Biol Invasions (2016) 18:3495–3512
DOI 10.1007/s10530-016-1241-z

ORIGINAL ARTICLE

Native richness and species level trophic traits predict establishment of alien freshwater fishes

J. H. Liew · L. R. Carrasco · H. H. Tan ·
D. C. J. Yeo

Received: 16 September 2015 / Accepted: 24 July 2016 / Published online: 8 August 2016

Abstract Community level ecological traits are thought to affect invasibility as more diverse communities with complex trophic interactions may be associated with greater biotic resistance. Elucidation of the nature of this relationship is often hampered by difficulties in characterising food webs, particularly where field data are lacking. We attempted to overcome this by coupling food web modelling with information-theoretic analysis of the modelled webs. In addition, we also investigated the possibility that species level trends in trophic traits of established aliens might reflect exploitation of empty niches. We constructed hypothetical food webs of 26 natural and artificial lentic habitats from a data set consisting of 370 fish species representing 71 families. Using these food webs, we investigated associations at the community level between food web traits and network topology and number of alien fish species using an information-theoretic approach based on a set of competing a priori hypotheses. At the species level, we similarly tested for trends in trophic traits of established alien fishes using the information-theoretic approach in addition to *nMDS* of diet data. We found that native species richness in a community was the most important determinant of the number of alien fish taxa, displaying an inverse relationship. Our data also show that alien fish generally feed lower down the food web. Our findings suggest that the biotic resistance hypothesis, though scale dependent, can result in observable effects in animal communities. Moreover, we also found that the ability to exploit low energy yield food sources could favour the establishment of alien species via avoidance of resistive forces from native taxa.

Keywords Biotic resistance · Aquatic food webs · Biological invasion · Invasibility · Competitive exclusion

Introduction

Biological invasions are a major driver of species loss, contributing to up to 54 % of extinctions with documented causes (Clavero and García-Berthou 2005). The ecological damage often attributed to biological invasions, and the need to prevent and manage invasions, has motivated studies seeking to characterise the invasion process and identify factors which favour biological invasions (Lodge et al. 2006).

Electronic supplementary material The online version of this article (doi:10.1007/s10530-016-1241-z) contains supplementary material, which is available to authorized users.

J. H. Liew · L. R. Carrasco · D. C. J. Yeo (✉)
Department of Biological Sciences, National University of Singapore, 14 Science Drive 4, Singapore 117543, Republic of Singapore
e-mail: dbsyeod@nus.edu.sg

H. H. Tan
Lee Kong Chian Natural History Museum, National University of Singapore, 6 Science Drive 2, #03-01, Singapore 117546, Republic of Singapore

While anthropogenic activity resulting in elevated alien propagule pressure (Colautti et al. 2006) or habitat disturbance (Davis et al. 2000) is often identified as a driver of biological invasions, some habitats are inherently more susceptible to the successful establishment of alien species than others (Johnson et al. 2008). The lack of biotic resistance, characterised as resistance to introduction of alien species resulting from interactions with native biota, is among widely discussed hypotheses explaining this observation (Moyle and Light 1996). The resistance of native biota against aliens is thought to be pertinent in the initial introduction, as well as at the spread stage of an invasion process (Lodge et al. 2006) through several forms of interaction, including competition (Levine et al. 2004; Dzialowski et al. 2006).

Being an important determinant of competition, trophic interactions and their components are commonly studied in relation to biological invasions (Marks et al. 2011; Cucherousset et al. 2012) in addition to a wide range of human disturbances such as species loss (Dunne et al. 2002a), habitat degradation (Henley et al. 2000), and eutrophication (Hadwen and Bunn 2005). Clear associations between trophic structure and the susceptibility of a habitat to biological invasions are yet to be conclusively determined, with current studies suggesting that invasibility of a habitat in relation to pre-existing communities are often scale dependent (Byers and Noonburg 2003). However, on a small spatial scale, there is some evidence to suggest that the trophic ecology of native biota can influence the success or failure of a biological invasion (Lake and Dowd 1991; Kennedy et al. 2002; Dzialowski et al. 2006).

The complexity of food webs and community level trophic interactions are among the major stumbling blocks in elucidating their association with alien species establishment. Consequently, studies testing the biotic resistance hypothesis tend to be theoretical (Tilman 2004; Romanuk et al. 2009; Baiser et al. 2010), while empirical studies have focused primarily on plant systems (Tilman 1997; Byers and Noonburg 2003). This bias is often compounded by the paucity of substantial field data pertaining to the community of interest, as exemplified by lentic habitats in Southeast Asia where little of the ecology is known despite an extensively studied diversity (Johnson 1973; Kottelat et al. 1993; Rainboth 1996; Rintelen et al. 2007).

To address this gap in knowledge of biological invasions, we applied a novel approach which couples food web modelling with statistical analyses of an extensive data set consisting of 370 fish species from 26 lakes from the Southeast Asian region where empirical food webs are largely unknown. As models of trophic interactions are widely applied (Pace et al. 1999; Williams and Martinez 2000) (see Rossberg et al. (2006) for limitations) and can be useful when community data from the field are lacking, we constructed literature-derived food web models based on algorithms dictated by organism size and diet as a basis for investigating the association between community and species level trophic traits with the successful establishment of alien fish taxa. The latter was done primarily by adopting the information-theoretic approach which is a comparatively robust and informative method when testing ecological questions (Lukacs et al. 2007; Sodhi et al. 2008). Using a combination of these techniques, we attempted to answer the following research questions: (1) is the presence of alien fish taxa associated with community level food web traits; and (2) is there a trend in species level trophic traits of the alien fish found in the habitats we studied?

Materials and methods

Data collection

We examined a total of 26 lentic habitats—20 artificial (i.e., man-made via excavations or river impoundments) and six natural—in the Southeast Asian region (Fig. 1) (Appendix A in ESM). Species lists of fishes of lentic habitats were compiled from various sources for Cambodia (Lim et al. 1999), Indonesia (Thomas 2005), Malaysia (Zakaria-Ismail and Lim 1995; Ali 1996; Mohd et al. 1996; Sim 2002), the Philippines (Aquino et al. 2011; Papa and Mamaril 2011), Singapore (Ng and Tan 2010), and Thailand (Chookajorn et al. 1999; Pholprasith and Sirimongkonthaworn 1999). Species checklists were verified against records on FishBase (Froese and Pauly 2015) and Catalog of Fishes (Eschmeyer 2013) to account for possible misidentifications. Uncertain records were excluded from subsequent analyses, after which, 970 entries of 370 fish species from 71 families remained (Appendix C in ESM).

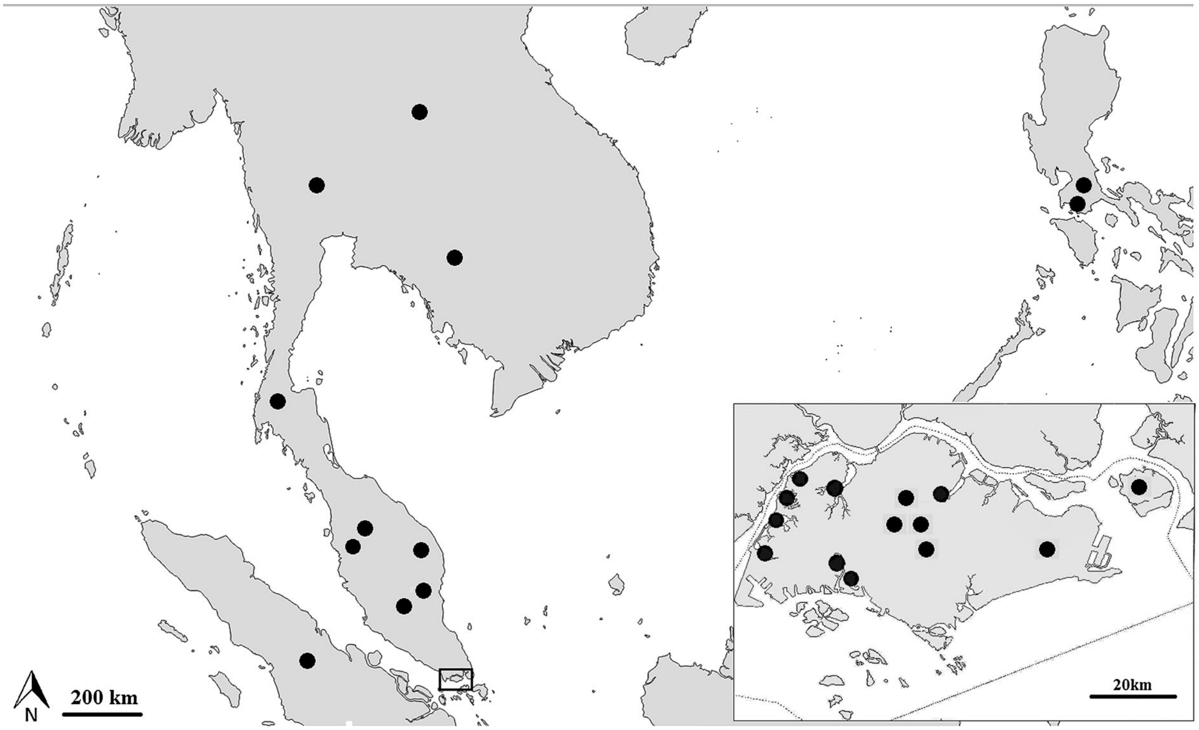

Fig. 1 Map of lakes we analysed on our study. Singapore, marked in a *black box* on the main map, is represented in the *inset*

From the collated species list, ecological traits, i.e., dietary habits, maximum recorded size (l_{max}) and status (native or alien) of the fishes were determined from several published sources (Appendix C in ESM) (Kottelat et al. 1993; Rainboth 1996). When dietary data were unavailable, dietary ecology was inferred from congeners of similar size. Owing to the incongruence of resolution in literature derived dietary data, we categorised food items under the following general groups: detritus, periphyton, plant matter, phytoplankton, zooplankton (microinvertebrates), macroinvertebrates and fishes. Fish taxa were assigned to the following feeding guilds as a function of their dietary components: benthic herbivore (i.e., species feeding on periphyton), detritivore (i.e., species feeding on detritus), herbivore (i.e., species feeding on various combinations of plant matter, periphyton and phytoplankton), macroinvertivore (i.e., species feeding on macroinvertebrates and zooplankton), omnivore/generalist (i.e., species feeding on a combination of various plant and animal food sources), pelagic planktivore (i.e., species feeding on zooplankton, or phytoplankton, or both), generalist predator (i.e., species feeding on combinations of zooplankton, macroinvertebrates and fishes), and piscivore (i.e., species feeding on fish). Trophic levels indicated on FishBase (referred to as FishBase trophic level) (Froese and Pauly 2015) were also recorded to complement dietary data as a general indicator of trophic niche.

Construction of food webs

We constructed hypothetical cumulative food webs (Schoenly and Cohen 1991) of each habitat reviewed in the form of predation matrices (described in Appendix D in ESM). As our study focusses on fish community, and considering the absence of data pertaining to non-fish taxa, our hypothetical food webs consisted primarily of fish species present in the lentic habitats. Other taxa/components included in the food webs were: detritus (i.e., dead organic matter of plant or animal origin), plant matter (i.e., all non-algal producers), phytoplankton (i.e., pelagic producers consisting of all species of phytoplankton), periphyton (i.e., benthic or encrusting producers), zooplankton (i.e., all species of zooplankton), and macroinvertebrates (e.g., decapod crustaceans and aquatic insect larvae). Trophic interactions in the matrices were a function of dietary data based on literature. For all piscivores, a size-constrained model in which a predator–prey size ratio of 4:1 was assumed (Scharf et al. 2000; Turesson et al. 2002). All species in the data set were ascribed with their common length (l_{com}), the most numerically abundant size class in a population, and this was calculated with the following formula; $l_{com} = 0.65 \times Maximum\ length$ (Pauly 2000). We analysed the resultant hypothetical food web using the *foodweb* package in the *R* environment (Perdomo et al. 2012) to generate associated food web network topology and other descriptors, namely; *trophic species richness* (w_{rich}), *connectance* (w_c), *total links* (w_{tl}), *link density* (w_d), *index of omnivory* (w_o), *proportion of herbivores* (w_h), *proportion of basal taxa* i.e., primary producers (w_b), *proportion of intermediate taxa*, i.e., primary and secondary consumers (w_i), *proportion of top taxa* i.e., apex predators (w_t), *ratio of prey to predator* (w_{pp}) and number of *trophic levels* (w_l) (Appendix B in ESM). Using the same package, we also calculated species trophic levels (s_l) from the hypothetical webs by averaging trophic levels of prey-items, where basal food sources (i.e., primary producers) were designated $s_l = 1$ (Williams and Martinez 2004). Unlike FishBase trophic level (s_f), calculated trophic level of a single species (s_l) can differ between lakes, as a function of the local food web structure, thus offering a more accurate, site-specific reflection of the trophic ecology of a species.

Approximations of propagule pressure and lake sizes

The likelihood of biological invasions is commonly attributed to propagule pressure (Colautti et al. 2006; Simberloff 2009) although data quantifying propagule pressure are often lacking and this necessitates the use of proxy measurements (Rouget and Richardson 2003). Similarly, we were not able to obtain empirical data measuring propagule pressure of all alien fish taxa present at all the habitats surveyed, thus we attempted to statistically control for propagule pressure by estimating the accessibility of the lakes following the (research supported) assumption that propagule pressure is positively correlated with human activity (Marchetti et al. 2004a; Bossenbroek et al. 2007). We approximated accessibility of the lakes by measuring the following two variables: (1) average travel time to population centre of 50,000 people or more (Nelson 2009); and (2) proportion of tree cover in buffer area consisting of riparian zones up to 1 km away from shore. We computed (1) by adopting the *GIS* raster layer from Nelson (2009), following which, time taken to travel to population centres of 50,000 was averaged across all 1 arc-minute grids occupied by the lakes, respectively. Variable (2) was computed from Global Forest Change (Hansen et al. 2013) tree cover *GIS* raster layer where tree cover data was first simplified by recoding the original continuous format (i.e., 0–100 % values in each 1 arc-second grid) in a binary form (i.e., 1 or 0) assuming substantial tree cover was only present in 30 m^2 grids with average tree cover greater than 20 %. Following the simplification of tree cover data, we approximated the proportion of tree cover in a 1 km buffer area around the lakes using the formula: *tree cover* (t_j) = ($\sum$Covered grids in buffer area$_j$) × ($\sum$Number of grids in buffer area$_j$)$^{-1}$, where a t_j value of 1 represents complete tree cover in the buffer area around lake *j*. In order to prevent over parameterising our models in subsequent analyses, we summarised both variables (1) and (2) using *Principal Components Analysis* on the *Ade4* statistical package (Dray and Dufour 2007) where a single covariate (principal component 1) was used as a proxy for habitat accessibility (*accessibility*). In addition, we also wanted to account for the potential scale dependence of biotic resistance (Byers and Noonburg 2003), and this was done by approximating lake area (*area*) based on Google Earth satellite images. All spatial analyses (i.e., construction of polygons approximating lake area, construction of buffer areas measuring 1 km away from lake shores, conversion of tree cover data, and summing of grids positive for tree cover as well as total number of grids present in buffer area) were conducted on the *QGIS*2.10* geographic information system (QGIS Development Team 2014).

Statistical analyses

To answer our first research question (i.e., is the presence of alien fish taxa associated with community level food web traits?), we narrowed down the list of variables potentially predictive of the number of native species in a habitat from among the values generated from our hypothetical food webs to the following: w_{rich}, w_{native}, w_c, w_d, w_l, w_o, w_h, w_i, and w_t.

These variables were selected considering the frequency of use in food web literature and potential ecological importance as proxies of biotic resistance. The relevance of these variables to our analyses are summarised in Table 1.

We tested the association between number of alien species present with variables describing food web traits and network topology by fitting multiple generalized linear mixed-effects models (*glmm*) in an inferential framework, from which the model(s) which best described our data was (were) selected (Burnham and Anderson 2002; Johnson and Omland 2004; Fox and Weisberg 2011). Our models consisted of combinations of variables described in Table 1 and were built according to plausible a priori hypotheses (Appendix E in ESM). The response variable in all the models was total number of alien species present in the community (i.e., *total aliens*). As our response variable is a count data, we applied poisson error structures in all our models. Habitat type (i.e., artificial or natural) was coded as a random-effect, within which the models were nested. This was to address potential confounders resulting from the distinct natural histories of the two habitat types, which may include, but are not restricted to: age, colonisation history, proximity to human activities, and heterogeneity of riparian zones (Gopal and Ghosh 2009). In addition to that, *accessibility* was also added to our models as a random slope variable to control for differences in public accessibility of the lakes as an approximation of human activity, which correlates with propagule pressure (Marchetti et al. 2004a). Moreover, we also split our models into two groups, assuming the presence and absence of scale dependence, respectively, where the latter includes *area* (km^2) as a covariate (Appendix E in ESM).

All predictor variables in our models were scaled to avoid potential biases resulting from differences in magnitudes. We also avoided building models with more than three predictor variables to prevent over-parameterising our models, as the co-dependent nature of the variables describing food webs (i.e., proportion of basal, intermediate and top taxa will necessarily sum to 1) means that high levels of multicollinearity exist in the data set. This prevents the inclusion of large numbers of variables (e.g., a saturated model in which all variables are included). We also addressed the issue of multicollinearity by computing variance inflation factors (*vif*) of equivalent generalized linear models (i.e., same set of predictor variables excluding random nesting effect) using the *car* package (Fox and Weisberg 2011) ensuring that all predictive variables in the models had a *vif* value of < 3. One of the more problematic collinearities (should it be significant) was the relationship between *area* and w_{rich} in view of its potential to confound assessments pertaining to the scale dependence of the association between number of alien species and community level food web traits and network topology. Therefore, in addition to ensuring a *vif* value of < 3 for all models, the linear relationship between *area* and w_{rich} was also tested by fitting the following generalised linear model: $area \sim w_{rich}$; and we found that the association between the two variables were not statistically significant (p value $= 0.201$). All our models were built with the *lme4* statistical package (Bates et al. 2015).

In order to determine the predictive ability of our parameterised models (i.e., models describing a priori hypotheses associating combinations of native species richness and food web traits and network topology to number of alien species present) relative to the null models (i.e., model describing the null hypothesis which assumes no association between number of alien species present and variables representing native species richness and food web traits and network topology) (Appendix E in ESM), we calculated Kullback–Leibler information loss based on Akaike's information criteria corrected for small sample sizes (AIC$_c$) (Burnham and Anderson 2002). Information loss relative to the null model was defined as $\Delta_i = \mathrm{AIC}_{ci} - \mathrm{AIC}_{cMin}$ where AIC$_{ci}$ represents the AIC$_c$ value of the ith model while AIC$_{cMin}$ represents the AIC$_c$ value of the most parsimonious model (i.e. lowest AICc value) (Lukacs et al. 2007). The probability of the model given the data (Akaike weights) was then computed with the following formula: $w_i = \frac{\exp\left(-\frac{1}{2}\Delta_i\right)}{\sum_{j=i}^{N} \exp\left(-\frac{1}{2}\Delta_i\right)}$, where exp represents the exponential function (Lukacs et al. 2007). In addition to that, we also calculated evidence ratios (e): $\frac{w_i}{w_{Null}}$ where w_{Null} represents the Akaike weight of the null model, allowing us to determine the likelihood of the ith model in comparison to the null model given our data (i.e., a value of 10 indicates that the *ith* model is ten times more likely to be true as compared to the null model). In order to best represent our data, we selected

Table 1 Summary of variables describing the traits and network topology of our food web models

Variable	Definition	Ecological relevance
Trophic species richness (w_{rich})	Total number of taxa (producers, invertebrates, and fishes) present at a habitat	Species richness has been shown to increase the resistance of a habitat to biological invasions (Stachowicz and Tilman 2005)
Native species richness (w_{native})	Total number of native taxa present at a habitat	A variant of w_{rich}. Greater native diversity has been shown to increase resistance against biological invasions (Stachowicz and Tilman 2005)
Connectance (w_c)	Fraction of realised link over total number of possible links (Dunne et al. 2002a)	High levels of *connectance* in a food web indicates an increase in web complexity (i.e., more links between taxa), which is thought to increase its robustness (Dunne et al. 2002b) and resistance to biological invasions (Galiana et al. 2014)
Link density (w_d)	Average number of links present per taxa (Scotti et al. 2009)	High levels of *link density* in a food web indicate an overall higher number of links per taxa (i.e., more links per taxa in the web), which may reflect higher niche utility contributing to competitive resistance against alien species (Dzialowski et al. 2006). Moreover, high link density also suggests greater food web complexity which reduces the likelihood of invasion (Galiana et al. 2014)
Trophic levels (w_l)	Number of trophic levels present	Number of trophic levels present may indicate complexity of food webs or resource availability. The former may prevent invasion (Galiana et al. 2014) while the latter could have the opposite effect of favouring the establishment of alien species exploiting surpluses in resources
Index of omnivory (w_o)	Proportion of species feeding on prey from multiple trophic levels (e.g. a fish species that feeds on producers and primary consumers, i.e. trophic levels 1 and 2 respectively) (Goldwasser and Roughgarden 1993)	High levels of omnivory may indicate high levels of stability in the community, which increases its resistance to disturbances (Fagan 1997)
Proportion of herbivores (w_h)	Proportion of taxa in a community consisting of primary consumers	Higher proportions of herbivores in a community may competitively preclude the establishment of herbivorous aliens (Dzialowski et al. 2006)
Proportion of intermediate taxa (w_i)	Proportion of taxa in a community consisting of secondary or tertiary consumers	Higher proportions of secondary or tertiary consumers in a community may preclude the establishment of alien fish taxa belonging to the same/similar trophic niches via a range of different mechanisms (Baltz and Moyle 1993)
Proportion of top taxa (w_t)	Proportion of taxa in a community consisting of apex predators	Higher proportions of apex predators in a community may prevent the establishment of alien predators via competitive exclusion. High diversity of apex predators may also prevent the establishment of aliens via predation (Harvey et al. 2004)

the best models by setting a cut-off point of $\Delta\mathrm{AIC_c} = 2$ (where $\Delta\mathrm{AIC_c}$ refers to differences in $\mathrm{AIC_c}$ values) from the model with the lowest $\mathrm{AIC_c}$ value (Burnham and Anderson 2002). Should there be more than one model selected using this criteria, the most parsimonious models were averaged using via the *MuMIn* package (Barton 2013). Further, we assessed general model fits by calculating marginal and conditional R^2 values for all the models (Nakagawa and Schielzeth 2013). The relationship between predictor variables and the response variable (*total aliens*) is linear, so a coefficient value of 1 suggests that a one unit increase in the associated predictor variable would result in a concomitant single unit increase of *total aliens*.

To answer our second research question at a species level, we conducted non-metric dimensional scaling (*nMDS*) of the literature derived dietary components of 370 fish species using the *vegan* package (Oksanen et al. 2013) to visualise potential dietary separation between native and alien fishes. Clusters of native and alien fishes in ordinal space were represented by dispersion ellipses calculated based on the standard error (*s.e.*) of the average scores. We tested for statistical significance in the separation between native and alien fishes using PERMANOVA with the *adonis* function on the *vegan* statistical package (Oksanen et al. 2013). Further, we constructed a contour plot derived from smooth surface thin-plate splines from a general additive model (*gam*) of *calculated trophic level* (s_l) (Marra and Wood 2011).

Besides testing for potential differences in the dietary component of alien fishes in comparison to native taxa, we also tested if native and alien species had significantly different species-specific trophic traits. We did this by conducting information-theoretic analyses on a data set consisting of 970 data points of 370 fish species (a single species may occur in multiple habitats), using combinations of species specific trophic traits (Table 2) as predictor variables and the status of the fish (i.e., native or alien) as a response variable. All predictor variables were again scaled prior to analysis. As our response variable is binary, we applied binomial error variance structures in all our models (i.e., logistic regression), and controlled for *family* and *locality* (i.e., habitat from which the species was recorded) by including them as random nesting factor. This allowed us to minimise potential confounders caused by phylogeny and habitat specific stochastic events (e.g., fish stocking). The list of models we built and tested based on a priori hypotheses are summarised in Appendix F in ESM. The parameterised models (i.e., models describing a priori hypotheses associating combinations of species-specific trophic traits with the status of a fish) were compared to the null model (i.e., model which assumes no association between any species-specific trophic traits with the status of a fish) and quantified by calculating Akaike weights and evidence ratios. Here again, we estimated the general fit of the models. In our species level analyses, the association between predictor variables and the response variable (*status*)

Table 2 Summary of species specific trophic related traits we included in our information-theoretic analyses

Variable	Definition	Ecological relevance
Feeding guild	General grouping of fish taxa, which is a function of their dietary components	Fishes belonging to certain feeding guilds may be more likely to invade successfully by exploiting "empty niches" (sensu Proches et al. 2008)
Fishbase trophic level (s_f)	Trophic level value obtained from FishBase (Froese and Pauly 2015). Species specific value that is uniform across habitats	Fishbase trophic level corresponds closely to general dietary composition of a species, and therefore is also indicative of alien fishes' potential ability to exploit empty trophic niches where present
Calculated trophic level (s_l)	Habitat specific trophic level which is a function of food web models	Fishes feeding at certain trophic levels may be more likely to invade successfully due to lack of competition and/or abundance in resource availability
Maximum length	Maximum length recorded in published literature	Trophic positions of fishes are often correlated to size (Akin and Winemiller 2008), and may provide insights into associations between trophic traits and the successful establishment of alien species
Family	Family of species included in analyses	Controls for potential confounders caused by, or related to, phylogeny

was assessed via logistic regression, thus a coefficient value of 1 suggests that a one unit increase in the associated predictor variable is e^1 times more likely to be true for the non-intercept *status* (i.e., native), where *e* represents the mathematical constant, *Euler's number*. All statistical analyses were conducted on the *R* statistical environment * 2.15.1 (R core team 2015).

Results

Out of the 34 models we constructed, two models, which cumulatively accounted for nearly 100 % of the Akaike's posterior weights, best represented our data at the community level. This suggests that *total native richness* (w_{native}) was the most informative trait in predicting the number of alien species in the community, with an evidence ratio indicating that the models were 2.48×10^9 and 1.92×10^9 times more likely than the null model (Table 3). The *total native richness* (w_{native}) of a community reflected a significant negative relationship (p value < 0.05) to number of alien species (Fig. 2; Table 4). In addition to that, models which were controlled for lake size (*area*) also generally outperformed their counterparts, suggesting the importance of accounting for spatial scale of the habitats.

At the species level, the results of our *nMDS* (stress value = 0.096) revealed distinct, separate clusters of native and alien fishes (Fig. 3), suggesting the potential dietary segregation between the two groups of fishes. We also observe qualitatively that alien fishes appear to feed at lower trophic levels (i.e., overlaps contour line representing trophic level 3.5). The clustering and segregation between the two groups of fishes was statistically significant (p value <0.0005), with detritus (57 %), macroinvertebrates (20 %), and plant matter (9 %), the food items accounting for most of the variance in our data.

Our qualitative assessments were also supported by the more quantitative information-theoretic approach where results reveal that the model describing associations between *fishbase trophic level* (s_f) and *maximum length* with the status of a fish (i.e., native or alien) was the most parsimonious, representing 95 % of the total posterior weights in our data (Table 5) and was 2.58×10^{13} times more likely to be true compared to the null model (*SpNull*). This suggests that *fishbase trophic level* (s_f) and *maximum length* were important variables in predicting the status of a fish. Other predictor variables which made up the most parsimonious models include s_l which was our alternative (more flexible) measure of trophic level. We found that the alien fishes were

Table 3 Summary of the five most parsimonious models describing the relationship between variables describing traits and network topology with the proportion of native species present in 26 lentic habitats

Model	*glmm*	AICc	Marginal R^2	Conditional R^2	Akaike weight	Evidence ratio
ComNull	*Total aliens* ~ 1 + (*accessibility*|*habitat type*)	239.2	0.000	0.483	<0.001	1.00
Com2	*Total aliens* ~ w_{native} + *area* + (*accessibility*|*habitat type*)	195.9	0.380	0.766	**0.563**	$\mathbf{2.48 \times 10^9}$
Com19	*Total aliens* ~ w_{native} + (*accessibility*|*habitat type*)	196.4	0.395	0.669	**0.437**	$\mathbf{1.92 \times 10^9}$
Com23	*Total aliens* ~ w_d + w_{rich} + *area* + (*accessibility* |*habitat type*)	221.6	0.237	0.666	<0.001	6.45×10^3
Com17	*Total aliens* ~ w_d + w_{rich} + (*accessibility*|*habitat type*)	223.9	0.190	0.517	<0.001	2.10×10^3
Com19	*Total aliens* ~ w_h + w_{rich} + *area* + (*accessibility*|*habitat type*)	224.3	0.224	0.726	<0.001	1.71×10^3

Models (with the exception of the null model) are ranked according to increasing AICc values (i.e. smaller values indicate higher parsimony), while the Akaike weights indicate percentage of posterior weight accounted for by the model. The four community traits represented in these models are *total natives* (w_{native}), *total species richness* (w_{rich}), *link density* (w_d), and *proportion of herbivores* (w_h). Marginal R^2 is indicative of proportion variance explained by fixed factors in the model while Conditional R^2 incorporates variance explained by random effects. The Akaike weights and evidence ratios of the most parsimonious models are written in bold fonts

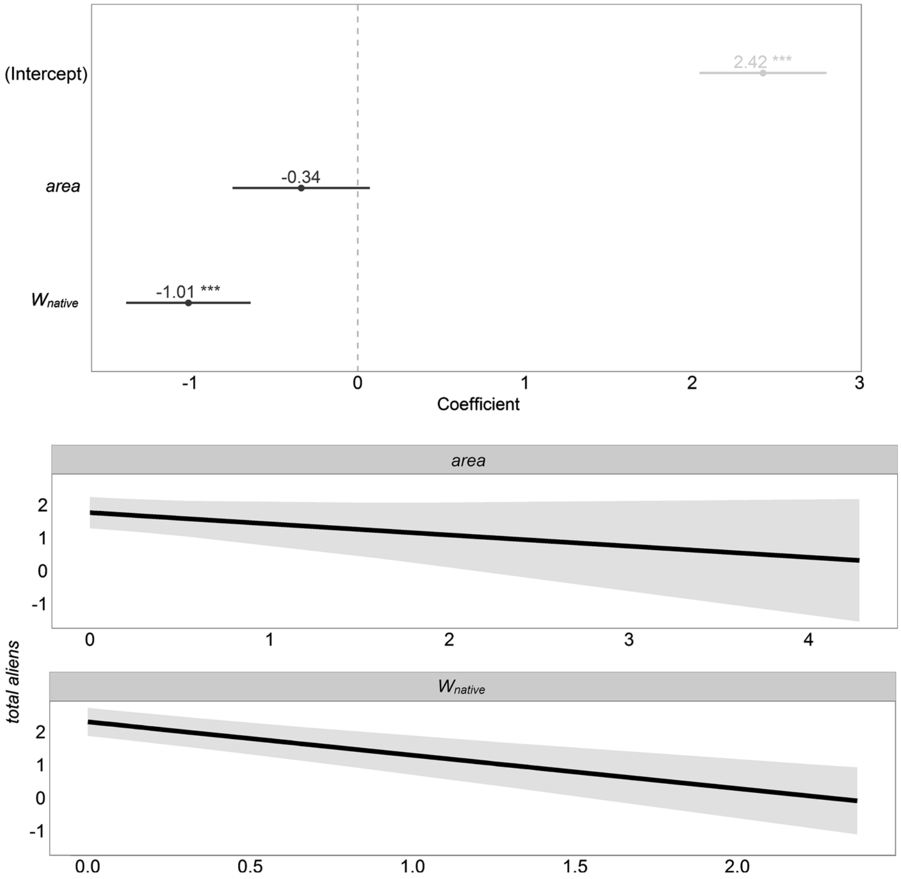

Fig. 2 *Plots* representing coefficients (*top*) and predicted relationships (*bottom*) between *total aliens* and predictor variables in our most parsimonious community level model. Associated errors (95 % confidence intervals) are denoted by whiskers and *grey* zones respectively

Table 4 Details of the averaged model derived from two models of greatest parsimony describing community level trends

Model	Variable	Coefficient	Standard error	p value	Random factor variance
Com2, *Com19*	W_{native}	−1.023	0.185	<0.001*	
	Area	−0.338	0.209	0.129	
	Accessibility				1.587
	Habitat type				3.236

Cumulatively, both models account for almost 100 % of the posterior weights. Coefficient values indicate both the direction and magnitude of the relationship between predictor and response variables

* Statistical significance at $\alpha = 0.05$

associated with lower *trophic levels* and greater *maximum length* (Figs. 4, 5; Table 6). To further explore the differences observed, we calculated the calculated Cohen's *d* and obtained medium effect sizes of 0.34 and 0.41 for s_f and *maximum length*, respectively.

Discussion

Community level food web traits

Our findings suggest that at the community level, native species richness appeared to be the most

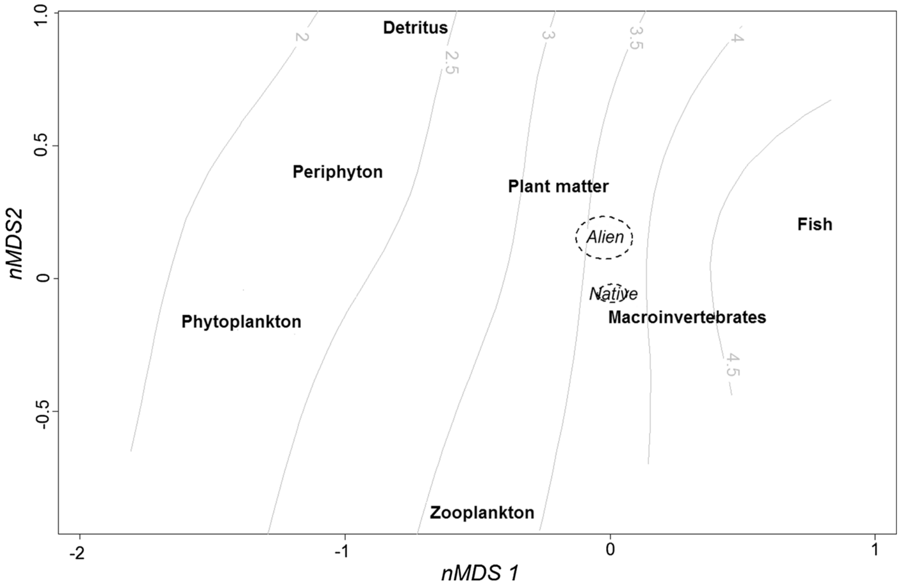

Fig. 3 Non-metric dimensional scaling (nMDS) plot of the dietary components of 370 fish species from 26 lentic habitats in Southeast Asia. Ellipses on the plots represent standard errors (s.e.) of average ordinal scores while *contour lines* represent smooth surface thin-plate splines from a general additive model (*gam*) of calculated species trophic level. Food items of the fishes are represented by *bold letterings* on the plot

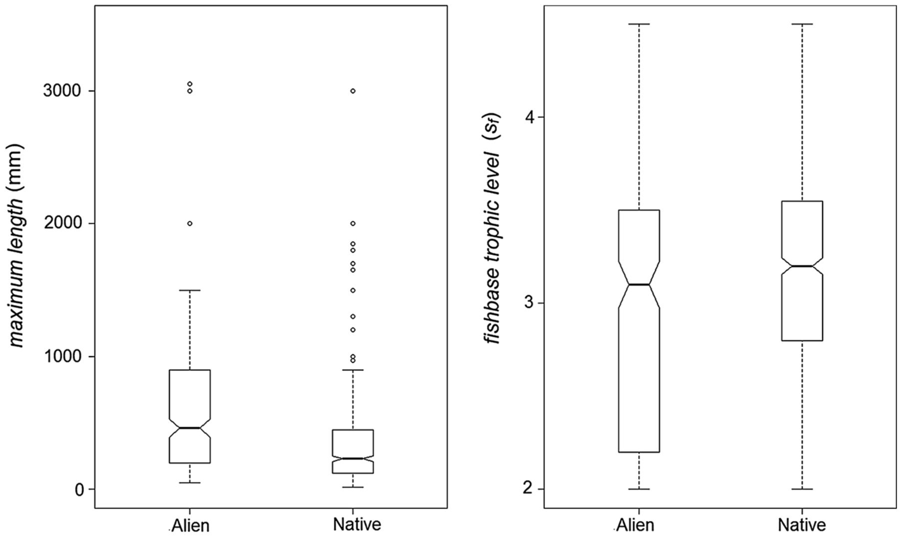

Fig. 4 *Boxplots* showing the distribution of *maximum length* and *fishbase trophic level* (s_f) of native and alien fishes in our data set consisting of 970 data points representing 370 fish species in 26 lentic habitats

important determinant of the invasiblity of a habitat, where an inverse relationship was observed between the total number of native and alien species. This observation concurs with early studies discussing the relationship between the diversity of native communities and their biotic resistance against invasions (Elton 1958; Moulton and Pimm 1983). The negative relationship between native species richness and the number of alien species we observed can likely be attributed to a lack of competition in less species rich communities resulting from a lower degree of resource utilisation (Tilman 1997, 2004). Communities which have lower species richness are also likely to have vacant or unsaturated niches with unexploited resources which favours the establishment of introduced taxa (Wiens 2011). Moreover, less species rich communities are more vulnerable to stochastic disturbances (Petchey 2000) that could result in disruptions to ecosystem function, which may in turn be exploited by biological invaders (Shea and Chesson 2002). While one may fairly assume that the negative relationship observed between richness of native and alien fish species may be a product, rather than a driver of invasion, this is less likely to be the case in our study

Table 5 Summary of the five most parsimonious models describing the relationship between the status of a fish (i.e. native or alien) and species specific trophic related variables in 26 lentic habitats

Model	*glmm*	AICc	Marginal R^2	Conditional R^2	Akaike weight	Evidence ratio
SpNull	*Status* ~ 1 + (1|*locality*/*family*)	685.0	0.000	0.775	<0.001	1.00
Sp8	*Status* ~ s_f + *maximum length* + (1|*locality*/*family*)	623.2	0.066	0.796	**0.950**	$\mathbf{2.58 \times 10^{13}}$
Sp9	*Status* ~ s_l + *maximum length* + (1|*locality*/*family*)	633.8	0.054	0.794	0.005	1.31×10^{11}
Sp2	*Status* ~ s_f + (1|*locality*/*family*)	653.5	0.042	0.753	<0.001	6.90×10^{6}
Sp4	*Status* ~ *maximum length* + (1|*locality*/*family*)	659.2	0.026	0.786	<0.001	4.00×10^{5}
Sp3	*Status* ~ s_l + (1|*locality*/*family*)	672.3	0.015	0.738	<0.001	5.71×10^{2}

Models (with the exception of the null model) are ranked according to increasing AIC_c values (i.e. smaller values indicate higher parsimony), while the Akaike weights indicate percentage of posterior weight accounted for by the model. Marginal R^2 is indicative of proportion variance explained by fixed effects in the model while Conditional R^2 incorporates variance explained by random effects. The Akaike weight and evidence ratio of the most parsimonious model is written in bold fonts

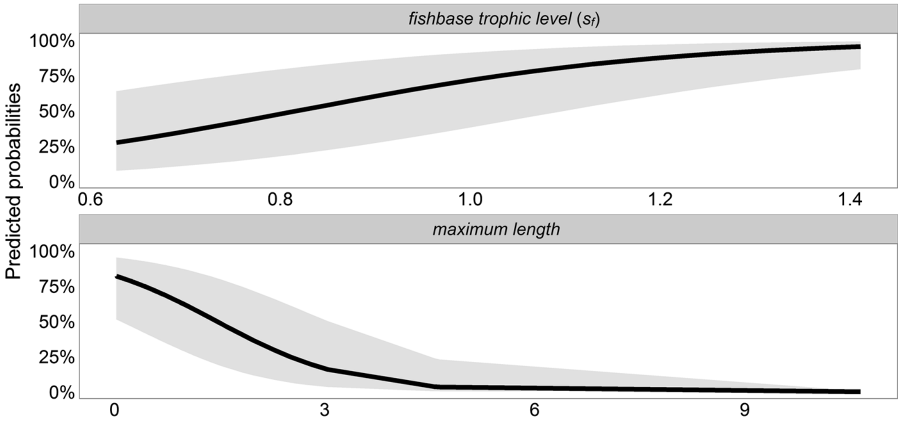

Fig. 5 Plot of predicted probability of a fish species being native as a function of predictor variables associated with our most parsimonious species level model, namely, *fishbase trophic level* (s_f) and *maximum length*

Table 6 Details of the most parsimonious model describing species level trends

Model	Variable	Coefficient	Standard error	p value	Random factor variance
Sp8	s_f	5.102	1.019	<0.001*	
	Maximum length	−1.054	0.223	<0.001*	
	Locality				11.82
	Family				3.55

Alien fishes were coded as the intercept, therefore, positive coefficients signify that greater predictor variable values are more likely in native fishes and vice versa

* Statistical significance at $\alpha = 0.05$

as biological invasions have not been shown to cause native extirpations in Southeast Asian habitats (Brook et al. 2003; Sodhi et al. 2004).

Despite the seemingly intuitive nature of the resistance hypothesis suggesting an inverse relationship between the diversity of native species and the probability of biological invasions (Elton 1958; Stachowicz and Tilman 2005), some recent studies disagree with the hypothesis and suggest that at larger scales, the opposite trend, termed the "biotic acceptance" hypothesis, is true (Byers and Noonburg 2003; Jeschke 2014). Others proposed that native species density rather than diversity was a more important determinant of resistance against invaders (Levine et al. 2004; Capers et al. 2007). However, evidence supporting the deterrent properties of biotic resistance (represented by community diversity) against invasion at smaller spatial scales is considerable (Kennedy et al. 2002; Stachowicz and Tilman 2005; Oakley and Knox 2013), suggesting that biotic resistance is not a universal phenomenon and is only observable in studies conducted at certain scales. The data collected in our study appears to lend further support to the scale dependence of the biotic resistance hypothesis as evidenced by how, with all other factors being equal, controlling for lake area resulted in greater model performance (Table 3). Even at relatively restricted range of spatial scale (i.e., all data points were at the local, single habitat level), findings from our study demonstrate the importance of contextualising (e.g., spatial scale or organisation level) findings pertaining to biotic resistance. This may reconcile our findings with previous studies suggesting "biotic acceptance" in animal models, which were surveyed at larger spatial scales (Poessel et al. 2013), considering that disproportionately large increases in resources available relative to the potential increase in interspecific interactions with increasing spatial scales (Byers and Noonburg 2003) could potentially reverse the directionality of relationships between native and alien species richness (i.e., from negative to positive).

In addition, contrasting observations made in studies proposing the "biotic acceptance" hypothesis were largely conducted on plant models (Levine et al. 2004; Capers et al. 2007; Jauni and Hyvo 2012; Lowry et al. 2013), potentially explaining the opposing trends reported. The different criteria for resource utility between plants and animals, which are arguably less narrow in the former, may affect the intensity of competition, which is an important determinant of resistance against biological invasion (Levine et al. 2004). To illustrate, while an autotrophic invader is capable of exploiting surpluses in nutrients (Huenneke et al. 2014) or light (Parendes and Jones 2000), a heterotrophic alien is constrained by its dietary requirements. Consequently, the intensity of competition among heterotrophic taxa is elevated, thus increasing the potency of biotic resistance against invaders. Although this line of reasoning is speculative based on current knowledge, the logic is consistent with diminishing resources (i.e., energy) up the trophic levels (Lindeman 1942; Pauly and Christensen 1995), and with field studies showing that interspecific competition is more commonly observed in marine and freshwater vertebrates as compared to marine, freshwater, and terrestrial plants (Connell 1983). Comparisons with terrestrial plants are especially relevant considering the model systems studied in a large proportion of "biotic acceptance" proponents. This again suggests that the negative association between native diversity and biotic resistance may remain valid, at least in animal models (Dzialowski et al. 2006; Taylor and Duggan 2012), given the appropriate spatial scale, and at the very least, merits further testing.

One limitation in this section of our study was the absence of data directly quantifying anthropogenic activity such as fish stocking, particularly in view of the presence of some evidence suggesting fish stocking activity in several of the habitats we studied (Yang 1989; Goltenboth and Lehmusluoto 2006). We attempted to address this by including habitat type as a random intercept with the assumption that artificial habitats, such as reservoirs, experience a greater level of anthropogenic impacts. In addition, a survey of aquaculture literature revealed that of the 74 species which were recorded as alien in at least one of the 26 habitats we analysed, only 11 (i.e., *Barbonymous gonionotus*, *Clarias batrachus*, *Cyprinus carpio*, *Ctenopharyngodon idella*, *Gambusia affinis*, *Hypothalmichthys molitrix*, *Hypothalmichthys nobilis*, *Labeo rohita*, *Oreochromis mossambicus*, *Oreochromis niloticus*, and *Pangasianadon gigas*) were historically stocked in Southeast Asia, though not necessarily in any of the 26 habitats included in our study (De Silva 1987; Balayut 1999; De Silva and Funge-Smith 2005; Arthur et al. 2010). The 11 species mentioned above were also native in some of the habitats we analysed and will not confound our analyses. Moreover, even in habitats where they were not native (e.g., *P. gigas* is native in Tonle Sap but not in Lake Taal), these species were not always successful in forming established populations (Balayut 1999; De Silva and Funge-Smith 2005), suggesting that fish stocking is not an important driver of biological invasions, at least in lentic water bodies in the region.

Confounding effects resulting from differences in anthropogenic activities were also minimised by our measures of controlling for accessibility of the lakes with the assumption that the level of human activities correlate with propagule pressure (Meyerson and Pys 2013; Roux et al. 2013). Should our control measures fail to completely account for all facets of anthropogenic disturbances, our assertions remain relevant, as a known consequence of habitat disturbance is species loss, which results in reduced ecosystem functioning (Duffy 2003), and consequently favouring biological invasions (Stachowicz and Tilman 2005). Therefore, even when assuming anthropogenic disturbances other than what we attempted to account for to be the ultimate driver of biological invasions, biotic resistance is likely to be one of the more important proximate factors determining habitat invasibility. To further illustrate this point, disturbed habitats are inherently less suitable for native taxa adapted to status quo in their native ranges and are thus likely to suffer impacts to abundance and richness (in cases where extirpations occur). We argue that the "passenger theory" pertaining to biological invasions and habitat change (Didham et al. 2005; MacDougall and Turkington 2005) should not necessarily be viewed as being exclusive of biotic resistance, as an impacted native community would logically be less able to repulse invading aliens via mechanisms such as competition or predation. In short, the "passenger" status of habitat degradation should apply to both alien and native species, albeit with opposite effects (i.e., in favour of the former but not the latter), giving rise to more synergistic/interactive consequences (Didham et al. 2007). Having said that, we believe that the relative importance and exact interactions in the effects of abiotic (habitat disturbance) and biotic resistance in predicting biological invasions is an important avenue for research and warrants future experimental and empirical work.

Finally, the paucity of high-resolution food web data at our study sites necessitated the use of modelling approaches to approximate food web structure. While this approach has been shown to be a relatively reliable (Pace et al. 1999; Williams and Martinez 2000), there remain shortcomings, particularly in its tendency to oversimplify trophic relationships and aggregate species (Polis 1991). Although our most important finding, which is the negative relationship between the richness of native and alien fish present, will not be affected by potential lack of resolution in our food webs, it is important to note that food web traits and network topology may be more important in predicting the invasibility of communities than our findings suggest. Despite the likelihood that these traits were underestimated, our findings suggest that w_d was one of the more important predictors of total number of aliens present (Table 3; *Com23*), and the model parameterised with it was 6.45×10^3 times more likely to be true compared to the null model (i.e., *ComNull*) and had a negative albeit not statistically significant (p value $= 0.14$) relationship.

As all our food webs were constructed using identical methods, we also have no reason to believe that increasing food web resolution (i.e., less species aggregation and increase number of links attributed to ontogeny) would change the directionality of relationships between food web traits and alien species richness, thus the central thesis of our community level inferences is likely to remain unchanged. However, we note that the inability to further taxonomically resolve invertebrate taxa may result in the inability to detect potential differences in food web structure in our analyses, and this may be relevant in comparisons between communities that have vastly different assemblages of non-fish taxa.

Species trophic traits

In addition to the association between native species richness and the invasibility of a habitat, our data also suggest that at the species level, alien taxa with certain trophic traits are more likely to become established. In both our *nMDS* (Fig. 2) and information-theoretic analyses, we found that alien species fed lower down the food web in comparison to native taxa. This observation raises three possible scenarios: (1) native species feeding at lower trophic levels are more likely to be displaced by alien fauna; (2) alien species occupying lower trophic levels are more likely to be released (i.e., introduced), thus increasing propagule pressure; or 3) alien species feeding lower down the food chain are more likely to be established in lentic habitats in the region because of the availability of poorly exploited resource niches. While (1) is possible, there is again little direct evidence to support the occurrence of fish extirpations resulting from biological invasions (Brook et al. 2003; Sodhi et al. 2004), particularly, as a result of competitive exclusion (Sax and Gaines 2008). This leaves the competing hypotheses (2) and (3) as the more likely factors underlying our observations, both with their own merits. While (2) describes a likely scenario in aquaculture (Tacon et al. 2009) attributable to the relative ease in growing low trophic level species, we believe that fish stocking is not an important driver of biological invasions in the lakes we studied due to reasons discussed in preceding paragraphs. We cannot, however, preclude the possibility that species feeding at lower trophic levels are being released at a disproportionately higher rate from the ornamental fish trade, though there is no data currently available to suggest that this is true. Anecdotally, fish occupying high trophic levels are just as likely to be released as unwanted pets (e,g., *Scleropages formosus*) or as angling species (e.g., *Cichla orinocensis*), as are low trophic level taxa (e.g., *Pterygoplichthys pardalis*). Unless further evidence is made available, we argue that (3) is the most well supported explanation as species feeding lower down the food web have been shown to be more likely to overcome resource limitations by utilising low quality food sources with low energy yield (Marchetti et al. 2004b; Gido and Franssen 2007). The association between alien taxa and food items of low energy yield (i.e., detritus and plant matter which collectively accounts for 66 % of the variance in our data) further supports this line of argument (Fig. 3). Our findings are consistent with theoretical (Dunne et al. 2002b; Romanuk et al. 2009) and empirical (Moyle and Light 1996; Gido and Franssen 2007) studies demonstrating a higher likelihood of invasion success among species that are capable of exploiting resources available at lower trophic levels, which suggests that competition and resource utilisation were the primary mechanisms underlying biotic resistance, at least in the fish communities we assessed.

We also observed a discrepancy of sizes between native and alien taxa suggesting that the ability to attain size refuge and consequently achieve predator avoidance is an important factor favouring successful alien establishment. As predation by native taxa is one of the factors contributing to biotic resistance (Harvey et al. 2004), this finding was not unexpected. Alternatively, the differences observed could again be attributed to local natural history as native species in certain areas (e.g., Singapore) are largely small forest stream specialists (Yeo and Lim 2011) and are necessarily more diminutive. Local natural history is another possible mechanism underlying the disparity between alien and native fishes belonging to the pelagic planktivore feeding guild (Table 6) where regions with no large rivers or lakes are not likely to have native planktivorous fish (Goldstein and Meador 2004).

We attempted to minimise potential confounding effects by controlling for locality as a random intercept in our *glmm* analysis with the assumption that the different habitats will have different propagule pressures. This is especially applicable to reservoirs in Singapore where high connectivity between water bodies and high public accessibility of reservoirs may increase propagule pressure (Yeo and Lim 2011). Further we observed substantially lower marginal R^2 values in comparison with conditional R^2 scores in all the models suggesting that at the species level, much of the variance in the data is associated with location and phylogeny, both random factors we controlled for in all our models.

Conclusions: biotic resistance revisited

Testing of the biotic resistance hypothesis in relation to food web traits or network topology often faces the challenge of inherent complexities in elucidating complex food webs. Consequently, many published studies of this nature use simulated food webs (Byers and Noonburg 2003; Romanuk et al. 2009; Baiser et al. 2010) as model systems. In our study, we applied a combination of (1) modelling food webs using data from literature and (2) statistical analyses to answer two research questions where we found trends in the establishment of alien freshwater fishes at both the community and the species level. At the community level, we found that communities with high native species richness were associated with lower numbers of aliens, while at the species level, we found that alien fishes fed at lower trophic levels compared to the natives. Both these observations corroborate the role of biotic resistance in deterring the establishment of alien species as our findings suggest that empty niches or a surplus of resources, which is likely to be more common in less speciose communities (Stachowicz and Tilman 2005; Jeschke 2014) and in lower trophic levels (Sinclair 1975), favour the establishment of alien species. Moreover, the differences in species level trophic traits between alien and native fishes suggest that the main mechanism underlying biotic resistance in the habitats we studied were likely to be related to resource utilisation. In addition to other known drivers of biological invasion such as propagule pressure (Simberloff 2009), and anthropogenic disturbances (Mack et al. 2000), our study shows that biotic resistance remains an important factor, which should not be overlooked when assessing the successful establishment of alien species in a community.

Acknowledgments We thank two anonymous reviewers for constructive suggestions and comments which substantially improved the manuscript. We also gratefully acknowledge PUB, Singapore's national water agency, and the members of the National University of Singapore (NUS) Reservoir Biodiversity team for data of fish fauna from Singapore reservoirs; and the National Research Foundation and the Economic Development Board (SPORE, COY-15-EWI-RCFSA/N197-1), PUB (NUS Grant No. R-154-000-619-490), and an AcRF Tier 1 Grant from the Singapore Ministry of Education (NUS Grant No. R-154-000-465-133) for financial support.

References

Akin S, Winemiller KO (2008) Original article body size and trophic position in a temperate estuarine food web. Acta Oecologia 33:144–153

Ali AB (1996) Chenderoh Reservoir, Malaysia: the conservation and wise use of fish biodiversity in a small flow-through tropical reservoir. Lakes Reserv Res Manag 2:17–30

Aquino LMG, Tango JM, Canoy RJC et al (2011) DNA barcoding of fishes of Laguna de Bay, Philippines. Mitochondrial DNA 22:143–153

Arthur RI, Lorenzen K, Homekingkeo P et al (2010) Assessing impacts of introduced aquaculture species on native fish communities: Nile tilapia and major carps in SE Asian freshwaters. Aquaculture 299:81–88

Baiser B, Russell GJ, Lockwood JL (2010) Connectance determines invasion success via trophic interactions in model food webs. OIKOS 119:1970–1976

Balayut EA (1999) Introduction and fish stocking in lakes and reservoirs in Southeast Asia: a review. In: van Densen WLT, Morris MJ (eds) Fish and fisheries of lakes and reservoirs in southeast Asia and Africa. Westbury Academic and Scientific Publishing, Otley, pp 117–142

Baltz DM, Moyle PB (1993) Invasion resistance to introduced species by a native assemblage of California stream fishes. Ecol Appl 3:246–255

Barton K (2013) MuMIn: multi-model inference. R package version 1.15.1. http://CRAN.R-project.org/package=MuMIn

Bates D, Meechler M, Bolker B (2015) Fitting linear mixed-effects models using lme4. J Stat Softw 67(1):1–48

Bossenbroek JM, Johnson LE, Peters B et al (2007) Forecasting the expansion of zebra mussels in the United States. Conserv Biol 21:800–810

Brook BW, Sodhi NS, Ng PKL (2003) Catastrophic extinctions follow deforestation in Singapore. Nature 424:420–426

Burnham KP, Anderson DR (2002) Model selection and multimodel inference: a practical information-theoretic approach. Springer, New York

Byers JE, Noonburg EG (2003) Scale dependent effects of biotic resistance to biological invasion. Ecology 84:1428–1433

Capers RS, Selsky R, Bugbee GJ et al (2007) Aquatic plant community invasibiity and scale-dependent patterns in native and invasive species richness. Ecology 88:3135–3143

Chookajorn T, Duangsawadi S, Chansawang B et al (1999) The fish community of Ubolratana Reservoir, Thailand. In: van Densen WLT, Morris MJ (eds) Fish and fisheries of lakes and reservoirs in southeast Asia and Africa. Westbury Publishing, Great Britain, pp 95–103

Clavero M, García-Berthou E (2005) Invasive species are a leading cause of animal extinctions. Trends Ecol Evol 20:110

Colautti RI, Ia Grigorovich, MacIsaac HJ (2006) Propagule pressure: a null model for biological invasions. Biol Invasions 8:1023–1037

Connell JH (1983) On the prevalence and relative importance of interspecific competition: evidence from field experiments. Am Nat 122:661–696

Cucherousset J, Bouletreau S, Martino A et al (2012) Using stable isotope analyses to determine the ecological effects of non-native fishes. Fish Manag Ecol 19:111–119

Davis MA, Grime JP, Thompson K (2000) Fluctuating resources in plant communities: a general theory of invasibility. J Ecol 88:528–534

De Silva SS (1987) Reservoir fishery management and development in Asia. In: De Silva SS (ed) November edn. IDRC, Kathmandu, pp 23–28

De Silva SS, Funge-Smith S (2005) A review of stock enhancement practices in the inland water fisheries of Asia. Asia-Pacific Fishery Commision, Bangkok

Didham RK, Tylianakis JM, Hutchinson MA et al (2005) Are invasive species the drivers of ecological change? Trends Ecol Evol 20:470–474

Didham RK, Tylianakis JM, Gemmell NJ et al (2007) Interactive effects of habitat modification and species invasion on native species decline. Trends Ecol Evol 22:489–496

Dray S, Dufour AB (2007) The ade4 package: implementing the duality diagram for ecologists. J Stat Softw 22:1–20

Duffy JE (2003) Biodiversity loss, trophic skew and ecosystem functioning. Ecol Lett 6:680–687

Dunne JA, Williams RJ, Martinez ND (2002a) Food-web structure and network theory: the role of connectance and size. Proc Natl Acad Sci USA 99:12917–12922

Dunne JA, Williams RJ, Martinez ND (2002b) Network structure and biodiversity loss in food webs: robustness increases with connectance. Ecol Lett 5:558–567

Dzialowski AR, Lennon JT, Smith VH (2006) Food web structure provides biotic resistance against plankton invasion attempts. Biol Invasions 9:257–267

Elton CS (1958) The ecology of invasions by animals and plants. Methuen, London

Eschmeyer WN (2013) Genera, species, references. In: California Academy of Sciences. Accessed 20 March 2013

Fagan WF (1997) Omnivory as a stabilizing feature of natural communities. Am Nat 150:554–567

Fox J, Weisberg S (2011) An *R* companion to applied regression. Sage, Thousand Oaks

Froese R, Pauly D (eds) (2015) Fishbase. World wide web electronic publication. www.fishbase.org

Galiana N, Lurgi M, Montoya JM et al (2014) Invasions cause biodiversity loss and community simplification in vertebrate food webs. OIKOS 123:721–728

Gido KB, Franssen NR (2007) Invasion of stream fishes into low trophic positions. Ecol Freshw Fish 16:457–464

Goldstein RM, Meador MR (2004) Comparisons of fish species traits from small streams to large rivers. Trans Am Fish Soc 133:971–983

Goldwasser L, Roughgarden J (1993) Construction and analysis of a large Caribbean food web. Ecology 74:1216–1233

Goltenboth F, Lehmusluoto P (2006) Lakes. In: Goltenboth F, Timotius KH, Milan PP, Margraf J (eds) Ecology of insular southeast Asia. Elsevier, Amsterdam, pp 96–138

Gopal B, Ghosh D (2009) Lakes and reservoirs of Asia. In: Likens GE (ed) Encyclopedia of inland waters. Elsevier, Amsterdam, pp 501–512

Hadwen WL, Bunn SE (2005) Food web responses to low-level nutrient and 15 N-tracer additions in the littoral zone of an oligotrophic dune lake. Limnol Oceanogr 50:1096–1105

Hansen MC, Potapov PV, Moore R et al (2013) High-resolution global maps of 21st-century forest cover change. Science 342:850–853

Harvey BC, White JL, Nakamoto RJ (2004) An emergent multiple predator effect may enhance biotic resistance in a stream fish assemblage. Ecology 85:127–133

Henley WF, Patterson MA, Neves RJ et al (2000) Reviews in fisheries science effects of sedimentation and turbidity on lotic food webs : a concise review for natural resource managers. Rev Fish Sci 8:125–139

Huenneke LF, Hamburg SP, Koide R et al (2014) Effects of soil resources on plant invasion and community structure in Californian serpentine grassland. Ecology 71:478–491

Jauni M, Hyvo T (2012) Positive diversity—invasibility relationships across multiple scales in Finnish agricultural habitats. Biol Invasions 14:1379–1391

Jeschke JM (2014) General hypotheses in invasion ecology. Divers Distrib 20:1229–1234

Johnson DS (1973) Freshwater life. In: Chuang SH (ed) Animal life and nature in Singapore. University Press, Singapore, pp 103–127

Johnson JB, Omland KS (2004) Model selection in ecology and evolution. Trends Ecol Evol 19:101–108

Johnson PT, Olden JD, Vander Zanden MJ (2008) Dam invaders: impoundments facilitate biological invasions into freshwaters. Front Ecol Environ 6:357–363

Kennedy TA, Naeem S, Howe KM et al (2002) Biodiversity as a barrier to ecological invasion. Nature 417:636–638

Kottelat M, Whitten AJ, Kartikasari SN et al (1993) Freshwater fishes of Western Indonesia and Sulawesi. Periplus Editions, Hong Kong

Lake PS, Dowd DJO (1991) Red crabs in rain forest, Chirstmas Island: biotic resistance red crabs in rain forest, to snail invasion by an exotic snail. OIKOS 62:25–29

Levine JM, Adler PB, Yelenik SG (2004) A meta-analysis of biotic resistance to exotic plant invasions. Ecol Lett 7:975–989

Lim P, Lek S, Tana S et al (1999) Diversity and spatial distribution of freshwater fish in Great Lake and Tonle Sap river (Cambodia, Southeast Asia). Aquat Living Resour 12:379–386

Lindeman RL (1942) The trophic-dynamic aspect of ecology. Ecology 23:399–417

Lodge DM, Williams S, MacIsaac HJ et al (2006) Biological invasions: recommendations for US policy and management. Ecol Appl 16:2035–2054

Lowry E, Rollinson EJ, Laybourn AJ et al (2013) Biological invasions: a field synopsis, systematic review, and database of the literature. Ecol Evolut 3:182–196

Lukacs PM, Thompson WL, Kendall WL et al (2007) Concerns regarding a call for pluralism of information theory and hypothesis testing. J Appl Ecol 44:456–460

MacDougall AS, Turkington R (2005) Are invasive species the drivers or passengers of change in degraded ecosystems? Ecology 86:42–55

Mack RN, Simberloff D, Lonsdale WM et al (2000) Biotic invasions: causes, epidimiology, global consequences and control. Ecol Appl 10:689–710

Marchetti MP, Light T, Moyle PB et al (2004a) Fish invasions in California watersheds: testing hypotheses using landscape patterns. Ecol Appl 14:1507–1525

Marchetti MP, Moyle PB, Levine R (2004b) Invasive species profiling? Exploring the characteristics of non-native fishes across invasion stages in California. Freshw Biol 49:646–661

Marks JC, Williamson C, Hendrickson DA (2011) Coupling stable isotope studies with food web manipulations to predict the effects of exotic fish: lessons from Cuatro Cienegas, Mexico. Aquat Conserv Mar Freshw Ecosyst 21(4):317–323

Marra G, Wood SN (2011) Practical variable selection for generalized additive models. Comput Stat Data Anal 55:2372–2387

Meyerson LA, Pys P (2013) Manipulating alien plant species propagule pressure as a prevention strategy for protected areas. In: Foxcroft LC, Pysek P, Richardson DM, Genovesi P (eds) Plant invasions in protected areas. Springer, Netherlands, pp 473–486

Mohd SK, Lee KY, Cramphon P et al (1996) Freshwater fishes of the Pahang River Basin, Malaysia. Wetlands International-Asia Pacific, Kuala Lumpur

Moulton MP, Pimm SL (1983) The introduced hawaiian avifauna: biogeographic evidence for competition. Am Nat 121:669–690

Moyle PB, Light T (1996) Biological invasions of fresh water: empirical rules and assembly theory. Biol Conserv 78:149–161

Nakagawa S, Schielzeth H (2013) A general and simple method for obtaining R^2 from generalized linear mixed-effects models. Methods Ecol Evol 4:133–142

Nelson A (2009) Accessibility model and population estimates. Background paper and digital files prepared for the World Development report

Ng HH, Tan HH (2010) An annotated checklist of the non-native freshwater fish species. COSMOS 6:95–116

Oakley CA, Knox JS (2013) Plant species richness increases resistance to invasion by non-resident plant species during grassland restoration. Appl Veg Sci 16:21–28

Oksanen J, Blanchet FG, Kindt R et al (2013) Vegan: community ecology package. R package version 2.0-6

Pace M, Cole J, Carpenter Sr et al (1999) Trophic cascades revealed in diverse ecosystems. Trends Ecol Evol 14:483–488

Papa RDS, Mamaril A Sr (2011) History of the biodiversity and limno-ecological studies on Lake Taal with notes on the current state of Philippine limnology. Philipp Sci Lett 4:1–10

Parendes LA, Jones JA (2000) Role of light availability and dispersal in exotic plant invasion along roads and streams in the HJ Andrews Experimental Forest, Oregon. Consrv Biol 14:64–75

Pauly D (2000) Box 29, Fishbase. In: Froese R, Pauly D (eds) Fishbase. World wide web electronic publication. www.fishbase.org

Pauly D, Christensen V (1995) Primary production required to sustain global fisheries. Nature 374:255–257

Perdomo G, Thompson R, Sunnucks P (2012) Food web: an open-source program for the visualisation and analysis of compilations of complex food webs. R package version 4.2

Petchey OL (2000) Species diversity, species extinction, and ecosystem function. Am Nat 155:696–702

Pholprasith S, Sirimongkonthaworn R (1999) The fish community of Ubolratana Reservoir, Thailand. In: van Densen WLT, Morris MJ (eds) Fish and fisheries of lakes and reservoirs in southeast Asia and Africa. Westbury Publishing, Great Britain, pp 95–102

Poessel SA, Beard KH, Callahan CM et al (2013) Biotic acceptance in introduced amphibians and reptiles in Europe and North America. Glob Ecol Biogeogr 22:192–201

Polis GA (1991) Complex trophic interactions in deserts: an empirical critique of food-web theory. Am Nat 138:123–155

Proches S, Wilson JRU, Richardson DM et al (2008) Searching for phylogenetic pattern in biological invasions. Global Ecol Biogeogr 17:5–10

QGIS Development Team (2014) QGIS geographic information system. Open Source Geospatial Foundation Project

R Core Team (2015) A language and environment for statistical computing. R foundation for statistical computing. R Core Team, Vienna

Rainboth WJ (1996) Fishes of the cambodian mekong. FAO, Rome

Rintelen KV, Rintelen TV, Glaubrecht M (2007) Molecular phylogeny and diversification of freshwater shrimps (Decapoda, Atyidae, Caridina) from ancient Lake Poso (Sulawesi, Indonesia)—the importance of being colourful. Mol Phylogenet Evol 45:1033–1041

Romanuk TN, Zhou Y, Brose U et al (2009) Predicting invasion success in complex ecological networks. Philos Trans R Soc Lond B Biol Sci 364:1743–1754

Rossberg AG, Yanagi K, Amemiya T et al (2006) Estimating trophic link density from quantitative but incomplete diet data. J Theor Biol 243:261–272

Rouget M, Richardson DM (2003) Inferring process from pattern in plant invasions: a semimechanistic model incorporating propagule pressure and environmental factors. Am Nat 162:713–724

Roux PC, Ramaswiela T, Kalwij JM et al (2013) Human activities, propagule pressure and alien plants in the sub-Antarctic: tests of generalities and evidence in support of management. Biol Conserv 161:18–27

Sax DF, Gaines SD (2008) Species invasions and extinction: the future of native biodiversity on islands. Proc Natl Acad Sci USA 105:11490–11497

Scharf FS, Juanes F, Rountree RA (2000) Predator size-prey size relationships of marine fish predators: interspecific variation and effects of ontogeny and body size on trophic-niche breadth. Mar Ecol Prog Ser 208:229–248

Schoenly K, Cohen JE (1991) Temporal variation in food web structure: 16 empirical cases. Ecol Monogr 61:267–298

Scotti M, Bondavalli C, Bodini A et al (2009) Using trophic hierarchy to understand food web structure. OIKOS 118:1695–1702

Shea K, Chesson P (2002) Community ecology theory as a framework for biological invasions. Trends Ecol Evol 17:170–176

Sim CH (2002) Fish of Tasek Bera. Wetlands International-Malaysia Programme, Kuala Lumpur

Simberloff D (2009) The role of propagule pressure in biological invasions. Annu Rev Ecol Evol Syst 40:81–102

Sinclair ARE (1975) The resource limitation of trophic levels in tropical grassland ecosystems. J Anim Ecol 44:497–520

Sodhi NS, Koh LP, Brook BW et al (2004) Southeast Asian biodiversity: an impending disaster. Trends Ecol Evol 19:654–660

Sodhi NS, Bickford D, Diesmos AC et al (2008) Measuring the meltdown: drivers of global amphibian extinction and decline. PLoS ONE 3:1–8

Stachowicz JJ, Tilman D (2005) Species invasions and the relationships between species diversity, community saturation, and ecosystem functioning. In: Stachowicz JJ, Gaines SD, Sax DF (eds) Species invasions: insights into ecology, evolution, and biogeography. Sinauer Associates, Massachusetts, pp 41–64

Tacon AGJ, Metian M, Turchini GM et al (2009) Responsible aquaculture and trophic level implications to global fish supply. Rev Fish Sci 18:94–105

Taylor CM, Duggan IC (2012) Can biotic resistance be utilized to reduce establishment rates of non-indigenous species in constructed waters ? Biol Invasions 14:307–322

Thomas P (2005) Fishes and ecological aspects in the southern region of Lake Toba and its associated rivers, Sumatra, Indonesia. Malay Nat J 57:81–89

Tilman D (1997) Community invasibility, recruitment limitation, and grassland biodiversity. Ecology 78:81–92

Tilman D (2004) Niche tradeoffs, neutrality, and community structure: a stochastic theory of resource competition, invasion, and community assembly. Proc Natl Acad Sci USA 101:10854–10861

Turesson H, Persson A, Bronmark C (2002) Prey size selection in piscivorous pikeperch (*Stizosteidon lucioperca*) includes active prey choice. Ecol Freshw Fish 11:223–233

Wiens JJ (2011) The niche, biogeography and species interactions. Philos Trans R Soc Lond B Biol Sci 366:2336–2350

Williams RJ, Martinez ND (2000) Simple rules yield complex food webs. Nature 404:180–183

Williams RJ, Martinez ND (2004) Limits to trophic levels and omnivory in complex food webs: theory and data. Am Nat 163:458–468

Yang SL (1989) Bighead carp culture in floating net-cages and water quality at seletar reservoir—a case study. PUB R&D J 1:28–33

Yeo DCJ, Lim KKP (2011) Freshwater ecosystems. In: Ng PKL, Corlett RT, Tan HTW (eds) Singapore biodiversity. Editions Didier Millet, Singapore, pp 52–63

Zakaria-Ismail M, Lim KKP (1995) The fish fauna of Tasik Temenggor and its tributaries south of Banding, Hulu Perak, Malaysia. Malay Nat J 48:319–332