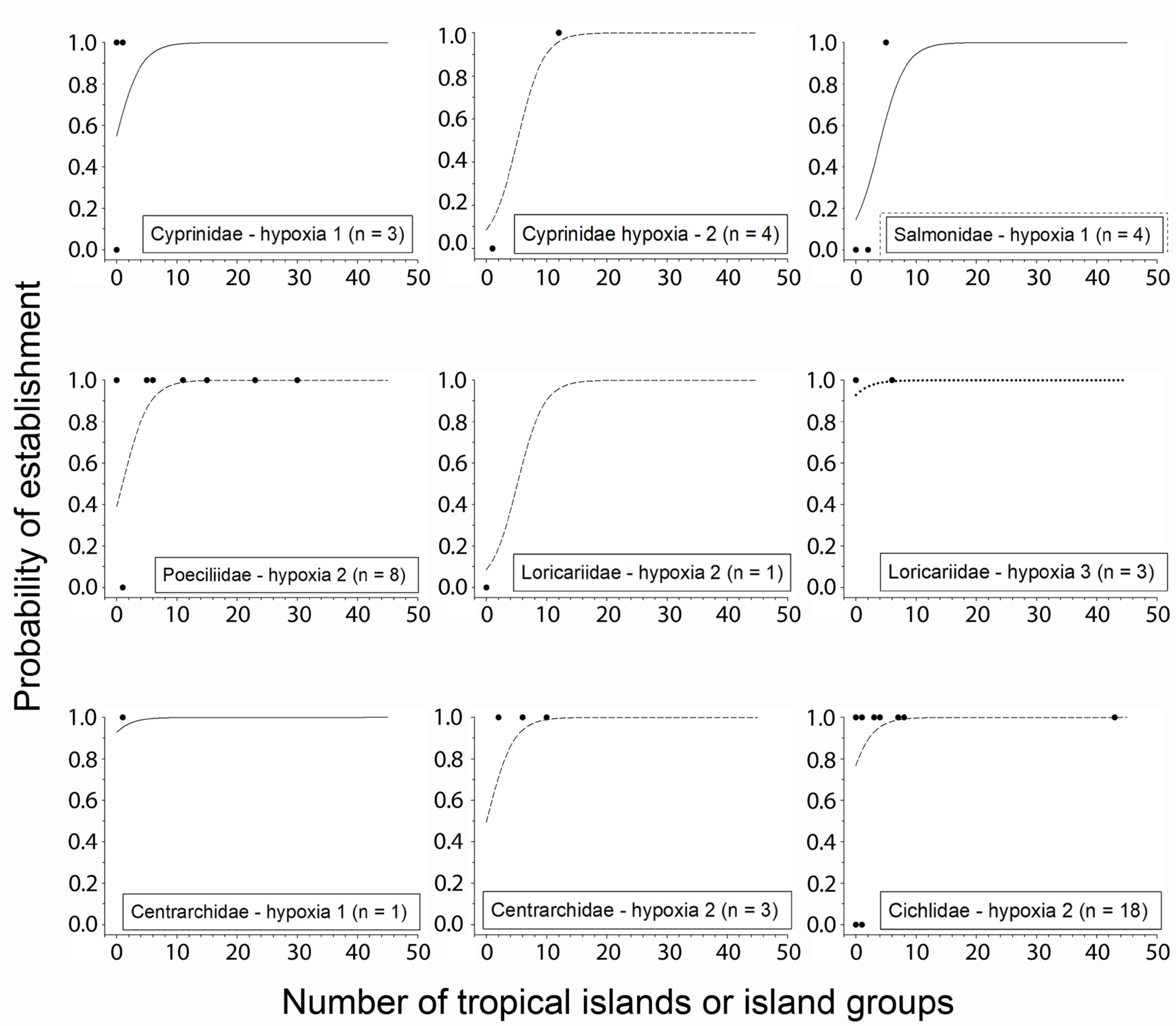

Fig. 3. Probability of establishment of non-native fishes of selected families introduced to inland waters of Hawaii and Guam as a function of number of tropical islands/island groups on which a species is established, excluding Hawaii and Guam, hypoxia tolerance, and family effect used as intercept. N – number of species for each family/hypoxia score combination.

We also plotted estimated probability of establishment for selected families with emphasis of those represented by more than three species in our data set (Fig. 3). Members of the family Cyprinidae with a hypoxia score of one had an establishment probability of 0.55 when not established on other islands/island groups. For cyprinids with a hypoxia score of two, probability was < 0.13 when not established on other islands/island groups but was 0.96 when established on 12 or more islands/island groups, due to widespread introductions of the goldfish *Carassius auratus*, and the common carp. Species of the family Salmonidae, all with hypoxia scores of one, had a probability of 0.15 when not established on other islands/island groups, with the probability increasing to 0.30 and 0.63 when established on two or five island/island groups, respectively. The family Poeciliidae, all species with hypoxia score of two, had a probability of 0.39 when not established on other islands/island groups, but the probability increased to 0.86 and 0.99 when established on five or ten island/island groups. Air-breathing members of the Loricariidae had a 0.93 probability of establishment when not established on other island/island groups, and this probability increased to 0.99 when established on three island/island groups; no loricariids with a hypoxia score of two were reported to occur on other island/island groups. The Centrarchidae (hypoxia scores of one and two) had high establishment probabilities, ranging from 0.71-0.94 if established on two to six other islands/island groups and reaching 0.99 if established on ten island/island groups. The Cichlidae, all with hypoxia score of two, also had high estimated probabilities of establishment ranging from 0.77 if not established on any other islands/island groups, increasing to 0.84, 0.93 and 0.99 if established on no, one, or five other islands/island groups, respectively.

The air-breathing family Channidae had an estimated establishment probability of 0.90 when not established elsewhere (as previously noted, the two snakehead species reported for Hawaii and Guam were treated as a single taxon in our model). Species of the *Channa* complex were established on seven other tropical islands/island groups and the fitted value of establishment probability for this taxon was 0.99 (Table S1).

Using our best-fit model we scored parameters for a set of nine taxa not known to be currently established in Hawaii or Guam to assess possibility

Table 5. Estimated establishment probability of selected fish taxa not known to be currently established in Hawaii or on Guam using parameters of best-fit model (#23). Shading indicates taxa on Guam Division of Aquatic and Wildlife Resources white list permitted for importation.

Family	Scientific name	Common name	Tropical island groups on which established	Hypoxia tolerance score	Establishment probability	Standard deviation
Clariidae	*Heteropneustes* spp.	Stinging or air-sac catfishes	0	3	0.95	0.11
Callichthyidae	*Hoplosternum littorale*	Brown hoplo	0	3	0.92	0.17
Notopteridae	*Notopterus*/*Chitala* spp.	Featherbacks	1	3	0.77	0.35
Lepisosteidae	*Lepisosteus*/*Atractosteus* spp.	Gars	0	3	0.75	0.37
Polypteridae	*Polypterus* spp.	Bichirs	0	3	0.75	0.37
Osteoglossidae/ Arapaimidae	*Scleropages*/*Heterotis* spp.	Australasian/African bonytongues	2	3	0.74	0.36
Mastacembelidae	*Mastacembelus*/*Macrognathus* spp.	Spiny eels	1	2	0.25	0.36
Cyprinidae	*Mylopharyngodon piceus*	Black carp	0	2	0.07	0.11
Cyprinidae	*Pimephales promelas*	Fathead minnow	0	2	0.07	0.11

of future establishment (Table 5). These taxa were selected based on their known or presumed likelihood of presence in pathways of concern, primarily popularity or novelty in the aquarium trade and species used for aquaculture, food, bait, or as biocontrol agents. We also sought to include some species that are on a white list maintained by the Guam Division of Aquatic and Wildlife Resources, which are species that are permitted for importation (Miller 2014). The establishment probability for six of the taxa was greater than 70% with two greater than 90%. The remaining three taxa had an establishment probability of 25% or less. There was considerable imprecision in some of these estimations given the relatively high standard deviations of predicted probability of establishment. This was primarily due to greater relative importance of hypoxia tolerance scores and low numbers of tropical islands/island groups on which the species are established (none for six taxa, one for two taxa, and two for one taxon). Nevertheless, this procedure illustrates how the modelling method can be applied to provide a general estimate of establishment likelihood for taxa of possible concern.

Discussion

In this study the best probability model of establishment success included: a phylogenetic component, indicated by the family to which a species belongs; a history component, characterized by the number of occurrences in which a species previously became established on other tropical islands/island groups globally; and a categorical score of tolerance to low levels of dissolved oxygen (i.e. hypoxia tolerance). Our modelling results were generally consistent with aspects of numerous other studies that examined non-native fish establishment success relative to historical factors and trait-based characters.

Like other oceanic islands with permanent freshwater habitats, Hawaii and Guam have depauperate native freshwater fish faunas (Pippard 2012) and most indigenous species have an amphidromous or catadromous life cycle involving life-history stages requiring both fresh and salt water (McDowall 1988, 2004). In contrast, most fish species introduced to these islands are strictly freshwater in their native environments. However, there are notable exceptions, such as the euryhaline Mozambique tilapia, a species that can survive and reproduce in fresh, brackish, and marine environments and may occasionally make forays into reef habitats (Lobel 1980, Nelson & Eldredge 1991). Nearly all the fish species introduced to Hawaii and Guam belong to families not represented by native species on these islands.

Not unexpectedly, the family-level composition of many fish species introduced and successful at becoming established in Hawaii and Guam includes groups of substantial human value and interest, especially commercially important food species raised in aquaculture, sport fishes, species in the ornamental trade, and species introduced for biocontrol (Maciolek 1984, Eldredge 1994, 2000). This taxonomic and economic bias is common in studies of introduced fishes in other parts of the world (Rahel 2002, 2007, Alcaraz et al. 2005, Jeschke & Strayer 2005, 2006, García-Berthou 2007, Strayer 2010), and such economic-linked introduction pathways are common for freshwater fishes in general (Fuller 2003, García-Berthou et al. 2005, Kerr et al. 2005, Gertzen et al. 2008, Jiao et al. 2009, Strecker et al. 2011, Lapointe et al. 2016, García-Díaz et al. 2018, Piria et al. 2018). Numerous species that became established in Hawaii, on Guam, and many other tropical islands in the Pacific and globally were legal importations and many were intentionally introduced into the wild, often by natural-resource management agencies or entities associated with commercial interests (Nelson & Eldredge 1991, Fuller et al. 1999, Eldredge 2000, Yamamoto & Tagawa 2000). Introductions of fishes and other freshwater species on tropical Pacific islands fall into major chronological periods associated with development and expansion of human activities in the region (Maciolek 1984, Eldredge 1992, 1994, 2000). Although introductions of freshwater fishes to Pacific Islands began in the late 1800s, most introductions occurred from the mid-1900s to the present. It is easiest to identify intentional introductions based on many records for which good sources of published information exist. However, in many cases information is lacking, especially in cases where introductions or establishment were unintentional. We surmise that most cases of unintentional establishment of freshwater fishes on tropical Pacific islands were the result of released aquarium fish, escapement from captive holding facilities, and contaminants associated with intentional introductions. Thus, although there are far fewer studies of freshwater fish introductions to tropical island regions compared to continental faunas, our results corroborate that many of the same factors operate globally in contributing to successful establishment of freshwater fishes in novel regions.

Propagule pressure is widely regarded as a primary determinant of establishment success of non-native species and is a driver for other stages of the invasion process (Kolar & Lodge 2001, Leung et al. 2004, Lockwood et al. 2005, 2009, Colautti et al. 2006, Drake & Lodge 2006, Simberloff 2009, Brockerhoff et al. 2014). Herein, we did not have a specific measure of propagule pressure, given uncertainty or lack of data for most species about total numbers of individuals introduced, frequency of introductions, and numbers of sites where released. However, we consider two conditions in our study to be indirect indicators of relatively high propagule pressure and successful fish establishment: number of tropical islands/island groups on which species were previously established, and number of different pathways through which various species are transported. Many of the non-native fish species that successfully colonized Hawaii and Guam are also established on many other tropical island/island groups globally. The historical component is obviously important and, as such, our best logistic model is congruent with other studies of freshwater fishes that identify prior invasion success as a reliable indicator of successful establishment in other regions. Prior invasion success generally represents a human-interest component (Jeschke & Strayer 2005, 2006). In the Laurentian Great Lakes of North America, introduced fishes with a prior history of invasiveness outside of their native range were more likely to become established (Kolar & Lodge 2002, Rixon et al. 2005, Snyder et al. 2014). In California, the invasion history of introduced fishes has an inherent multivariate dimensionality, with prior invasion success – defined as the number of countries where a species was introduced and became established – indicative of successful establishment (Marchetti et al. 2004a, b, Moyle & Marchetti 2006). On the Iberian Peninsula, prior invasion success of introduced fishes was a good indicator of establishment success as well as other stages of the invasion process (Alcaraz et al. 2005, Ribeiro et al. 2008). In a study of 1,678 introductions of 280 freshwater fish species globally, the number of countries where a species was introduced was a significant estimator of establishment success, and all species (n = 46) introduced to nine or more countries had an established population in at least one country (Bomford et al. 2010).

In terms of pathways, the origins, sources, purposes, approximate dates, and general fate of most intentional introductions of non-native fishes to inland habitats of Pacific islands, including Hawaii and Guam, were reviewed in many publications from which we assembled our data matrix (Brock 1960, Maciolek 1984, Devick 1991, Eldredge 1994, 2000, Englund 2002). As noted, intentional introductions of non-native fishes to inland waters of Hawaii and Guam were primarily to stock sport or game species or their prey, establish breeding populations of food fish in aquaculture facilities or natural water bodies, and biocontrol. This is reflected by several of the families and their respective species listed in Table S1. For example, many of the species introduced for sport or game fishing include cichlids (*Cichla ocellaris*), centrarchids (*Micropterus* spp., *Lepomis* spp.), ictalurids (*Ameiurus nebulosus*, *I. punctatus*), and salmonids (*Oncorhyncus mykiss*, *Oncorhyncus tshawytscha*, *S. trutta*, *Salvelinus fontinalis*). Examples of species stocked to serve as forage base for other fishes, both native and introduced, include clupeids (*Dorosoma petenense*), centarchids (*Lepomis* spp.) and poeciliids (*Xiphophorus* spp.). Included among the many species introduced into inland waters either purposefully or as unintended releases in association with aquaculture or intention to establish populations for harvest as food were cyprinids (*C. carpio*, *C. auratus*, *Hypophthalmichthys nobilis*), clariids (*Clarias* spp.), cichlids (*Oreochromis* spp., *Tilapia* spp.), and channids (*Channa* spp.). Species introduced for biocontrol, typically to manage invasive plants, phytoplankton, other fishes, and mosquito control include cyprinids (*Ctenopharyngodon idella*), cichlids (*Oreochromis* spp., *Tilapia* spp.) and poeciliids (*Gambusia* spp., *Poecilia* spp., *Xiphophorus* spp.). In Australia, most of the earliest (pre-1970) introductions of fishes that became established were species introduced intentionally for purposes such as angling and biocontrol, whereas more recent introductions and establishments (post-1970) were transported via the ornamental trade (García-Díaz et al. 2018). Introductions and establishment of fishes in Hawaii and Guam appears to show the same trend.

Many freshwater fish species present in Hawaii and Guam were introduced via multiple pathways and often repeatedly, a pattern similar to fish introductions on other oceanic islands. This is the case with tilapia (*Oreochromis* spp. and *Tilapia* spp.) that were repeatedly and widely distributed among Pacific islands to establish aquaculture stocks for food, biological control agents, for use as live bait (e.g. tuna fishery), as prey for native species, to enhance fisheries, and for research purposes (Gillett 1990, Nelson & Eldredge 1991, Szyper et al. 2000, De Silva et al. 2004, Nandlal & Pickering 2004). However, tracking the precise pattern of introduction and subsequent dispersal of the different tilapia taxa is problematic due to the existence of numerous hybrids and incorrect identifications. Molecular studies of both captive and naturalized populations indicate that at least seven distinct tilapia lineages currently exist in Hawaii, including both Nile tilapia *Oreochromis niloticus* and *O. mossambicus*, with wild populations exhibiting disproportionate hybridization and introgression among species compared to captive stocks (Szyper et al. 2000, Wu & Yang 2012). In recent decades, the Nile tilapia has replaced Mozambique tilapia as the most common and widely distributed tilapia in aquaculture, partly due to its rapid growth and feed efficiency (De Silva 2012). Like other tilapia species and many other cultured fish taxa, characteristics that make Nile tilapia attractive for aquaculture contribute to its tendency to be highly invasive.

Numerous freshwater fishes found on Pacific Islands are associated with the ornamental garden and aquarium trade and we presume that their presence in the wild is primarily due to releases by pet owners or escapement from ponds (Table S1). Many ornamental species exhibit high propagule pressure, and most species popular in the aquarium trade are tropical and relatively cold intolerant (Courtenay & Stauffer 1990, Padilla & Williams 2004, Rixon et al. 2005, Duggan et al. 2006, Gertzen et al. 2008, Strecker et al. 2011). Given that Hawaii, Guam, and circum-equatorial Pacific islands have a climate that matches regions where most aquarium species are native, it is not surprising that insular areas of Oceania and other tropical areas of the Pacific with substantial human habitation are especially vulnerable to establishment by ornamental freshwater fishes that primarily originate from tropical and subtropical continental regions of Asia, Africa, and South America. Further evidence of the substantial propagule pressure represented by many of the popular aquarium taxa represented in our data set is their disproportionately high representation among ornamental freshwater species introduced into the United States (Chapman et al. 1997), as well as widespread introduction throughout numerous countries of the world (Welcomme 1981, 1988, 1992). Of 32 ornamental species that dominated the trade in the United States by numbers imported and monetary value (Chapman et al. 1997; Table 3), 14 (44%) of the species in Table S1, or a closely related congener, were introduced to Hawaii and/or Guam, of which all but two became established (*Pterophyllum* sp. and *Osteoglossum bicirrhosum*). Moreover, there are large numbers of fish and other aquatic species in the ornamental fish trade that are regularly introduced on a spatial and temporal basis globally to areas where they have not previously been recorded (Mangiante et al. 2018, Chan et al. 2019), suggesting that Pacific Islands, like other freshwater regions of the world with suitable climate, will continue to experience establishment of non-native aquarium fishes in the future.

Unlike previous studies (see Table 2), our *a priori* prediction that life-history attributes such as body size, reproductive mode, or trophic category might influence establishment success of fishes introduced to Hawaii and Guam was not supported by our modelling approach. There are different possible reasons for this. Our data set includes a relatively limited number of species but with a broad range of life-history attributes, such that similarities in traits did not weigh proportionally as in other factors that ranked high in our best models, family and prior establishment history (Table 4). Additionally, there could be multicollinearity between some of our variables. Interspecific comparisons can be compromised by phylogenetic nonindependence, and species-specific variables such as body size or diet can be linked erroneously to invasion risk among taxonomically related species that are invasive for other reasons (Ruesink 2005). Colautti et al. (2006) noted that many introductions of non-native organisms are non-random, and that interpretation of patterns associated with invasiveness may be confounded by “propagule bias”. Our data set clearly includes examples of such non-random introductions, especially groups of fishes (e.g. centrarchids, cichlids, cyprinids, poecilids) exhibiting taxonomic relatedness, conserved life-history features as a result of phylogeny (family membership), and taxa where propagule pressure was particularly high.

Modelling results that support high establishment probability for air-breathing species (hypoxia score 3) conformed to our prediction. However, our model estimate of a higher establishment probability for species with a hypoxia tolerance score of 1 than for species with a score of 2 was unexpected; we predicted species with a score of 1 to have the lowest establishment probability. One possibility for this result is that most natural habitats in Hawaii and Guam are perennial streams characterized by moderate to swift currents and high dissolved oxygen levels. An abundance of such types of streams provides favourable conditions for establishment of species that successfully thrive in normoxic water conditions. However, Hawaii and Guam also have many man-made reservoirs and other artificial aquatic environments that experience frequent drops in dissolved oxygen, conditions that favour non-native air-breathing and hypoxia-tolerant species. It is also possible that the suite of species in our data matrix is comprised of taxa for which there is not a clear differentiation between those with a low to intermediate tolerance of hypoxia and those moderately tolerant of hypoxia, a seemingly good likelihood given the close proximity of the fitted lines (Fig. 2). Tolerance to low dissolved oxygen is commonly associated with invasive fishes. For example, two questions in the Fish Invasiveness Screening Kit (FISK) pertain to these tolerance attributes: 1) are any life stages likely to survive out of water transport, and 2) does the species tolerate a wide range of water-quality conditions, in particular oxygen depletion and high temperature (Copp et al. 2005b)? Moreover, many specialized air-breathing fishes occur in tropical fresh waters where seasonal droughts and hypoxia has selected for a large diversity of aerial respiratory adaptations (Graham 1997). Thus, given that most freshwater fishes introduced to Hawaii, Guam, and other Pacific islands originate from tropical or subtropical regions, it is expected that air-breathing species have a favourable advantage in successfully becoming established.

Our study focused on establishment success of introduced non-native freshwater fishes but did not address subsequent spread and impacts (i.e. invasiveness). Because many invasive fishes seem to have high tolerance to environmental perturbation, further work that examines in detail the competitive advantage of non-native fishes over native species within impaired *vs.* pristine natural habitats would help improve understanding of establishment success. An impact analysis, especially one that might include all 81 species listed in Table S1, would require more detailed information on distributions, abundance, and ecological effects – an analysis beyond the scope of the present study. Nevertheless, certain non-native fishes established in Guam, Hawaii, and other tropical islands are clearly invasive. Many are widespread and abundant and there is a mix of direct or indirect evidence of their ecological impacts. A few of the more harmful island invaders are members of families Poeciliidae, Cichlidae (especially the tilapias), and Loricariidae. For instance, field studies reveal that poeciliids have a marked negative effect on the ecosystem structure, function, and native species abundance of streams and anchialine pool habitats in Hawaii (Englund 1999, Capps et al. 2009, Havird et al. 2013). Some of the affected invertebrates are endemic species, shrimps (Atyidae) and damselflies, a few of which have only recently been added to the United States' list of federally endangered species (USFWS 2016). The widespread introduction of Mozambique tilapia to many islands of the Pacific for aquaculture purposes, beginning with Hawaii in 1951, was later considered an environmental disaster (Nelson & Eldredge 1991). In response, over recent years authorities have eradicated or attempted to eradicate localized island populations of tilapia (Nico & Walsh 2011). There are ongoing efforts to eradicate a number of tilapia and poecilid populations inhabiting wetlands and anchialine pools in Hawaii (Nico et al. 2015).

As in other hotspot areas, the ecological impacts from the many different foreign fish species present in Hawaii and Guam can be considered diverse, complex, often not readily observed, and in many instances unpredictable (Maciolek 1984, Englund 1999, Eldredge 2000, Yamamoto & Tagawa 2000, Capps et al. 2009, Nico et al. 2015). More is known about the detrimental effects of introduced fish populations in Hawaii compared to that of Guam. However, there is anecdotal evidence that streams in Guam with abundant non-native fish species have either fewer native fishes or their distribution patterns differ from historical conditions (GDAWR 2006). Like other regions of the world, the primary impacts that established non-native freshwater fishes are thought to have on native aquatic communities of Pacific islands are the result of predation, competition, habitat alteration, and introduction of parasites and pathogens (Maciolek 1984, Eldredge 2000, Englund et al. 2000, Englund 2002, 2008, Brasher et al. 2006, MacKenzie & Bruland 2012). However, most of these factors are not well studied on tropical Pacific islands and there would be potential benefit for focused research in this area.

The geographic isolation of Hawaii and Guam from major land masses is reflected in the unique biogeographic and evolutionary histories of their faunas, including their fishes (e.g. McDowall 2003). In general, isolated oceanic islands, have few, if any, native animals that prey on fish or other vertebrates. The few native fishes that penetrate inland freshwater habitats of these islands are mostly small-bodied species that feed largely on invertebrates, whereas large-bodied, native piscivorous fishes tend to be absent or uncommon in freshwater environments of the more isolated islands. For instance, Hawaii has only five indigenous freshwater fish species, all gobiiforms that feed on invertebrates and algae, and that spend only part of their life in streams, with the remainder in marine habitats (Kido 1996, 1997). A general lack of native piscivores, presence of numerous man-made artificial aquatic habitats (e.g. reservoirs, concrete channels), degradation of natural habitats, and a tropical climate all contribute to greater likelihood that introduced fish will become established. In Hawaii, perturbation to natural habitats (including presence of non-native fishes) strongly affects community composition of aquatic insects (Englund et al. 2007). Moreover, in modern times, because both Hawaii and Guam rely extensively on imported goods, overseas resources, and tourism, there exists numerous and frequent vectors and pathways available to introduced aquatic species. The type, ease, and rapidity of invasion on tropical islands *vs.* continental and temperate regions all likely differ. For example, the isolation and perennial conditions conducive for spawning on small tropical island ecosystems may result in the establishment and rapid spread of an invasive species over an entire island. Consequently, compared to continental and temperate regions, direct and indirect impacts of invaders often extend across the entire island ecosystem. Tools such as the establishment-potential model in the present study can inform critical preventive measures for invasive species management in these invasion-prone regions.

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Supplementary online material

Appendix S1. Variable selection.

Appendix S2. Results of model fitting procedure.

Table S1. Status of nonindigenous freshwater fishes known to have been introduced into Hawaii and Guam since the late 1800s. Status: 0 – introduced, not known to be established; 1 – established, defined as a self-sustaining, wild population. Species of questionable identity indicated by use of "cf.," "?," "sp.," or "complex." Shading indicates air-breathing species. Fitted values for best model (#23) of establishment success in risk analysis (see text).

Table S2. List of tropical and subtropical islands, island groups, and/or country names, excluding Hawaii and Guam, reviewed for records of non-native inland fish species introductions.

Table S3. Data matrix used in frequentist models for risk assessment of establishment success for non-native inland fishes of Hawaii and Guam. HS, status in Hawaii; GS, status in Guam (0 – introduced, not established; 1 – established). Variable codes correspond to Table 1; sum – total number of pathways (variable 3).

Table S4. Parameter estimates from the best model of establishment success of non-native inland fishes in Hawaii and Guam. Included is the estimate for the fixed intercept (no family effect) and estimates for each family (random intercept).

(https://www.ivb.cz/wp-content/uploads/JVB-vol.-70-4-2021-Walsh-et-al.-Appendix.-S1-S2-Table-S1-S4.pdf)

Fig. S1. Error rate for the best model. A vertical dashed line connects the predicted and observed dots for the seven species that were misclassified by the model. Horizontal solid line indicates probability of establishment = 0.50 (https://www.ivb.cz/wp-content/uploads/JVB-vol.-70-4-2021-Walsh-et-al.-Fig.-S1.jpg).

Fig. S2. Of 1,000 simulated data sets generated using the most general model, 57.5% contained more species that failed to establish than the 38.8% present in the actual data (horizontal line) (https://www.ivb.cz/wp-content/uploads/JVB-vol.-70-4-2021-Walsh-et-al.-Fig.-S2.jpg).

Fig. S3. Numerical scoring by possible pathways for model data set of fishes introduced and established in inland waters of Hawaii and Guam (https://www.ivb.cz/wp-content/uploads/JVB-vol.-70-4-2021-Walsh-et-al.-Fig.-S3-scaled.jpg).