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R E V I E W

Empirical Predictions of the Trophic Consequences of Non-Native Freshwater Fishes: A Synthesis of Approaches and Invasion Impacts

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Abstract

Predicting the ecological impacts of invasive fishes is crucial for understanding their risks in the environment. Experimental approaches that provide empirical data on invasion impacts provide both theoretical insights and data of high management utility for prioritising high-risk invaders. Here, a synthesis of some experimental approaches that predict invasion impacts of non-native fish is presented, where the focus is on impacts relating to the trophic impacts of the invader on either native trophically analogous fishes or prey populations. Experiments in tank aquaria are advantageous in providing homogenous and controlled conditions that also enable high replication. Competition-based studies can determine invasion impacts via exposure of fish to fixed food rations, although these experiments tend to produce results in intensely competitive conditions that might not occur in the wild. Comparative functional response experiments in tank aquaria have been successfully applied to determining the relative impacts of invaders compared with native species on prey populations, and have revealed high resource efficiency in globally invasive piscivorous fishes. Experiments completed in mesocosms and small ponds have the advantage of providing replicated systems in semi-natural conditions. They have been successful in revealing that rather than competing with native fishes, many invasive fishes show strong patterns of trophic niche partitioning. These patterns are also evident in these fishes when in natural invaded communities. Thus, whilst it is often suggested invasion impacts from non-native fishes result from inter-specific competition, evidence for this from experimental and field-based predictions is equivocal.

Introduction

Predicting the ecological impacts of invasive fishes is integral to understanding and managing their risks in the environment (Kumschick *et al.*, 2012; Leung *et al.*, 2012). Approaches that predict the invasion impacts on native populations and communities are especially important, as they help explain the underlying processes that are driving the observed patterns (Britton, Ruiz-Navarro, Verreycken & Amat-Trigo, 2017). The utility of predictive approaches to impact assessment is that when they are coupled with horizon scanning and surveillance programmes, they should enable management resources to be rapidly directed to controlling the presence and dispersal of newly introduced high-risk species prior to their establishment (Simberloff *et al.*, 2013; Lampert, Hastings, Grosholz, Jardine, & Sanchirico, 2014; Roy *et al.*, 2014).

Allied to their management utility, predictive approaches in invasion biology also enable the testing of ecological theory using invasive species. A wide

range of theory can be tested using invasive species (Catford, Jansson & Nilsson, 2009; Jeschke, 2014; Enders, Hütt & Jeschke, 2018), including propagule pressure (Lockwood, Cassey & Blackburn, 2005; Britton and Gozlan 2013), biotic resistance (Britton, 2012), and the enemy release hypothesis (Sheath, Williams, Reading & Britton, 2015). Regarding the introduction of a new species into a native food web, there are a series of niche-based hypotheses that potentially explain how the introduced species integrates into the community and how native species can coexist in sympatry with the invader (Ricciardi, Hoopes, Marchetti & Lockwood, 2013). For example, the release of a new species into a species-poor community that has unexploited resources would enable the invader to utilise these resources, avoiding competitive interactions with native species and enhancing their ability to integrate into the food web (Mason, Cooke, Moles & Leishman, 2008; Juncos, Milano, Macchi & Vigliano, 2015). When the introduction is into a community where resources are fully exploited and potentially limiting, theory predicts that the interactions between the introduced and native species will result in both their trophic niches becoming constricted and divergent through dietary specialisms (Bolnick *et al.*, 2010; Tran, Jackson, Sheath, Verreycken & Britton, 2015; Jackson, Grey, Miller, Britton, & Donohue, 2016). Conversely, these increases in competitive interactions might result in the species exploiting a wider resource base and thus resulting in larger trophic niches (Svanbäck and Bolnick, 2007). If the introduced species is a superior competitor then their exploitation of the resources potentially results in the competitive exclusion of native species (Bøhn, Amundsen & Sparrow, 2008; Tran *et al.*, 2015).

A major issue in predicting the ecological impacts of invasive species for testing ecological theory and applying the results to management is that impact assessments are often variable between contexts and systems. In wild situations, post-invasion scenarios often lack pre-invasion data, making before-and-after-impact assessments challenging, especially in the absence of control sites (Britton, Davies & Harrod, 2010; de Moura Queirós, Hiddink, Johnson, Cabral, & Kaiser., 2011). Correspondingly, where predictions of impacts are reliant only on field case studies, the context dependency of approaches and outcomes often inhibit the derivation of robust predictions for application beyond the study system (Alexander, Dick, Weyl, Robinson & Richardson, 2014; Dick *et al.*, 2014).

Consequently, the aim of this review was to synthesise a range of extant studies that predicted the impacts of invasive freshwater fishes using *in-* and *ex-situ* approaches. The focus was on predicting trophic impacts, either between fishes of the same trophic guild or at similar trophic levels, or impacts of predation on prey populations and how they vary between invasive and native trophic analogues. Rather than providing a comprehensive review of all of the studies completed using these approaches, the aim was to synthesise information across a range of approaches for application to studies on invasion-mediated trophic impacts. These studies were based on invasive and native fishes present in temperate Western European freshwaters, with focus often on British freshwaters by work completed by the author. Each approach includes demonstration of how they have been applied and how they enhance impact prediction. Note that throughout the review, the focus was on empirical experimental approaches and so modelling approaches that predict invasion impacts and/ or outcomes, such as agent-based models, were not considered.

Approaches, Model Species and Experimental Design

Approaches to empirical experiments to predict invasion impacts of non-native fishes can be completed across a range of spatial scales (Table 1). The smallest of these tend to be experiments completed in tank aquaria (microcosms). These simulate the interactions between the invader and native species across a range of competitive and/ or predator-prey scenarios in order to develop understandings of the impact processes that then help explain the impact patterns detected at larger spatial scales (Dick *et al.*, 2014). Their benefit is that they can be completed in homogenous, controlled conditions with high replication of treatments and controls. Their experimental designs should then provide relatively high statistical power in analyses. The next spatial experimental scale tends to be small ponds and mesocosms. Here, the ecological complexity of the experimental arenas is increased (at least compared to aquaria experiments), but with the approach still enabling the use of replicated controls and treatments in the experimental design. This ensures greater precision in impact prediction than in experiments completed at larger spatial scales, where the ability for true replication is more constrained. The final experimental approach outlined here are large-scale field based experiments where, for example, before-after-control-impact (BACI) experiments can be utilised to better understand the ecological impacts of the invasive fish in wild conditions, but where replication can be more difficult.

Irrespective of the experiment, the model species requires consideration. This species might be a specific non-native fish for which there is minimal extant information on their impacts in wild situations and thus the experiment aims to predict their potential impacts for invasive species that can be used as the basis of invasion impact assessments (Copp *et al.*, 2009, 2016). Alternatively, the focal non-native fish can be used as a model that is representative of a wider range of non-native taxa that enables conclusions to be drawn on impact predictions that are relevant beyond the study system (Dick *et al.*, 2017a). Irrespective of the focal

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Table 1. A summary of the spatial scale of some experimental approaches that can be used to predict the impact of invasive freshwater fishes. The spatial scales of the experimental systems (as volume or area) are provided as examples to highlight differences between the approaches, rather than representing definitive size limits

Spatial scale	Testing	Example	
Tank aquaria (Indoor; < 200 L)	Competitive interactions and consequences	Native *Carassius carassius* versus invasive *Cyprinus carpio* and *Carassius auratus*	Busst and Britton (2015)
	Functional response parameters within comparative functional responses	Consumption rates of invasive *Micropterus salmoides* versus native *Sandelia capensis*	Alexander et al. (2014)
Mesocosms (Outdoor, > 200 L, < 2000 L)	Trophic consequences of invasion of non-native fish on native fishes via assessment of altered characteristics of trophic niches	Invasive *Pseudorasbora parva* versus native fishes	Tran et al. (2015)
	Biotic resistance to a fish introduction	Introduced *Pseudorasbora parva* versus *Cyprinus carpio*	Britton (2012)
	Trophic impacts on prey communities and ecosystem function	Invasive *Pseudorasbora parva*	Jackson et al. (2015)
Pond systems (Outdoor, > 15 m²)	Trophic consequences of invasion of non-native fish on native fishes via assessment of altered characteristics of trophic niches	Invasive *C. carpio* and *C. auratus* versus native *Tinca tinca*	Britton et al. (2017)
		Invasive *Lepomis gibbosus* versus native pond fishes	Copp et al. (2017)
Wild systems	Trophic consequences of invasion of non-native fish on native fishes via assessment of altered characteristics of trophic niches	Invasive *Barbus barbus* versus native *Squalius cephalus*	Bašić and Britton (2016)

non-native fish being used in the study, the ethos of the three 'R's of animal experimentation ('replace, reduce and refine') need to be embedded within experimental designs. This ensures that the most appropriate number of fishes is used in accordance with the power requirements of statistical analyses, and that the use of live fishes can be justified in the context of the benefits the research delivers (Metcalfe and Craig, 2011).

Where experiments aim to predict competitive consequences resulting from trophic interactions of the invasive and native fishes, then growth rate metrics should be utilised. This is because fish growth is indeterminate and strongly influenced by both biotic and abiotic conditions. Thus, assuming that experimental abiotic conditions are constant, differences in growth rates between treatments should only result from biotic differences between the treatments according to the experimental design. Indeed, Ward, Webster & Hart (2006) suggested that as fish are adaptable and tractable experimental organisms, they represent strong model species for use in studies on competitive interactions.

Predictive Approaches in Tank Aquaria

The utilisation of tank aquaria experiments to predict invasion impacts in the wild provides the opportunity for experiments to utilise high replication in the experimental control and treatments and in conjunction with controlled conditions (e.g. temperature, day-length, prey supply, water quality, refugia). However, the size of aquaria will limit the size and numbers of individual fish that can be used experimentally. Here, the application of experiments completed in tank aquaria to invasion impact

prediction is demonstrated by two approaches: competitive interactions between species at the same trophic level and/ or feeding guild, and predator-prey relationships according to comparisons of consumption rates on prey populations between invasive fishes and native trophically analogous fishes.

Competitive Interactions

In fishes where the mode of competition tends to be exploitative rather than antagonistic, experiments can be designed whereby the *per capita* daily food supply to the fish is kept constant, but the number and/ or combination of species present in the experimental treatments differ, with growth rate metrics then used as powerful analytical tools to assess the outcome of competitive interactions (Ward *et al.*, 2006). For example, to predict the outcome of competitive interactions between a non-native and native species, a simple experiment could comprise each species in allopatry (N = 10) and then in sympatry (n = 5 of each species). Each would be replicated at least three times in tank aquaria (e.g. 45 L), exposed to fixed daily rations of prey at above maintenance levels but below *ad libitum* (e.g. mean 2 % body weight per day), and completed over a fixed timeframe (e.g. 30 days). The change in mean body mass and/ or fish length per species and treatment over the experimental timeframe can then be assessed to determine whether the competitive interactions between the species were symmetric (growth rates are not significantly different between the species and their allopatric and sympatric treatments) or asymmetric (growth rates are significantly different between species and their allopatric and sympatric treatments). Complexity in experimental design can

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then, for example, increase the number of treatments by using different combinations of fish numbers, adding other fishes, using different food rations or food items, increasing environmental complexity, and/ or manipulating water temperature and day length. Integral to these experiments is the measurement of individual or batch weights of the fish in each replicate before and after the experiment; where information is required at the individual level then a tagging technique that enables individual recognition is recommended, such as insertion of passive integrated transponder (PIT) tags (Britton, Cucherousset, Grey & Gozlan, 2011). Changes in body length (e.g. as incremental length changes) and/ or mass (e.g. specific growth rates) can then assess growth rates.

An example of this type of experiment to predict invasion impacts is provided by Busst and Britton (2015). They used a tank aquaria experiment to predict the outcomes of competitive interactions between the native crucian carp *Carassius carassius* and its invasive trophic analogues, goldfish *Carassius auratus* and common carp *Cyprinus carpio*. In the wild, whilst the interactions of these fishes tend to result in genetic introgression (e.g. Hanfling, Bolton, Harley & Carvalho, 2005), their trophic interactions and consequences were less clear, but were hypothesised as to be detrimental due to competition resulting from their similar foraging behaviours and functional traits. An aquaria experiment completed over 30 days and using the fishes in allopatric and sympatric contexts under fixed food rations, revealed significantly depressed growth rates in *C. carassius* in all sympatric contexts compared to allopatry, suggesting asymmetric competitive interactions with the invaders (Busst and Britton, 2015).

Britton *et al*. (2011) used topmouth gudgeon *Pseudorasbora parva* and *C. carpio* in a range of treatments to determine how body size and biomass affected their competitive outcomes. The results indicated that the inter-specific competition imposed by *P. parva* was only as strong as the intra-specific competition within *C. carpio* when they were present at a similar biomass. These results reveal that in these types of competitive experiments, whilst the fish number per treatment is important, their biomass must also be considered carefully, as this can impact the outcomes of the experiment (Britton *et al*., 2011).

Comparative Behavioural Functional Responses

It has been argued that as many invasive species tend to have highly efficient resource use, the utilization of 'comparative functional responses', i.e. the comparisons between invasive and trophically analogous native species of the relationship between the resource use of a consumer and its availability, can predict invasion impacts on prey populations (Dick *et al*., 2014). By their description of the resource use of the species over a range of resource availabilities, these experiments provide foraging metrics capable of testing differences between the species, such as attack rates (*a*), food handling times (*h*) and maximum consumption rates (Dick *et al*., 2014, 2017a,b). There is then potential for testing of the likely population-level outcomes of invasions for affected species (Dick *et al*., 2014). In this context, these ecological impacts focus on the invasion impacts on prey populations and/ or communities (Guo, Sheath, Amat Trigo & Britton, 2017). Whilst there has been some conjecture over the utility of the approach to impact assessment (e.g. Vonesh, McCoy, Altwegg, Landi & Measey, 2017; Dick *et al*., 2017b,c), these experiments can provide a rapid impact assessment tool capable of predicting ecological impacts of invasive fishes and other non-native taxa (e.g. Alexander *et al*., 2014; Penk *et al*., 2017).

These comparative functional response (CFR) experiments tend to be completed in small tank aquaria (e.g. 10 L) that provide uniform habitats at constant temperatures (Guo *et al*., 2017). Fish are usually used individually and are exposed to fixed prey densities (e.g. 2 to 96 per tank; minimum three replicates) of the same prey type (e.g. Chironomid larvae or Daphnia spp.) and over a fixed timeframe (e.g. 1 hour) (Laverty *et al*., 2017). The amount of food consumed in that unit of time according to the initial prey density is then defined as the consumption rate of that individual. Values of the CFR parameters attack rate (*a*) and handling time (*h*) can then be estimated using, for example, the Random Predator Equation (Rogers, 1972) that assumes a Type II functional response and the non-replacement of prey ($N_e = N_0 (1 - \exp(a(N_e h - T)))$, where N_e is the number of prey eaten, N_0 is the initial density of prey, *a* is the attack rate, *h* is the handling time and T is the total time available). The asymptote of the curve (i.e. the maximal consumption rate) can be determined from ($1/h$) (Laverty *et al*., 2017). Differences in *a* and *h* between the invader and native species can then be tested for their statistical significance (Dick *et al*., 2014, 2017a; Barrios-O'Neill *et al*., 2016; Guo *et al*., 2017; Laverty *et al*., 2017). This testing can be completed in specific R packages, such as 'Functional responses in R' (*Frair*; Pritchard, 2014; Pritchard, Paterson, Bovy & Barrios-O'Neill, 2017).'

The utility of the approach for testing high impact invaders was revealed by Alexander *et al*. (2014), who compared FRs of the largemouth bass *Micropterus salmoides*, a globally invasive piscivorous fish with reported impacts on native prey communities (e.g. Gratwicke and Marshall, 2001), with a South African trophically-analogous native fish, the Cape kurper *Sandelia capensis*, as well as an emerging invasive catfish *Clarias gariepinus* (also invasive in many areas of the world; Kadye and Booth, 2012), with the South African river goby *Glossogobius callidus*. They detected that both invaders consumed more prey (as tadpoles, *Hyperolius marmoratus*), with significantly lower

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handling times that resulted in significantly higher maximum consumption rates.

Whilst demonstrating the potential high utility of the method for discriminating high impact piscivorous invasive fishes (e.g. Alexander *et al.*, 2014), results for invaders versus native omnivorous fishes have been less clear. For example, differences in maximum consumption rates were not being significantly different between invasive *C. carpio* and *C. auratus* versus native trophic analogues in Britain, such as tench *Tinca tinca* (Guo *et al.*, 2017). However, this does not necessarily mean these invaders have negligible trophic impacts via their predation, as these results only provide *per capita* consumption rates. Thus, Laverty *et al.* (2017) revealed how *per capita* data might be scaled up to population level impacts. For example, they demonstrated that whilst consumption rates of individual invasive *P. parva* might be relatively low, their propensity for forming highly abundant populations (Britton *et al.*, 2010) means that when scaled up to population levels, their relative impact potential (Dick *et al.*, 2017a) is substantially elevated and of high ecological concern. Indeed, the development of more nuanced experimental and analytical protocols for comparative functional responses for non-native fishes that are, for example, omnivorous and exploitative competitors, enables increased ecological complexity and realism within predictions, thus providing a more robust and powerful predictive tool (Dick *et al.*, 2017a; Laverty *et al.*, 2017; Penk *et al.*, 2017).

Mesocosm and Pond Experiments

A mesocosm can be defined as any outdoor experimental system that is based in natural environmental conditions. Mesocosms are generally smaller than natural ponds (Table 1), and have greater control of their environmental conditions. They are usually larger than tank aquaria (Table 1), but have less control of their conditions. For assessments of the trophic impact of non-native fishes, it is likely that mesocosms would be situated outside and of sufficient number to enable an experimental design that would comprise replicated controls and treatments. The mesocosms are also likely to provide homogenous habitats across the replicates, including refugia and water chemistry, and be seeded with the same invertebrate fauna. Correspondingly, the only differences between the mesocosms of the control and treatments should the numbers and/ or species of fish involved. Similarly, larger, pond-based experiments should also aim to achieve homogenized physical, chemical and biotic conditions across replicates, although given the larger spatial scale this can be more difficult to achieve (Copp *et al.*, 2017). Experiments completed within enclosures situated within a single, larger pond can help overcome this (Britton *et al.*,

2017).

The duration of experiments will be dependent upon the research questions and analytical tools being applied. Studies that seek to assess the trophic interactions of native and non-native fishes might utilise stable isotope (SI) analysis (e.g. δ^{13}C and δ^{15}N), as this can provide a temporally integrated assessment of diet (Cucherousset, Boulêtreau, Martino, Roussel & Santoul, 2012). This will, however, mean that the experiment will need to be of sufficient duration for sufficient isotopic turnover in the tissues to ensure the SI data reflects the diet of the fishes within the mesocosms/ ponds and not their previous diets (Busst and Britton, 2018). Where assessments of impacts on zooplankton communities or decomposition rates are required, experimental length can be shorter, with the application of, for example, 'leaf packs' for assessing cascading impacts on decomposition rates (Jackson, Ruiz-Navarro & Britton, 2015).

A series of experiments using stable isotope analysis to assess the trophic interactions and impacts of invasive fishes on native fishes completed in mesocosms and small ponds have consistently revealed that rather than the fishes sharing resources and so having high trophic niche convergence, patterns of niche partitioning have generally been strongly evident. Trophic niche partitioning between invasive and native fishes have been demonstrated in studies involving invasive *P. parva*, *C. carpio*, *C. auratus*, pumpkinseed *Lepomis gibbosus* and European barbel *Barbus barbus* (Tran *et al.*, 2015; Bašić and Britton, 2016; Britton *et al.*, 2017; Copp *et al.*, 2017; Gutmann Roberts, Bašić, Amat Trigo & Britton, 2017). In the case of sympatric *P. parva*, *C. carpio* and *L. gibbosus*, this trophic niche partitioning was also coincident with constricted niche sizes compared with the species in allopatry, indicating more specialised diets in sympatry and thus some consistency with the niche variation hypothesis (Tran *et al.*, 2015; Copp *et al.*, 2017). Conversely, an experiment testing the relative effects of increased intra- versus inter-specific competition involving the presence of invasive fishes revealed whilst increased fish abundances significantly altered the position of the trophic niches of all fishes, the niche sizes were relatively unaffected (Britton *et al.*, 2017). Thus, across all of these studies, whilst patterns of niche partitioning were evident in all species, there was some context dependency in whether niche constriction also occurred. In addition, the predicted patterns of niche partitioning in the experiments were generally similar to the patterns of trophic niche partitioning evident in more complex wild fish communities where the invader was present, indicating their general applicability and utility (Britton, Tran & Ruiz-Navarro, 2015; Britton *et al.*, 2017).

Jackson *et al.* (2015) tested how the population density of *P. parva* impacted a range of biological characteristics of invaded pond mesocosms and

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revealed that the severity of impacts was both linear and non-linear. For example, whilst the relationship between *P. parva* density and zooplankton body mass was described by a low-threshold curve, with higher impacts at low densities than predicted linearly, the relationship between density and zooplankton biomass and abundance was also non-linear but with a high-threshold, indicating a lower impact than a linear relationship would predict. Although impacts on phytoplankton metrics were linear, impacts on benthic invertebrate abundance and decomposition rates were described by s-shaped curves. These experimental results were underpinned by dietary analyses that indicated that *P. parva* increasingly relied on zooplankton resources as density increased, a consequence of resource depletion (Jackson *et al.*, 2015).

The increased complexity and more natural conditions provided by these systems when compared with tank aquaria also enables the results from tank aquaria experiments to set testable hypotheses for testing in more complex environments. For example, it was outlined above that in the presence of fixed food rations in tank aquaria, the competitive interactions of native *C. carassius* with invasive *C. carpio* and *C. auratus* were asymmetric, resulting in depressed growth rates of the native fish (Busst and Britton, 2015). Their interactions and growth rates were then tested in a pond enclosure experiment (Busst and Britton, 2017). For *C. carassius* and *C. auratus*, their trophic niche sizes and positions were not significantly different between allopatric and sympatric contexts, with high niche overlap. Whilst this suggested that there was potential for competition to occur, this was not evident in their growth rates, a contrast to the tank experiment (Busst and Britton, 2015). This suggests that both species were exploiting similar resources that were sufficiently abundant not to result in depressed growth rates. These results were also in line with those of Tarkan, Cucherousset, Zięba, Godard, & Copp (2010), who suggested that across four invaded wild ponds, there was no difference in the growth rates of *C. carassius* in *C. auratus* when compared with ponds where *C. auratus* was absent. However, when *C. carassius* was sympatric with *C. carpio* in the pond experiment, their isotopic niche shifted to a higher trophic position compared with allopatry and their growth rate was significantly depressed (Busst and Britton, 2017). These results were thus more consistent with the tank aquaria experiment predictions.

In entirety, the results from these pond-based experiments suggest that when the ecological complexity of the experimental system is increased, such as using semi- wild contexts with natural food resources available, these can provide greater understandings of the outcomes of the trophic interactions of invasive and native fishes than tank aquaria experiments alone.

Field Experiments and Manipulations

The final experimental approach synthesised here is where large-scale natural systems are manipulated in order to make experimental predictions of impacts arising from the trophic interactions of invasive and native fishes. It should be noted that there are strong ethical and biosecurity issues associated with the release of non-native fish into freshwaters for research purposes and this should never be completed without full risk assessment and consents granted from relevant authorities. Moreover, it can be argued that if the driver of the introduction is only research, then it should not proceed given the unpredictable impacts that could result from the introduction. Consequently, these approaches are more suited to systems where the focal invasive fish is already present and where manipulations of their population sizes can be completed and/ or their presence/ absence across different systems provides a series of replicated natural 'control' and 'treatment' waters.

An example of a study using natural 'control' and 'treatment' waters is provided by Britton *et al*. (2010), where two adjacent angling ponds of similar size, depth and water chemistry provided a control (no *P. parva* present) and treatment (*P. parva* present in high abundance) system. Other than *P. parva*, the fish assemblages of the ponds were similar. The *P. parva* had been present in the invaded pond for approximately two years following an accidental release when a batch of larger fishes being stocked to enhance angling was contaminated (Davies, Gozlan & Britton, 2013). Stable isotope analysis revealed that in the invaded pond, there was high trophic overlap between *P. parva*, *C. carpio* and roach *Rutilus rutilus*. Analysis of temporal patterns in growth rates revealed that the growth rates of *R. rutilus* were significantly depressed in the period of high *P. parva* abundance versus the period prior to their introduction. Moreover, there were no significant patterns in the temporal growth rates of *R. rutilus* in the pond where *P. parva* were absent. These results suggested that the depressed growth of *R. rutilus* in the invaded pond was due to *P. parva* mediated inter-specific competition (Britton *et al.*, 2010). In addition, in the invaded pond, a number of native cyprinid fishes, including common bream *Abramis brama*, were approximately one trophic level higher than *P. parva*, suggesting these omnivorous fishes were predating on the highly abundant invaders, probably their young-of-the-year (Britton *et al.*, 2010). Indeed, other cyprinid fishes have been shown to resist the establishment of *P. parva* via predation of these life-stages (Britton, 2012).

Subsequent mesocosm and pond experiments have suggested that the extreme abundance of *P. parva* in the invaded pond of Britton *et al*. (2010) was likely to have resulted from high angling activities resulting in their baits providing strong trophic

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subsidies (Jackson, Allen, Pegg & Britton, 2013). These subsidies appear to significantly increase the growth and survival of young-of-the-year *P. parva*, enabling them to overcome the biotic resistance imposed from other cyprinid fishes (Britton *et al*., 2015). Where these angling trophic subsidies are lower or absent, then *P. parva* population sizes tend to be much lower, with the result that their inter-specific interactions with native fishes are less severe, and with patterns of trophic niche partitioning strongly evident (Tran *et al*., 2015).

The consequences of stocking indigenous fish into freshwaters within their natural range but where they are currently not present can also provide information suitable for testing hypotheses relating to invasion biology, given that the underlying establishment and colonisation processes are likely to be similar. An example was provided by Bašić and Britton (2016), where the effects of stocking of *B. barbus* (a species that is also invasive outside of its natural range) on chub *Squalius cephalus* were tested in its natural range in eastern England. This study used two experimental approaches, completed in pond mesocosms and two streams, with comparison of results to the wild populations in three lowland rivers. In pond mesocosms, there was the rapid formation of dietary specialisations and discrete trophic niches between the fish species. This pattern of niche partitioning was also apparent in both streams in the two years after their stocking with hatchery-reared *B. barbus*, where both streams did not have an established *B. barbus* population present prior to the stocking. These results were also consistent with larger fishes in the lowland rivers, where the two fishes revealed strong partitioning in their trophic niches (Bašić and Britton, 2016). Consequently, the two experimental approaches revealed that these hatchery-reared *B. barbus* incurred only minor consequences for the trophic ecology of *S. cephalus*, with consistent patterns of trophic niche partitioning and diet specialisation. These results can thus be applied to risk assessment processes for situations where *B. barbus* are proposed for release for the enhancement of angling in areas outside of their natural range (Copp *et al*., 2009).

Discussion

This study synthesised two main aspects of invasion impacts that can be predicted from empirical experiments:(1) interactions of invasive and native fishes that are functionally analogous and/ or at similar trophic positions, and (2) predator/ prey relationships. It was outlined that the interactions of functionally analogous fishes can be studied over a range of spatial scales, from relatively small tank aquaria up to field based, natural experiments (Bašić and Britton, 2016). For predator/ prey relationships and comparisons between invasive and native fishes, tank based approaches were described that were based on comparative functional responses. It was recognised that the complexity of these relatively simple experimental arenas can be increased in order to increase the robustness of the predictions for omnivorous or non-piscivorous fishes (Laverty *et al*., 2017).

An important outcome of the experiments that predicted impacts from the trophic interactions of native fishes and a functionally analogous invasive fish was that large trophic niche overlaps were rarely detected, with niche partitioning being the consistent prediction across most studies (e.g. Tran *et al*., 2015; Bašić and Britton, 2016; Britton *et al*., 2017; Copp *et al*., 2017; Gutmann Roberts *et al*., 2017). This consistent prediction is important, as it is contrary to a frequent assumption in fish invasion ecology that negative impacts of invasions from trophic interactions occurs via increased inter-specific competition for food resources (e.g. Gozlan, Britton, Cowx & Copp, 2010; Cucherousset *et al*., 2012). Whilst Britton *et al*. (2010) revealed depressed growth of *R. rutilus* in the presence of invasive *P. parva* when their stable isotope data suggested they were exploiting similar resources, the population density of the invader was extremely high. When their population densities were lower, these competitive interactions and outcomes were not detected (Tran *et al.,* 2015). An important finding was that tank experiments testing the outcome of competitive interactions abundance via feeding fixed food rations typically indicated asymmetric interactions, where the invader (e.g. *C. carpio* and *C. auratus*) advantageously accessed greater proportions of food resources and thus had faster growth rates than the native fish (e.g. *C. carassius*), with the latter fish growing significantly slower in sympatric treatments compared with their allopatric conspecifics (Busst and Britton, 2015). In pond-based experiments, however, whilst similar results were apparent for impacts of invasive *C. carpio*, they were not observed for invasive *C. auratus*, with it suggested that in the ponds, the food resources being exploited by the two fishes were not limiting (Busst and Britton, 2017), enabling their co-existence (Schulze, Dorner, Baade & Holker*,* 2012).

Experiments investigating the trophic impacts of *B. barbus* revealed the utility of using approaches over different spatial scales within the same study (Bašić and Britton, 2016). Results from both experimental and field data revealed consistent partitioning in their trophic niches with sympatric *S. cephalus*, a fish of similar body size and relatively similar functional traits, with no evidence that these fishes were sharing resources in either relatively short-term mesocosm experiments (100 days) or in the wild. This consistency in the results across these systems is again important, as the results from the field studies were similar to the ponds despite their greater complexity (e.g. the fishes were naturally present in a multi-species fish

community) and being subject to higher stochasiticity (Bašić and Britton, 2016). An issue with field studies alone is that they rarely enable data collection in the pre-invasion state and so it is challenging to infer the invasion-mediated trophic impacts without some aspect of manipulation or experimentation. This is important in the context of testing invasion ecological theory. For example, when invaders and native species are in sympatry, dietary specialisations and thus constricted niche sizes can result, even where niches are partitioned, with this detected in experiments utilising *P. parva* and *C. carpio* (Tran *et al*., 2015; Busst and Britton, 2017). Theory suggests this partitioning and increased specialisation is the process that enables the invader and native species to coexist when resources would otherwise be limiting (Chesson, 2000; Kylafis and Loreau, 2011). However, this niche constriction was not detected across all the synthesised studies (e.g. Britton *et al*., 2017).

The utilisation of experiments to predict invasion impacts can thus provide important theoretical insights and results of high utility to invasion risk management (Copp *et al*., 2009, 2016). However, an issue with some experimental ecological approaches is that they are completed under intense conditions in relatively short timeframes and are thus outside of ecological norms. This means that their results might not scale up to represent those in more complex and stochastic environments (Korsu, Huusko & Muotka, 2009; Spivak, Vanni & Mette, 2011). It has already been outlined that the results of the aquaria tank based experiments involving *Carassius* fishes were not consistent with those from pond experiments (Busst and Britton, 2017) or patterns observed in the wild (Tarkan *et al*., 2010). Whilst tank aquaria results still have some utility, their use of fixed food rations means that these are limited resources, with the pond experiment results suggesting that food resources are rarely limiting in more wild contexts. Moreover, even if food resources were limiting in the ponds, the fish have the option to exploit alternative food resources to maintain their energy intakes and growth rates, but with this not possible in the tanks. Indeed, pond and mesocosm experiments have been successfully applied to understand many ecological processes at larger spatial scales, with studies suggesting their outputs are often consistent and relevant for understanding wild processes (e.g. Spivak *et al*., 2011). This was also apparent in some studies discussed here, including Tran *et al*. (2015), Bašić and Britton (2016) and Britton *et al*. (2017).

Throughout all the pond and field experiments outlined here, stable isotope analyses were used as the primarily analytical tool to investigate the trophic interactions of the fishes. The utility of the stable isotopes of $\delta^{13}C$ and $\delta^{15}N$ to investigate trophic interactions is their provision of temporally integrated dietary assessments that cannot be obtained easily from stomach contents data (Cucherousset *et al*.,

2012). Their application can be completed on relatively low sample sizes and still provide important trophic insights, which is more difficult to achieve with stomach contents data. Moreover, they can be completed on tissues sampled non-lethally, such as fin tissues and scales (Busst *et al*., 2015; Busst and Britton, 2016), which this important for field experiments if, for example, there is a requirement for mark-recapture approaches. However, studies comparing fish diets across different methods, including stable isotopes and stomach contents, often provide some contrasting results (e.g. Hamidan, Jackson & Britton, 2016), for a number of reasons, including the difference between the food ingestion and assimilation rates (Locke, Bulté, Forbes & Marcogliese, 2013). Consequently, whilst stable isotope data have high utility in understanding energetic pathways in food webs, if changes in food web structure are to be measured then multi-method approaches might be preferable. In addition, throughout this synthesis, the term 'trophic niche' has been used in the context of describing the core diet of the fishes. However, in all cases, these niches were determined from stable isotope data and so, *sensu stricto*, the isotopic niche is being described (Jackson, Inger, Parnell & Bearhop, 2011; Jackson *et al*., 2012). Whilst the isotopic niche is generally considered as very similar to the trophic niche, the isotope niche is also influenced by, for example, fish growth and metabolism (Busst and Britton, 2017).

In summary, this synthesis of a range of experimental approaches to predict the impacts of invasive freshwater fishes revealed a range of approaches that can be utilised by researchers to better understand the implications of introducing novel and invasive fishes into new freshwater environments. The results provided strong theoretical and applied insights, with comparative functional response experiments demonstrating that empirical approaches can provide rapid predictions of impact. Correspondingly, where there is a need for robust impact prediction and assessment of invasive fishes, it is recommended that empirical experimental approaches are considered as integral components of the research approach.

References

Alexander, M.E., Dick, J.T.A., Weyl, O.L., Robinson T.B. & Richardson, D.M. (2014). Existing and emerging high impact invasive species are characterized by higher functional responses than natives. *Biology Letters*, 10, 20130946.
https://doi.org/10.1098/rsbl.2013.0946

Barrios-O'Neill, D., Kelly, R., Dick, J.T.A., Ricciardi, A., MacIsaac, H.J. & Emmerson, M.C. (2016). On the context-dependent scaling of consumer feeding rates. *Ecology Letters*, 19, 668–678. https://doi.org/10.1111/ele.12605

Bašić, T. & Britton, J.R. (2016). Characterizing the trophic

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Turk. J. Fish.& Aquat. Sci. 19(6), 529-539

niches of stocked and resident cyprinid fishes: consistency in partitioning over time, space and body sizes. *Ecology and Evolution*, 6, 5093-5104. https://doi.org/10.1002/ece3.2272

Bøhn, T., Amundsen, P.A. & Sparrow, A. (2008). Competitive exclusion after invasion? *Biological Invasions*, 10, 59-368. https://doi.org/10.1007/s10530-007-9135-8

Bolnick, D.I., Ingram, T., Stutz, W.E., Snowberg, L.K., Lau, O.L. & Paull, J.S. (2010). Ecological release from interspecific competition leads to decoupled changes in population and individual niche width. *Proceedings of the Royal Society of London B: Biological Sciences*, 277, 1789-1797. https://doi.org/10.1098/rspb.2010.0018

Britton, J.R. (2012). Testing strength of biotic resistance against an introduced fish: inter-specific competition or predation through facultative piscivory? *PloS One*, 7, e31707. https://doi.org/10.1371/journal.pone.0031707

Britton, J.R. & Gozlan, R.E. (2013). How many founders for a biological invasion? Predicting introduction outcomes from propagule pressure. *Ecology*, 94, 2558-2566. https://doi.org/10.1890/13-0527.1

Britton, J.R., Cucherousset, J., Grey, J. & Gozlan, R.E. (2011). Determining the strength of exploitative competition from an introduced fish: roles of density, biomass and body size. *Ecology of Freshwater Fish*, 20, 74-79. https://doi.org/10.1111/j.1600-0633.2010.00460.x

Britton, J.R., Davies, G.D. & Harrod, C. (2010). Trophic interactions and consequent impacts of the invasive fish Pseudorasbora parva in a native aquatic food web: a field investigation in the UK. *Biological Invasions*, 12, 1533-1542. https://doi.org/10.1007/s10530-009-9566-5

Britton, J.R., Tran, T.N.Q. & Ruiz-Navarro, A. (2015). Synergistic effects of propagule pressure and trophic subsidies overcome biotic resistance to a non-native fish. *Biological invasions*, 17, 3125-3131. https://doi.org/10.1007/s10530-015-0938-8

Britton, J.R., Ruiz-Navarro, A., Verreycken, H. & Amat-Trigo, F. (2017). Trophic consequences of introduced species: Comparative impacts of increased interspecific versus intraspecific competitive interactions. *Functional Ecology*. https://doi.org/10.1111/1365-2435.12978.

Busst, G.M.A. & Britton, J. R. (2015). Quantifying the growth consequences for crucian carp *Carassius carassius* of competition from non-native fishes. *Ecology of Freshwater Fish,* 24, 489-492. https://doi.org/10.1111/eff.12155

Busst, G.M.A. & Britton, J.R. (2016). High variability in stable isotope diet–tissue discrimination factors of two omnivorous freshwater fishes in controlled ex situ conditions. *Journal of Experimental Biology*, 219, 1060-1068. https://doi.org/10.1242/jeb.137380

Busst, G.M.A. & Britton, J.R. (2017). Comparative trophic impacts of two globally invasive cyprinid fishes reveal species-specific invasion consequences for a threatened native fish. *Freshwater Biology*, 62, 1587-1595. https://doi.org/10.1111/fwb.12970

Busst, G.M.A. & Britton, J.R. (2018). Tissue-specific turnover rates of the nitrogen stable isotope as functions of time and growth in a cyprinid fish. *Hydrobiologia*, 805, 49-60. https://doi.org/10.1007/s10750-017-3276-2

Catford, J.A., Jansson, R. & Nilsson, C. (2009). Reducing redundancy in invasion ecology by integrating hypotheses into a single theoretical framework. *Diversity and Distributions*, 15, 22-40. https://doi.org/10.1111/j.1472-4642.2008.00521.x

Chesson, P. (2000). Mechanisms of maintenance of species diversity. *Annual review of Ecology and Systematics*, 31, 343-366. http://doi.org/19,1146/annurev.ecolsys.31.1.343

Copp, G.H., Vilizzi, L., Mumford, J., Fenwick, G.V., Godard, M.J. & Gozlan, R.E. (2009). Calibration of FISK, an invasiveness screening tool for non-native freshwater fishes. *Risk Analysis*, 29, 457-467. https://doi.org/10.1111/j.1539-6924.2008.01159.x

Copp, G.H., Russell, I.C., Peeler, E.J., Gherardi, F., Tricarico, E., Macleod, A…Mumford, J. (2016). European Non-native Species in Aquaculture Risk Analysis Scheme – a summary of assessment protocols and decision support tools for use of alien species in aquaculture. *Fisheries Management and Ecology*, 23, 1-11. https://doi.org/10.1111/fme.12074

Copp, G.H., Britton, J.R., Guo, Z., Edmonds-Brown, V.R., Pegg, J., Vilizzi, L…Davison, P.I. (2017). Trophic consequences of non-native pumpkinseed Lepomis gibbosus for native pond fishes. *Biological Invasions*, 19, 25-41. https://doi.org/10.1007/s10530-016-1261-8

Cucherousset, J., Boulêtreau, S., Martino, A., Roussel, J.M. & Santoul, F. (2012). Using stable isotope analyses to determine the ecological effects of non-native fishes. *Fisheries Management and Ecology*, 19, 111-119. https://doi.org/10.1111/j.1365-2400.2011.00824.x

de Moura Queirós, A., Hiddink, J.G., Johnson, G., Cabral, H.N. & Kaiser, M.J. (2011). Context dependence of marine ecosystem engineer invasion impacts on benthic ecosystem functioning. *Biological Invasions*, 13, 1059-1075. https://doi.org/10.1007/s10530-011-9948-3

Davies, G.D., Gozlan, R.E. & Britton, J.R. (2013). Can accidental introductions of non-native species be prevented by fish stocking audits? *Aquatic Conservation: Marine and Freshwater Ecosystems*, 23, 366-373. https://doi.org/10.1002/aqc.2341

Dick, J.T., Alexander, M.E., Jeschke, J.M., Ricciardi, A., MacIsaac, H.J., Robinson, T.B…Paterson, R.A. (2014). Advancing impact prediction and hypothesis testing in invasion ecology using a comparative functional response approach. *Biological Invasions*, 16, 735-753. https://doi.org/https://doi.org/10.1007/s10530-013-0550-8

Dick, J.T., Laverty, C., Lennon, J.J., Barrios-O'Neill, D., Mensink, P.J., Britton, J.R…Caffrey, J. (2017a). Invader relative impact potential: a new metric to understand and predict the ecological impacts of existing, emerging and future invasive alien species. *Journal of Applied Ecology*, 54,1259-1267. https://doi.org/10.1111/1365-2664.12849

Dick, J.T., Alexander, M.E., Ricciardi, A., Laverty, C., Downey, P.O., Xu, M… Barrios-O'Neill, D. (2017b). Functional responses can unify invasion ecology. *Biological invasions*, 19, 1667-1672. https://doi.org/10.1007/s10530-016-1355-3

Dick, J.T., Alexander, M.E., Ricciardi, A., Laverty, C., Downey, P.O., Xu, M… Barrios-O'Neill, D. (2017c). Fictional responses from Vonesh *et al*. *Biological Invasions*, 19, 1677-1678.

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Turk. J. Fish.& Aquat. Sci. 19(6), 529-539

https://doi.org/10.1007/s10530-016-1360-6

Enders, M., Hütt, M. & Jeschke, J.M. (2018). Drawing a map of invasion biology based on a network of hypotheses. *Ecosphere*, 9, e02146.
https://doi.org/10.1002/ecs2.2146.

Gozlan, R.E., Britton, J.R., Cowx, I.G. & Copp, G.H. (2010). Current knowledge on non-native freshwater fish introductions. *Journal of Fish Biology*, 76, 751-786.
https://doi.org/10.1111/j.1095-8649.2010.02566.x

Gratwicke, B. & Marshall, B.E. (2001). The relationship between the exotic predators *Micropteru ssalmoides* and *Serranochromis robustus* and native stream fishes in Zimbabwe. *Journal of Fish Biology*, 58, 68-75.
https://doi.org/10.1111/j.1095-8649.2001.tb00499.x

Guo, Z., Sheath, D., Amat Trigo, F. & Britton, J.R. (2017). Comparative functional responses of native and high-impacting invasive fishes: impact predictions for native prey populations. *Ecology of Freshwater Fish*, 26, 533-540.
https://doi.org/10.1111/eff.12297

Gutmann Roberts, C., Bašić, T., Amat Trigo, F. & Britton, J.R. (2017). Trophic consequences for riverine cyprinid fishes of angler subsidies based on marine-derived nutrients. *Freshwater Biology*, 62, 894-905.
https://doi.org/10.1111/fwb.12910

Hamidan, N., Jackson, M.C. & Britton, J.R. (2016). Diet and trophic niche of the endangered fish *Garra ghorensis* in three Jordanian populations. *Ecology of Freshwater Fish*, 25, 455-464.
https://doi.org/10.1111/eff.12226

Hänfling, B., Bolton, P., Harley, M. & Carvalho, G.R. (2005). A molecular approach to detect hybridisation between crucian carp (*Carassius carassius*) and non-indigenous carp species (*Carassius* spp. and *Cyprinus carpio*). *Freshwater Biology*, 50, 403-417.
https://doi.org/10.1111/j.1365-2427.2004.01330.x

Jackson, A.L., Inger, R., Parnell, A.C. & Bearhop, S. (2011). Comparing isotopic niche widths among and within communities: Bayesian analysis of stable isotope data. *Journal of Animal Ecology*, 80, 595-602.
https://doi.org/10.1111/j.1365-2656.2011.01806.x

Jackson, M.C., Jackson, A.L., Britton, J.R., Donohoe, I., Harper, D.M. & Grey, J. (2012). Population level metrics of trophic structure based on stable isotopes and their application using invasion ecology. *PLoS One*, 7, e31757.
https://doi.org/10.1371/journal.pone.0031757

Jackson, M.C., Allen, R., Pegg, J. & Britton, J.R. (2013). Do trophic subsidies affect the outcome of introductions of a non-native freshwater fish? *Freshwater Biology*, 58, 2144-2153.
https://doi.org/10.1111/fwb.12197

Jackson, M.C., Ruiz-Navarro, A. & Britton, J.R. (2015). Population density modifies the ecological impacts of invasive species. *Oikos*, 124, 880-887.
https://doi.org/10.1111/oik.01661

Jackson, M.C., Grey, J., Miller, K., Britton, J.R. & Donohue, I. (2016). Dietary niche constriction when invaders meet natives: evidence from freshwater decapods. *Journal of Animal Ecology*, 85, 1098-1107.
https://doi.org/10.1111/1365-2656.12533

Jeschke, J.M. (2014). General hypotheses in invasion ecology. *Diversity and Distributions*, 20, 1229–1234.
https://doi.org/10.1111/ddi.12258

Juncos, R., Milano, D., Macchi, P.J. & Vigliano, P.H. (2015).

Niche segregation facilitates coexistence between native and introduced fishes in a deep Patagonian lake. *Hydrobiologia*, 747, 53-67.
https://doi.org/10.1007/s10750-014-2122-z

Kadye, W.T. & Booth, A.J. (2012). Detecting impacts of invasive non-native sharptooth catfish, *Clarias gariepinus*, within invaded and non-invaded rivers. *Biodiversity and Conservation*, 21, 1997-2015.
https://doi.org/10.1007/s10531-012-0291-5.

Korsu, K., Huusko, A. & Muotka, T. (2009). Does the introduced brook trout (*Salvelinusfontinalis*) affect growth of the native brown trout (*Salmo trutta*)? *Naturwissenschaften*, 96, 347-353.
https://doi.org/10.1007/s00114-008-0482-9

Kumschick, S., Bacher, S., Dawson, W., Heikkilä, J., Sendek, A., Pluess, T... Kühn, I. (2012). A conceptual framework for prioritization of invasive alien species for management according to their impact. *NeoBiota*,15, 69-100.
https://doi.org/10.3897/neobiota.15.3323

Kylafis, G. & Loreau, M. (2011). Niche construction in the light of niche theory. *Ecology Letters*, 14, 82–90.
https://doi.org/10.1111/j.1461-0248.2010.01551.x

Lampert, A., Hastings, A., Grosholz, E.D., Jardine, S.L. & Sanchirico, J.N. (2014). Optimal approaches for balancing invasive species eradication and endangered species management. *Science*, 344, 1028-1031.
https://doi.org/10.1126/science.1250763

Laverty, C., Green, K.D., Dick, J.T., Barrios-O'Neill, D., Mensink, P.J., Médoc, V… Gallagher, C. (2017). Assessing the ecological impacts of invasive species based on their functional responses and abundances. *Biological Invasions*, 19, 1653-1665.
https://doi.org/10.1007/s10530-017-1378-4

Leung, B., Roura-Pascual, N., Bacher, S., Heikkilä, J., Brotons, L., Burgman, M.A… Sol, D. (2012). Teasing apart alien species risk assessments: a framework for best practices. *Ecology Letters*, 15, 1475-1493.
https://doi.org/10.1111/ele.12003

Locke, S.A., Bulté, G., Forbes, M.R. & Marcogliese, D.J. (2013). Estimating diet in individual pumpkinseed sunfish *Lepomis gibbosus* using stomach contents, stable isotopes and parasites. *Journal of Fish Biology*, 82, 522-537.
https://doi.org/10.1111/j.1095-8649.2012.03497.x

Lockwood, J.L., Cassey, P. & Blackburn, T. (2005). The role of propagule pressure in explaining species invasions. *Trends in Ecology and Evolution*, 20, 223-228.
https://doi.org/10.1016/j.tree.2005.02.004

Mason, R.A., Cooke, J., Moles, A.T. & Leishman, M.R. (2008). Reproductive output of invasive versus native plants. *Global Ecology and Biogeography*, 17, 633-640.
https://doi.org/10.1111/j.1466-8238.2008.00402.x

Metcalfe, J. D. & Craig, J. F. (2011), Ethical justification for the use and treatment of fishes in research: an update. *Journal of Fish Biology*, 78, 393–394.
https://doi.org/10.1111/j.1095-8649.2010.02900.x

Penk, M., Saul, W-C, Dick, J.T.A., Donohue, I., Alexander, M.E., Linzmaier, S…Jeschke, J.M. (2017). A trophic interaction framework for identifying the invasive capacity of novel organisms. *Methods in Ecology and Evolution*, 8, 1786–1794.
https://doi.org/10.1111/2041-210X.12817

Pritchard, D.W. (2014). frair: Functional response analysis in R. R package version 0.4. http://CRAN.R-project.org/package=frair.

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Turk. J. Fish.& Aquat. Sci. 19(6), 529-539

Pritchard, D.W., Paterson, R.A., Bovy, H.C. & Barrios-O'Neill, D. (2017). frair: an R package for fitting and comparing consumer functional responses. *Methods in Ecology and Evolution*, 8, 1528–1534. https://doi.org/10.1111/2041-210X.12784

Ricciardi, A., Hoopes, M.F., Marchetti, M.P. & Lockwood, J.L. (2013). Progress toward understanding the ecological impacts of non-native species. *Ecological Monographs*, 83, 263-282. https://doi.org/10.1890/13-0183.1

Rogers D. (1972). Random search and insect population models. *Journal of Animal Ecology,* 41, 369-383. https://doi.org/10.2307/3474

Roy, H.E., Peyton, J., Aldridge, D.C., Bantock, T., Blackburn, T.M., Britton, R…Dobson, M. (2014). Horizon scanning for invasive alien species with the potential to threaten biodiversity in Great Britain. *Global Change Biology*, 20, 3859-3871.
https://doi.org/10.1111/gcb.12603

Schulze, T., Dorner, H., Baade, U. & Holker, F. (2012). Dietary niche paritioning in a piscivorous fish guild in response to stocking of an additional compeitiot – the role of diet specialisation. *Limnologica*, 42, 56-64. https://doi.org/10.1016/j.limno.2011.08.001.

Sheath, D.J., Williams, C.F., Reading, A.J. & Britton, J.R. (2015). Parasites of non-native freshwater fishes introduced into England and Wales suggest enemy release and parasite acquisition. *Biological Invasions*, 17, 2235-2246.
https://doi.org/10.1007/s10530-015-0857-8

Simberloff, D., Martin, J.L., Genovesi, P., Maris, V., Wardle, D.A., Aronson, J…Pyšek, P. (2013). Impacts of biological invasions: what's what and the way forward. *Trends in Ecology and Evolution*, 28, 58–66. https://doi.org/10.1016/j.tree.2012.07.013

Spivak, A.C., Vanni, M.J. and Mette E.M. (2011). Moving on up: can results from simple aquatic mesocosm experiments be applied across broad spatial scales? *Freshwater Biology*, 56, 279–291. https://doi.org/10.1111/j.1365-2427.2010.02495.x

Svanbäck, R. & Bolnick, D.I. (2007). Intraspecific competition drives increased resource use diversity within a natural population. *Proceedings of the Royal Society of London B: Biological Sciences*, 274, 839-844.
https://doi.org/10.1098/rspb.2006.0198

Tarkan, A.S., Cucherousset, J., Zięba, G., Godard, M.J. & Copp, G.H. (2010). Growth and reproduction of introduced goldfish Carassius auratus in small ponds of southeast England with and without native crucian carp *Carassius carassius*. *Journal of Applied Ichthyology*, 26, 102-108. https://doi.org/10.1111/j.1439-0426.2010.01506.x

Tran, T.N.Q., Jackson, M.C., Sheath, D., Verreycken, H. & Britton, J.R. (2015). Patterns of trophic niche divergence between invasive and native fishes in wild communities are predictable from mesocosm studies. *Journal of Animal Ecology*, 84, 1071-1080. https://doi.org/10.1111/1365-2656.12360

Vonesh, J., McCoy, M., Altwegg, R., Landi, P. & Measey, J. (2017). Functional responses can't unify invasion ecology. *Biological invasions*, 19, 1673-1676. https://doi.org/10.1007/s10530-016-1356-2

Ward, A.J., Webster, M.M. and Hart, P.J. (2006). Intraspecific food competition in fishes. *Fish and Fisheries*, 7, 231-261.
https://doi.org/10.1111/j.1467-2979.2006.00224.x