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Ecological determinants of parasite acquisition by exotic fish species

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Disease-mediated threats posed by exotic species to native counterparts are not limited to introduced parasites alone, since exotic hosts frequently acquire native parasites with possible consequences for infection patterns in native hosts. Several biological and geographical factors are thought to explain both the richness of parasites in native hosts, and the invasion success of free-living exotic species. However, the determinants of native parasite acquisition by exotic hosts remain unknown. Here, we investigated native parasite communities of exotic freshwater fish to determine which traits influence acquisition of native parasites by exotic hosts. Model selection suggested that five factors (total body length, time since introduction, phylogenetic relatedness to the native fish fauna, trophic level and native fish species richness) may be linked to native parasite acquisition by exotic fish, but 95% confidence intervals of coefficient estimates indicated these explained little of the variance in parasite richness. Based on R^2-values, weak positive relationships may exist only between the number of parasites acquired and either host size or time since introduction. Whilst our results suggest that factors influencing parasite richness in native host communities may be less important for exotic species, it seems that analyses of general ecological factors currently fail to adequately incorporate the physiological and immunological complexity of whether a given animal species will become a host for a new parasite.

Disease threats mediated by exotic host species frequently involve introduced parasites (Cunningham et al. 2003, Tompkins et al. 2003). However, as exotic species often lose their original parasites during translocation (MacLeod et al. 2010), their parasite burdens may be dominated by native parasites acquired in their new locality rather than those retained from their area of origin (Torchin et al. 2003, Kelly et al. 2009). This is the case, for example, for the many exotic fish species that have been translocated globally as parasite-free eggs or juveniles (e.g. *Oncorhynchus mykiss*, Ortubay et al. 1994; *Salmo trutta*, Hine et al. 2000). Disease threats mediated by exotic species are therefore likely to involve altered native host–parasite dynamics (Tompkins et al. 2011), which potentially result in either the spillback (Daszak et al. 2000, Kelly et al. 2009) or dilution of native infection (Telfer et al. 2005, Thieltges et al. 2009).

While native parasites can dominate the parasite communities of exotic host species, both the number and type (e.g. endo- or ecto-parasites) of acquired native parasites differ among exotic hosts (Kelly et al. 2009, Poulin et al. 2011). Two sets of factors may potentially influence such acquisition. First, several biological and geographical factors have been shown to influence parasite richness in fish species, including host size, diet, density and geographical range (Bell and Burt 1991, Poulin 1997, Sasal et al. 1997, Morand et al. 2000). Having influenced the acquisition and accumulation of parasite species by particular host lineages over evolutionary time, such factors may also be important in determining the shorter time-scale acquisition of native parasites by exotic host species. Second, biological factors determining the success of exotic free-living species after introduction to new regions have also been identified in the literature; in the case of fish, these include habitat, migratory behaviour and phylogeny, among others (Kolar and Lodge 2001). Understanding the importance of these factors appears essential for predicting and managing disease emergence. However, although such factors may also influence the richness of native parasites acquired by exotic fish, the latter hosts are frequently excluded from comparative studies of the determinants of parasite richness, as short-term geographic and historical influences can obscure the effect of basic biological traits on rates of parasite acquisition (Luque and Poulin 2007). When studies of parasite richness have included exotic fish, distinctions between traits and factors influencing native and exotic hosts have not been made (Price and Clancy 1983).

In order to predict which exotic fish species are likely to pose disease-mediated threats to sympatric native populations via spillback, it is necessary to identify the factors that increase the probability of exotic fish acquiring native parasites. This question is addressed here by analysis of a large database compiled from the literature. Specifically, we used an information-theoretic approach based on model selection to investigate the influence of a series of biological and geographical traits reported to affect the invasion success of exotic species and/or the parasite species richness of freshwater fish.

Methods

Data collection

Searches of both literature databases and the internet were performed to obtain freshwater fish parasite checklists (i.e. lists of the parasite species found in each fish species in a given area). Checklists were selected according to the following criteria: 1) publication in English or Spanish, 2) identification of the majority of parasites to species level, and 3) availability of supporting reference material. Fish parasite checklists from 10 geographical areas met these criteria and were searched for parasite species present in exotic freshwater fish (or those with a freshwater phase): Argentina (Patagonia only; Ortubay et al. 1994), Australia (Beumer et al. 1982), Canada (Margolis and Arthur 1979, McDonald and Margolis 1995), Chile (Olmos and Munoz 2006), Czech Republic and Slovak Republic (Moravec 2001), Hawaii (Font 2003), Ireland (Holland and Kennedy 1997), Puerto Rico (Bunkley-Williams and Williams 1994), Mexico (Salgado-Maldonado 2006) and New Zealand (Hine et al. 2000).

All native parasite taxa in exotic fish (present in both native and exotic fish in the exotic fish's introduced range only) were identified; to avoid incorrectly classifying the origin of a parasite species, only parasites with full taxonomic names were included. Parasites classified as introduced (present in the exotic fish's original range only), or of unknown/cryptic origin (distribution of parasite could not be verified from literature) were excluded. Parasites present in both the original and introduced range of an exotic fish were also excluded from analyses, as were those with worldwide distributions (to avoid incorrectly classifying parasites that might infect exotic fish in their original ranges but have not been detected due to low sampling effort). Furthermore, only monogeneans, trematodes, cestodes, nematodes, acanthocephalans and copepods, including all life stages, were included in analyses because other taxa, such as protozoa or myxosporea, were seldom sampled or infrequently reported.

The total number of native parasite species acquired by an exotic fish in each of its introduced ranges was determined. Although Poulin (2004) recommends distinguishing between endo- and ecto-parasites because different host traits are likely to influence whether parasites with direct or complex lifecycles are acquired by a fish, endo- and ecto-parasites were not analysed separately as relatively few ectoparasites were reported.

Sampling effort strongly influences estimates of parasite richness (Walther et al. 1995), but freshwater fish parasite checklists seldom report the number of hosts examined or the duration of sampling (e.g. seasons or years). To account for the effects of unequal sampling on parasite richness, an index of study effort was calculated by determining the number of publications for each exotic fish species per geographical region. The country of introduction, the exotic fish's Latin name and all known synonyms, extracted from FishBase (Froese and Pauly 2010), were used as keywords in a search of the Zoological Record (1864−), with the upper date limit set as the checklist's publication year. This measure of study effort provides an estimate of the research activity targeting a given fish species, and thus of the relative number of individual fish examined for parasites (Luque and Poulin 2007). As study effort values showed a right-skewed distribution, and because zero values were recorded during this period for some species, study effort was log $x + 1$ transformed to achieve a normal distribution. Zero values (i.e. no publications included in Zoological Record) indicate that some fish species have received very little research attention in their country of introduction.

Predictors of parasite richness

A series of factors that relate to the exotic fish's biological traits or their places of introduction were selected for analysis as outlined below. Although factors that may influence parasite richness were selected on the basis of our current understanding of the evolution of parasite faunas (Poulin 1997), it is acknowledged that native parasite richness in exotic fish may be influenced by additional factors not included in this study. With the exception of phylogenetic relatedness, all traits were parameterised from species data available from FishBase (Froese and Pauly 2010).

Biological traits

Six biological traits (host size [total length], host age, host diet, trophic level, phylogenetic relatedness with the native fish fauna, and migratory behaviour) were identified from previous studies as potential determinants of parasite richness. Host size in particular is frequently invoked as a determinant of parasite richness in fish (Price and Clancy 1983, Guégan et al. 1992, Poulin 1997, Lo et al. 1998), although this relationship may not be the same for endo- and ecto-parasites (Sasal et al. 1997). Host age may also influence parasite richness because long-lived hosts accumulate more parasites (Morand 2000), but note that there may be collinearity between host size and host age because large hosts tend to be long-lived. Host age was quantified as the maximum reported age (years), whereas for host size Length–Length relationship tables (Froese and Pauly 2010) were used to calculate the maximum total length (cm) when only standard or fork length was reported.

Host diet has also been shown to influence parasite richness. This is especially the case for endoparasites that rely on trophic transmission for completion of their life cycles, while it may be of less importance to ectoparasites that rely on direct transmission between host individuals. The diet of each exotic fish species was categorised as detritivore (detritus only), planktivore (phytoplankton only), zooplanktivore (zooplankton, or phyto- and zooplankton), omnivore (plant and invertebrates/fish), insectivore (invertebrates only), carnivore (invertebrates and fish) or piscivore (predominantly fish). Species consuming plants and detritus were considered omnivores because their diet may also include animal tissues. Fish consuming both phytoplankton and zooplankton were classified as zooplanktivores to reflect the presence of animals in the diet. Although host diet is known to change with host age, host diet was classified for adults because juvenile diet was seldom reported. The trophic level of a host is an alternative measure of the influence of diet, and has also been shown to be positively correlated with parasite richness (Luque and Poulin 2008). Trophic level was estimated from the number of energy transfer steps separating a fish species from basal resources; these were obtained for each fish species from FishBase (Froese and Pauly 2010).

Phylogenetic relatedness of an exotic fish to the native fish fauna may affect the probability of native parasite acquisition by exotic fish, because parasites adapted to a specific native fish genus or family may be more likely to be acquired by an exotic fish of the same genus or family than by more distantly related fishes (Freeland 1983). Given the absence of complete phylogenetic trees, phylogenetic relatedness was quantified as the number of taxonomical steps between an exotic species and the closest native species in the fauna of the country of introduction (exotic fish and closest native species are in the same genus = 1 step, same family = 2 steps, same order = 3 steps).

Migratory patterns of exotic fish also have the potential to influence native parasite acquisition, because fish moving between different freshwater habitats (potamodromous species) are likely to encounter different suites of parasites associated with different populations or species of native fish. Moreover, fish with a marine phase may acquire fewer native parasites because these hosts are only present in freshwater habitats for a portion of their life. This is especially true for anadromous species that utilise freshwater habitats for breeding but do not feed in freshwater environments, thus reducing their encounter rates with trophically-transmitted parasites. In contrast, the migration patterns of catadromous species, which spend the majority of their lives in freshwater environments, should have a lesser impact on the acquisition of native parasites because these only enter marine environments for breeding. Here, we separated exotic fish species into four categories: non-migratory, potamodromous, anadromous or catadromous.

Geographic factors

We identified four factors (latitude of introduced region, latitudinal difference between original and introduced regions, time since introduction, richness of native fish fauna) associated with the country of introduction that may influence native parasite acquisition. The difference between the mean latitude of an exotic fish's original distribution and that of the region of introduction was calculated. Freshwater fish from temperate regions have been shown to have greater parasite richness than those from tropical regions when the effects of host size and sampling effort are taken into account (Poulin 2001), suggesting that fish introduced to mid-latitude regions may acquire more native parasites due to the greater availability of parasite species.

Local parasite richness is often positively correlated with local host richness (Watters 1992, Krasnov et al. 2004, Thieltges et al. 2011); therefore, the number of native hosts present in a country may also influence the size of the pool of native parasites available for acquisition by exotic hosts. The probability of an exotic species acquiring native parasites may also increase with the length of time the exotic species has been in a new habitat. Time since introduction was calculated as the difference between the year of introduction and publication date of the parasite checklist.

Statistical approach

The influence of predictor variables on total number of native parasites acquired was analysed using a generalised linear mixed model (GLMM) fitted with a quasipoisson distribution (log link function), within a framework of quasi-Akaike information criterion (QAIC) and model averaging (Bolker et al. 2009). The QAIC was selected rather than an Akaike information criterion (AIC), because the quasi-poisson distribution in the former takes into account the over-dispersed nature of the response variable (number of native parasites acquired). As collinearity amongst explanatory variables can cause problems with model selection and parameter estimation (Freckleton 2010), potential collinearity between positively correlated predictors was investigated by preliminary data exploration. Each positively correlated predictor (e.g. host size and host age; host diet and trophic level; introduced latitude and richness of native fish fauna) was evaluated in separate preliminary GLMM's, with predictors with the strongest model values included in the global set to generate a sub-set of variables that could potentially influence parasite species richness in exotic fish species. Preliminary data exploration revealed that variation in migratory behaviour and latitudinal differences between original and introduced locations did not have strong influences on parasite richness and these were excluded from further analysis to avoid over-parameterising the model. The final set of explanatory variables included host length, trophic level, time since introduction, phylogenetic relatedness with the native fish fauna, and richness of the native fish fauna. Our final dataset included only fish species for which data for all explanatory variables were available because missing data prevents model averaging.

The global model included study effort as a random effect, to control for the influence of differential sampling on estimates of parasite richness. Fish species was also included as a random effect as some exotic fish species were introduced to multiple countries, and each introduction event was treated as a separate data point. No interaction terms were included in the global model because we did not hypothesise strong interactions between any of the explanatory factors. The global model that included the final set of explanatory variables was fitted using the package lme4 (Bates and Maechler 2009) of the program R. A set of all possible sub-models was created from the global model using the R package MuMIn functions (Barton 2010). The quasi-likelihood information criterion (QAICc) was calculated by hand, and was used in conjunction with model averaging ('zero' method) to rank all sub-models within 4 QAIC_C of the best model. The model-averaged parameter estimates, standard errors (SE), 95% confidence intervals and relative importance of each explanatory variable are reported for the top models.

Results

Our final data set comprised 39 exotic freshwater fish introductions involving 26 different fish species in the Cypriniformes (six introductions), Cyprinodontiformes (three), Perciformes (14) and Salmoniformes (16; Table 1). Exotic fish acquired on average 2.4 (range 1–8) native parasites per fish per introduced locality, of which the majority were endoparasites (86.6 %).

From the global model, a total of 32 possible models was produced from the data-dredging function in R, of which 13 models were found to be within 4 QAIC of the best supported model (Table 2). All predictor variables were included in at least one of these 14 top models; host length was included in all, while time since introduction was included in half. However, 95% confidence intervals for all predictor variables included zero, suggesting that no predictors included in our analyses explained a significant proportion of the variance in parasite richness (Table 3). R^2-values, calculated for each predictor variable, showed that a weak relationship existed only between the number of native parasites acquired and host size or time since introduction (Fig. 1).

Discussion

Although numerous studies have reported that parasite species richness is influenced by a number of factors associated with the host's biology or geography (Watters 1992, Poulin 1997, 2001, Morand et al. 2000), our study found that none were strong predictors of the number of native parasites acquired by exotic fish. Traits known to influence invasive species establishment also had little

Table 1. The number of native parasites acquired, and host and geographical characteristics for each exotic fish species according to country of introduction.

				Host characteristics		Geographical characteristics		
Country	Host	Native parasites	Study effort (log transformed)	Total length (cm)	Trophic level	Time since introduction (years)	Native fish species richness	Phylogenetic relatedness (steps)
Argentina	*Oncorhynchus mykiss*	8	1.000	120	4.42	90	485	4
	Salmo salar	1	1.176	150	4.43	90	485	4
	Salmo trutta	2	0.778	150	3.16	90	485	4
	Salvelinus fontinalis	3	0.903	95	3.14	90	485	4
	Salvelinus namaycush	1	0.000	150	4.29	90	485	4
Australia	*Carassius auratus*	1	0.954	59	2.00	107	319	4
	Oncorhynchus mykiss	1	1.204	120	4.42	89	319	4
	Salmo trutta	2	1.653	150	3.16	119	319	4
Canada	*Cyprinus carpio*	7	1.301	126	2.96	164	206	2
	Salmo trutta	4	1.623	150	3.16	90	206	2
Chile	*Oncorhynchus mykiss*	4	1.863	120	4.42	101	44	4
	Salmo trutta	4	1.491	150	3.16	101	44	4
Czech and Slovak Republics	*Carassius gibelio*	1	0.903	45	2.54	29	76	1
	Ctenopharyngodon idella	4	0.778	150	2.00	40	76	2
	Lepomis gibbosus	5	1.041	40	3.12	72	76	3
	Oncorhynchus mykiss	3	1.322	120	4.42	110	76	2
	Pseudorasbora parva	2	0.778	11	3.04	36	76	2
	Salvelinus fontinalis	4	1.079	95	3.14	111	76	2
	Thymallus baicalensis	1	0.699	35	3.53	42	76	1
Hawaii	*Poecilia reticulata*	1	0.954	8	3.20	103	7	4
	Xiphophorus helleri	1	0.699	14	3.19	81	7	4
Ireland	*Oncorhynchus mykiss*	3	1.146	120	4.42	97	21	2
Mexico	*Oreochromis aureus*	6	1.279	46	2.07	40	511	2
	Oreochromis mossambicus	4	1.146	47	2.00	40	511	2
	Oreochromis niloticus	2	1.114	76	2.00	40	511	2
	Oreochromis urolepis	1	0.778	31	2.00	26	511	2
	Tilapia zillii	1	0.778	52	2.00	59	511	2
New Zealand	*Carassius auratus*	2	0.954	59	2.00	134	40	4
	Oncorhynchus tshawytscha	2	1.875	150	4.40	124	40	4
	Perca fluviatilis	2	1.000	72	4.35	133	40	3
	Salmo trutta	5	2.053	150	3.16	133	40	4
Puerto Rico	*Lepomis auritus*	1	0.000	31	3.12	37	22	3
	Lepomis macrochirus	1	0.000	41	3.18	79	22	3
	Lepomis microlophus	1	0.000	43	3.39	37	22	3
	Micropterus coosae	1	0.000	47	3.60	36	22	3
	Oreochromis aureus	1	0.000	46	2.07	23	22	3
	Oreochromis mossambicus	2	0.477	47	2.00	36	22	3
	Poecilia reticulata	2	0.301	8	3.20	59	22	3
	Tilapia rendalli	1	0.000	45	2.18	31	22	3

Table 2. The 14 top-ranked models sorted by corrected quasi-Akaike information criterion (QAICc), with model deviance, difference in QAICc from the best model ($\Delta QAIC_C$) and model weights ($QAIC_W$). Models within 4 QAICc of the top model were considered in the top model set.

Response	Model	Deviance	$QAIC_C$	$\Delta QAIC_C$	$QAIC_W$
Parasites	Total length + Time since introduction	35.88	114.68	117.56	0.17
	Total length + Phylogenetic relatedness + Time since introduction	35.01	114.24	118.12	0.13
	Total length + Time since introduction + Trophic level	35.13	114.59	118.47	0.11
	Total length + Phylogenetic relatedness	36.27	115.79	118.68	0.10
	Total length + Trophic level	36.34	115.99	118.87	0.09
	Total length + Phylogenetic relatedness + Trophic level	35.53	115.70	119.58	0.06
	Total length + Native fish species richness + Phylogenetic relatedness	35.63	115.98	119.86	0.06
	Total length + Phylogenetic relatedness + Time since introduction + Trophic level	34.58	115.04	120.10	0.05
	Total length	37.71	117.83	119.89	0.05
	Total length + Native fish species richness + Time since introduction	35.72	116.23	120.11	0.05
	Total length + Native fish species richness + Phylogenetic relatedness + Time since introduction	34.72	115.42	120.49	0.04
	Total length + Native fish species richness + Trophic level	36.14	117.41	121.29	0.03
	Total length + Native fish species richness	37.21	118.42	121.30	0.03
	Total length + Native fish species richness + Time since introduction + Trophic level	35.06	116.40	121.46	0.02

power to predict whether exotic species subsequently acquire native parasites upon introduction to a new area. At best, both host size and time since introduction have weak influences on native parasite acquisition, with larger-bodied species or those introduced earlier having marginally more native parasites than recently introduced or smaller-bodied species. Neither of these relationships, if real, is unexpected. Host size is often considered a major determinant of parasite species richness in native fish (Price and Clancy 1983, Guégan et al. 1992, Lo et al. 1998), while the time since introduction has also been shown to affect parasite acquisition in fish when the time scale considered is relatively long (Guégan and Kennedy 1993). For exotic plants as well, time since introduction has a strong influence on pathogen acquisition, with species introduced 400 years ago acquiring over six times more pathogens than those introduced 40 years ago (Mitchell et al. 2010).

Diet and/or trophic level are often invoked as determinants of parasite species richness, especially for endoparasites that rely on trophic transmission. More specifically, Chen et al. (2008) demonstrated that host species with high parasite richness are characterised by having wider diet ranges or occupying food-chain positions that are either close to many prey species or that allow them to accumulate parasites from lower trophic levels. Although the majority of native parasites acquired by exotic fish in this study were endoparasites, neither trophic level nor diet was a strong determinant of parasite richness of exotic fish. Similarly, the presence of closely related species had no clear relationship with parasite acquisition, although host phylogenetic relatedness often constrains the spectrum of host species that a parasite can infect (Mitchell et al. 2010). For instance, both *Carassius gibelio* and *Thymallus baicalensis* introduced to the Czech and Slovak Republics, where native *Carassius* sp. and *Thymallus* sp. are present, acquired only one native parasite species each, while exotic fish with no close phylogenetic affinities to any species in the native fish communities showed highly variable native parasite acquisition.

The results of this study suggest that some predictors of parasite richness in native communities may be less important for exotic species. For example, while parasite species richness may be related to the diversity of native hosts, which itself is correlated to the size of available habitat (Thieltges et al. 2011), an exotic species may occupy only a small portion of this habitat and interact with only a fraction of the native fish fauna. This restricts the potential pool of parasites that an exotic species may encounter, making the overall number of native fish present or habitat size poor predictors of the potential to acquire native parasites. Measures of the relative area invaded or of the proportion of native fish actually encountered by an exotic fish species (both currently unavailable) may reveal stronger correlations with native parasite acquisition.

It is of course possible that other biological or geographical traits not considered here may determine native parasite acquisition by exotic hosts. To account for this potential bias, a wide set of biological and geographical traits were included in the initial model set, with traits subsequently removed from the global model based on collinearity. There is also a limit to the number of predictor traits that can be

Table 3. Standardized coefficients of model predictors for number of native parasites acquired by exotic freshwater fish, after model averaging of 14 top candidate models (Table 2).

Response	Predictor variable	Σ	Estimate	SE	95% CI
Parasite	Intercept		0.787	0.473	−0.455 to 1.402
	Total length	1.00	0.006	0.003	−0.003 to 0.008
	Time since introduction	0.58	−0.001	0.001	−0.0008 to 0.002
	Phylogenetic relatedness	0.44	−0.058	0.070	−0.067 to 0.208
	Trophic level	0.37	−0.051	0.067	−0.065 to 0.200
	Native fish species richness	0.22	6.889×10^{-5}	0.00015	−0.0001 to 0.0004

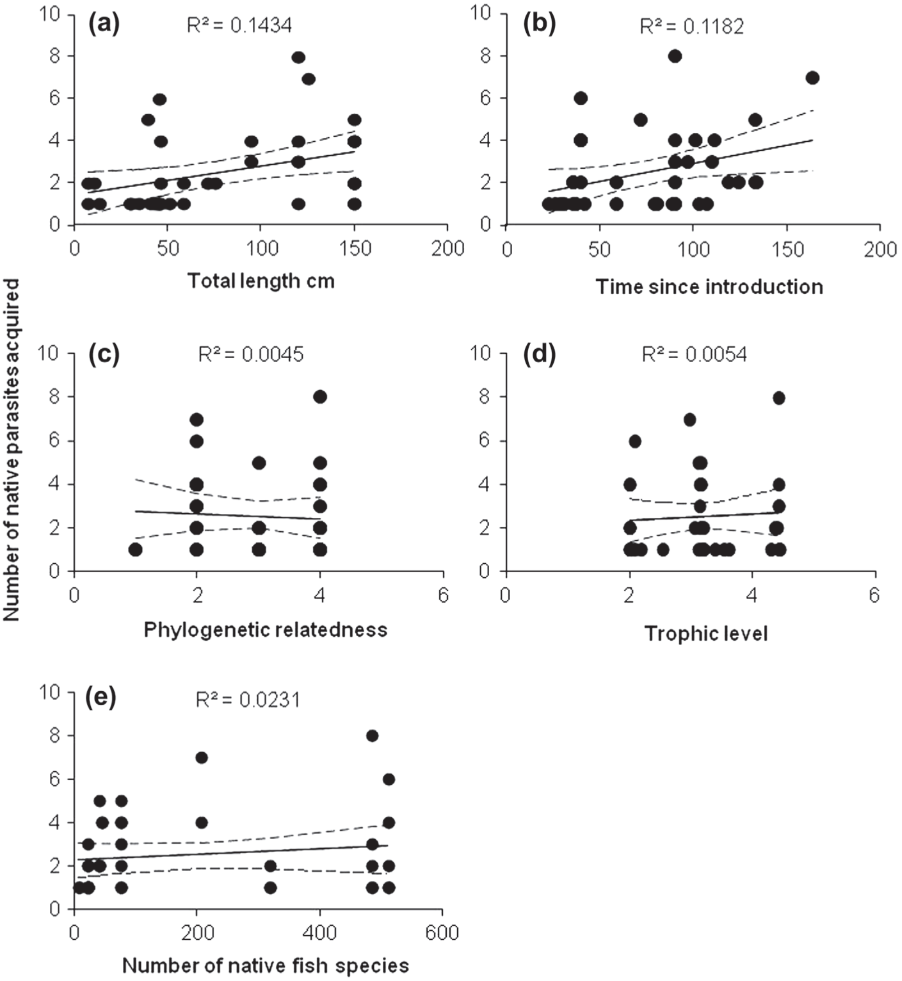

Figure 1. The relationships between the number of native parasites (raw data) acquired by exotic fish host species and (a) total length, (b) time since introduction, (c) phylogenetic relatedness with the native fish fauna, (d) trophic level and (e) the richness of the native fish fauna. R^2 values represent the proportion of the variance explained by each predictor. Confidence bands (95% confidence intervals - dashed lines) are displayed around the regression line (solid line).

included in GLMM's for a model to be fit, so only the traits with greatest influence on parasite richness in exotic fish (based on univariate exploratory analyses) were incorporated in the global model. Additionally, the statistical power necessary to detect which factors influence parasite acquisition may be reduced in situations such as this, where the acquisition of a native parasite by an exotic species is a relatively rare event (Torchin et al. 2003, Kelly et al. 2009).

Alternatively, it may be that the process of becoming a host for a new parasite depends on a complex set of interactions involving aspects of host biology and particular spatial and temporal scales that cannot be measured by a few generalised factors. For instance, the compatibility of a parasite for a novel host at the physiological or immunological levels is probably independent of that host's size, its latitude of origin, or how long it has been introduced to the parasite's area. In both the original region of the exotic species and in the native parasite's region, parasites have evolved adaptations over very long time scales that allow them to infect locally available hosts (Morand et al. 1996, Kaltz and Shykoff 1998). However, when exotic species are introduced to new localities, the evolutionary timescale for such adaptations to develop is relatively short. Host–parasite encounter may be strongly dependent on host ecology, but host–parasite compatibility allowing a parasite to establish inside a novel host will either require numerous generations to evolve or perhaps already exists, but independent of the ecological factors included in the present analysis. Host–parasite compatibility may therefore be unpredictable based on ecological variables, or at least those currently quantified. Furthermore, the likelihood that an exotic fish will acquire native parasites may also be a function of the proportion of generalist parasite species available in a locality, since these are more likely to be acquired by novel hosts (Poulin and Mouillot 2003, Kelly et al. 2009). If this is the case, disease threats mediated by the acquisition of native parasites by exotic hosts are likely to involve generalist parasites, while modified host–parasite dynamics resulting in parasite dilution could involve either generalist or specialist parasite species.

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