

REPORT

Indirect facilitation of an anuran invasion by non-native fishes

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Abstract

Positive interactions among non-native species could greatly exacerbate the problem of invasions, but are poorly studied and our knowledge of their occurrence is mostly limited to plant-pollinator and dispersal interactions. We found that invasion of bullfrogs is facilitated by the presence of co-evolved non-native fish, which increase tadpole survival by reducing predatory macroinvertebrate densities. Native dragonfly nymphs in Oregon, USA caused zero survival of bullfrog tadpoles in a replicated field experiment unless a non-native sunfish was present to reduce dragonfly density. This pattern was also evident in pond surveys where the best predictors of bullfrog abundance were the presence of non-native fish and bathymetry. This is the first experimental evidence of facilitation between two non-native vertebrates and supports the invasional meltdown hypothesis. Such positive interactions among non-native species have the potential to disrupt ecosystems by amplifying invasions, and our study shows they can occur via indirect mechanisms.

Keywords

Aeshnidae, amphibians, biological invasions, facilitation, fishes, indirect effects, *Lepomis macrochirus*, non-native species, pond communities, *Rana catesbeiana*.

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INTRODUCTION

Biological invasions threaten agriculture, commerce and biodiversity worldwide, and understanding mechanisms of invasions is one of the greatest challenges for ecology today (Soulé 1990; Lövei 1997). Positive interactions among non-native species could exacerbate the problem of invasions, contributing to what Simberloff & Von Holle (1999) termed an 'invasional meltdown'. Facilitation among invaders is thought to be common, but experimental evidence for positive interactions has been sparse and mostly limited to plant-pollinator and dispersal interactions (Simberloff & Von Holle 1999; Richardson *et al.* 2000). We combined a field experiment with field surveys to test the hypothesis that a coevolved, positive interaction with non-native sunfish is facilitating the invasion of bullfrogs (*Rana catesbeiana* Shaw).

Native to eastern North America, bullfrogs are broadly invading western North America and have also been introduced in Mexico, western Canada, Hawaii, Japan, Italy, the Netherlands, Cuba and Jamaica (Green 1978; Stebbins 1985; Stumpel 1992). They are often introduced deliberately for aquaculture but are then capable of rapid and widespread expansion on their own (Jennings & Hayes

1985). Movements of 2.8 km have been documented but bullfrogs are generally philopatric (Bury & Whelan 1984). They are voracious predators and are considered detrimental to native amphibians and other fauna (Moyle 1973; Bury & Luckenbach 1976; Rosen & Schwalbe 1995). In both their native and introduced range, bullfrogs are described as occupying a wide range of aquatic habitats including lakes, ponds, swamps, bogs and backwaters (Conant 1975; Stebbins 1985). Bullfrogs are highly aquatic and breeding appears generally confined to permanent water for the multi-season development of their larvae (Bury & Whelan 1984). Several authors suggest that bullfrogs may have a preference for human-created or human-altered waterbodies, such as millponds and reservoirs (Wright & Wright 1949; Bury & Luckenbach 1976; Jennings 1988), but this has seldom been tested (but see Zampella & Bunnell 2000).

In their native range, bullfrogs have been shown to have a positive association with centrarchid sunfish (Werner & McPeck 1994). Many eastern centrarchids have been widely introduced in western North America (Moyle 1986) representing a major, but often overlooked, ecosystem alteration (Rahel 2000; Schindler *et al.* 2001). In western North America, native fish are mostly riverine and most

ponds are presumed to have been fishless historically (Moyle 1986; Bahls 1992). For example, 95% of western montane lakes and ponds formerly lacked fish (Bahls 1992). The introduction of fishes can be detrimental to native organisms (Hurlbert *et al.* 1972; Knapp *et al.* 2001) and generally benefits organisms with specific behavioural, chemical or life-historical adaptations that allow coexistence with fish (Kats *et al.* 1988; Wellborn *et al.* 1996). Bullfrogs are such an organism; they are unpalatable to a variety of fishes (Kruse & Francis 1977) but are consumed by predaceous macroinvertebrates such as dragonfly nymphs (Aeshnidae, Odonata) and diving beetle larvae (Dytiscidae, Coleoptera) that are prey for some eastern warm-water fishes (Werner & McPeck 1994). The presence of fish gives bullfrogs a competitive advantage over other anuran larvae that sacrifice growth to avoid predation by both fish and macroinvertebrates (Werner & McPeck 1994; Kupferberg 1997).

Because of the coevolution of bullfrogs with centrarchids in eastern North America, we hypothesized that predation by introduced centrarchids on native macroinvertebrates is indirectly facilitating the survival of bullfrog tadpoles in their introduced range. Native fish in our area are small, gape limited, and rare relative to non-native fish in lentic sites where bullfrogs occur; they are not expected to impact populations of large-bodied, predaceous macroinvertebrates (Hynes 1950). We further hypothesized that an indirect positive effect of non-native fish is leading to higher bullfrog abundance and broader distribution in their introduced range. We investigated the role of non-native fish in bullfrog invasions using a manipulative field experiment and an analysis of bullfrog distribution and abundance from pond surveys in the Willamette Valley of Oregon, USA. The field experiment used a factorial design to test the predictions that: (1) non-native fish (bluegill, *Lepomis macrochirus* Rafinesque) lower the abundance of native dragonfly nymphs, (2) native dragonfly nymphs reduce the survival of bullfrog tadpoles and (3) survival of larval bullfrogs improves when a non-native fish is present. The field surveys were used to determine how the effect of non-native fish on bullfrogs compared with other factors could potentially relate to bullfrog distribution and abundance. Our findings provide the first experimental evidence of a positive interaction between two non-native vertebrates.

MATERIAL AND METHODS

Study area

Our research was conducted in the Willamette Valley, which is a 150-km stretch of the Willamette River flowing between the Cascade Range and the Coast Range from Eugene to Portland in western Oregon, USA. The valley is *c.* 30-km wide on average and is characterized by deep soil deposits

from the Missoula floods 12 000 years ago. It is predominately agricultural, but several urban centres including Portland and Eugene exist and are growing rapidly (Holland *et al.* 1995). Lentic habitats are numerous and are mostly riverine in origin or are constructed (i.e. excavated or impounded). They are a mix of ephemeral and permanent hydroperiods and tend to fill during fall rains and dry in mid to late summer. The climate is maritime and freezing temperatures occur annually but are rare. The average elevation is *c.* 150 m. *Rana catesbeiana* has invaded throughout the valley. Native fish are mostly riverine, but several species arrive at ponds via flooding or connections to lotic habitats with some regularity: *Richardsonius balteatus* (Richardson, 1836), *Gasterosteus aculeatus* Linnaeus, 1758 and *Cottus* spp. The Willamette Valley is sometimes considered a southward extension of the Puget Trough (Franklin & Dyrness 1988) in terms of flora and fauna, but soils and aquatic habitats differ considerably justifying its classification as a separate ecoregion (Omernik 1987).

Field surveys

We used data from a 3-year study (1999–2001) of the habitat associations of amphibians in the Willamette Valley of Oregon to explore the factors associated with bullfrog distribution and abundance. During the 3-year study, we surveyed a total of 85 ponds and wetlands (hereafter ponds) for bullfrogs and fish throughout the Willamette Valley using a combination of visual encounter surveys, dip-netting, and funnel trapping. Visual encounter surveys involved two observers searching for fish and amphibians by walking the perimeter of ponds in tandem and also walking a zig-zag pattern through the portion of ponds <0.75-m deep while searching for amphibians (Thoms *et al.* 1997). To allocate trapping and dip-netting effort within ponds, we identified one to five major habitat associations within each pond based on depth, vegetation and shading. We allocated traps proportionately to the habitats using a minimum of three traps for any habitat covering 50 m². We added an additional trap each time the area of the habitat >50 m² doubled (e.g. three traps for a 50-m² habitat, four for 100 m², five for 200 m², etc.; adapted from Adams *et al.* 1997). We also did three to five 2-m long sweeps with a long-handled dip net in each habitat. A breeding population of bullfrogs was considered present if eggs or larvae were detected by any method. Bullfrog abundance was the number of larvae captured in funnel traps per trap night. Native or non-native fish were considered present if they were detected by any method.

In addition to bullfrog and fish variables, we recorded eight pond characteristics thought to be associated with bullfrog distribution and abundance (variable names are in capital letters). We determined if ponds were permanent by

visiting in late summer to see if they had dried (PERM). Bullfrogs generally require permanent water for successful recruitment in our area (Bury & Whelan 1984). We visually estimated the percentage of a pond's surface area that had reed canarygrass (*Phalaris arundinacea* L.) which is an aggressive invader that grows in dense, emergent stands (PHALARIS). It often invades disturbed or created ponds, and we hypothesized that it would have a positive association with bullfrogs. As bullfrogs have the warmest thermal tolerance of any anuran in North America (Bury & Whelan 1984), we characterized SHADE by measuring the angle from the pond centre at eye height to the top of the tree line or horizon east, south and west using a handheld clinometer. We used the mean of these measurements as an index of shading.

We included three additional pond variables to test the assertion that bullfrogs are associated with large, deep waters that are altered or created by humans (Bury & Whelan 1984). We measured AREA in m² by obtaining coordinates for multiple points around the perimeter of each pond using a global positioning system and then by measuring the area within the points using ArcInfo. We visually estimated the percentage of a pond's surface area that had depth <0.75 m (SHALLOW). Finally, we classified the ORIGIN of each pond as naturally occurring, altered (if characteristics of the pond had been altered by onsite construction), or constructed (if the pond would not have existed without construction). We determined ORIGIN by visual inspection, queries of management agencies, and personal knowledge of a pond's history.

We also obtained two landscape-scale variables: percentage FOREST and length of ROADS per hectare. Both were measured using ArcInfo within a 1000-m belt around each pond. Forest coverage data were from the 1998 Willamette Valley Land Use/Land Cover Map available from the Oregon Department of Fisheries and Wildlife. Although bullfrogs are highly aquatic, we hypothesized that the adults may need upland forest for dispersal and aestivation. Road data were from 1999 and are available from the Bureau of Land Management (<http://www.or.blm.gov/gis/projects/transportation/gtrn.asp>). We included ROADS and a measure of development around each pond because bullfrogs have been described as a species well-adapted to human-altered landscapes (Zampella & Bunnell 2000).

While traditional hypothesis testing would have allowed a direct test of the association of bullfrogs with fish, we preferred to rank the ability of multiple competing models to approximate the observed distribution and abundance of bullfrogs in the Willamette Valley. Ranking competing models allows us to compare the importance of factors, including non-native fish, thought to be associated with the distribution and abundance of bullfrogs. Thus, we used an information theoretic approach (Burnham & Anderson

1998) to compare the ability of 71 models to describe each of two bullfrog response variables: (1) detected/not detected (hereafter DETECTED) and (2) relative abundance based on trap rate (hereafter ABUN). The 71 models consisted of 11 univariate regressions, all but two pairwise combinations of those 11 variables (see below), six interaction models and the null model containing only an intercept. The 11 variables used were the eight pond characteristics described above and the presence of native fish (NFISH), non-native fish (NNFISH), and any fish (FISH). The six interaction models consisted of each fish variable crossed with PHALARIS and with SHALLOW. These were included because we hypothesized that the effect of fish might depend on the structural characteristics of a pond. The two pairwise combinations of predictors that we excluded were NFISH + FISH and NNFISH + FISH because we could think of no unique interpretation for these models.

We used generalized linear modelling to fit each of the 71 models using binomial error when the response variable was DETECTED and using Poisson error when the response variable was ABUN. The latter was only approximately Poisson. We fit these models using S-Plus 2000 (Anonymous 1999). We used the function 'extractAIC', available in the MASS library of S-Plus (version 6.2) and created by Venables and Ripley (Venables & Ripley 1994), to calculate Akaike's Information Criterion (AIC) for each model. We then modified the output AIC to achieve the small sample version called AIC_c, which is recommended in cases such as ours when sample size divided by the number of parameters is <40 (Burnham & Anderson 1998).

The AIC_c provides a means of selecting the best model or set of models given the data from a set of *a priori* models (Burnham & Anderson 1998). It is a measure of the relative information content of a model given the number of parameters. After ranking the models, a probability that each model is the best of *R* competing models given the data, can be calculated based on the difference in AIC_c between the given model and the best model. This is termed the AIC_c weight (*w*) and can be calculated for model *i* as

$$w_i = \frac{\exp(-0.5\Delta\text{AIC}_i)}{\sum_{r=1}^R \exp(-0.5\Delta\text{AIC}_r)}$$

where ΔAIC is the difference between the given model and model with the lowest AIC (Burnham & Anderson 1998). The cumulative weight (w_{cum} ; Table 1) is the probability that the given model or one of the better models is the best model given the data.

We used *w* to further evaluate the results of our analysis. We considered $w \geq 0.9$ to strongly suggest that the given model is the best of the candidate models given the data. If multiple models were necessary to obtain a cumulative

Table 1 The top five models describing occurrence of bullfrog breeding populations (detected/not detected) in the Willamette Valley, OR, USA. Ranking of models is based on the small sample version of Akaike's Information Criterion (AIC_c). The null model, containing only the intercept, is shown for comparison. The weight (w) is the probability that a model is the best of the candidate models given the data, and w_{cum} is the cumulative sum of the w 's. df are shown as model, residual

Model	df	Residual deviance	AIC_c	w	w_{cum}
FISH + SHALLOW	3, 82	74.56	83.06	0.449	0.449
NNFISH + SHALLOW	3, 82	75.99	84.49	0.220	0.669
FISH \times SHALLOW	4, 81	74.50	85.26	0.149	0.818
NNFISH \times SHALLOW	4, 81	75.25	86.01	0.103	0.921
FISH + ROADS	3, 82	79.05	87.55	0.048	0.969
Null	1, 84	115.17	119.32	<0.001	1.000

weight of 0.9 or higher, we concluded that the analysis did not support a single model alone and then evaluated the similarities and dissimilarities of the set of models with $w_{cum} \leq 0.9$ (including the first model to exceed this limit). To assess fit, we give the deviance for the best five models and for the null model. Deviance is a measure of goodness-of-fit, and residual df divided by residual deviance is expected to be ≈ 1 for a well fit model (McCullagh & Nelder 1989). Deviance is equivalent to variance for normal error.

Field experiment

The experimental units were $96 \times 132 \times 107$ cm wood-frame enclosures completely covered with grey, fibreglass window screen (mesh size ≈ 2 mm) which was removable on top to provide access to the interior. To create structure, we added three 70-cm, leaved willow stems (*Salix* sp.) and a 2-m length of nylon rope tied at opposite, upper corners of each enclosure and allowed to hang in a U-shape draped on the bottom of the enclosure. Four blocks of four enclosures were set within a 24-year-old excavated pond in Corvallis, OR, USA. Water depth was ≈ 1 m and did not vary over time because of a stand pipe that regulated water level in the pond. Treatments followed a factorial design, and factors were fish (none or one bluegill) and aeshnid dragonfly nymphs (none or 15). Bluegills were chosen because they are the most common introduced centrarchid and because they were shown to facilitate bullfrog survival in their native range (Werner & McPeck 1994).

The dragonfly nymphs were comparably sized mid- and late-instar *Aeshna multicolor* Hagen, 1861, *Aeshna californica* Calvert, 1895 and *Anax junius* (Drury, 1773). The density of dragonfly nymphs varies widely in nature with densities as high as $150\text{--}290\text{ m}^{-2}$ in lakes and 25 m^{-2} in experimental enclosures with fish present (Johnson *et al.* 1996). Densities in our region have not been reported, but one study found up to 9.2 late instar nymphs per m^2 using dip-netting, which likely undersamples density (C. Beatty, Oregon State

University, unpublished data). We used 12 mid-instar nymphs (9.2 m^{-2}) and three late-instar nymphs, making a total density of 11.5 m^{-2} . Most of the late-instar nymphs ($\bar{x} = 2.3$, range 1–3), as expected, emerged within 11 days of initiating the experiment.

The experiment began with the addition of 50 bullfrog tadpoles (2 days post-hatching) on 28 June 2000. We then randomly assigned each of the four treatment combinations to an enclosure within each block. Aeshnids were added 24 h after the tadpoles and fish were added 24 h after the aeshnids. We terminated tests on 7 August (two blocks) and 8 August 2000 (remaining two blocks) by pulling the enclosures from the water and preserving all tadpoles, fish and aeshnids for quantification in the laboratory. At the beginning of the experiment, aeshnids averaged 29.7 mm total length (SD = 7.4); bluegill averaged 26.6 g (SD = 1.7) and had gapes averaging 6.3 mm (SD = 0.5). All the bluegill survived. A variety of alternative prey species for fish and aeshnids invaded the enclosures (e.g. chironomid larvae, amphipods, microcrustaceans) during the experiment, but 12 zygopteran larvae (damsfly; total length 10–17 mm) were added to all enclosures on three occasions to ensure availability of larger prey items.

Response variables were the proportion of tadpoles and the proportion of aeshnids surviving till the end of the experiment. Proportional responses are best modelled using logistic regression, which incorporates binomial error and uses a logit link to make the model linear (McCullagh & Nelder 1989). We used the GLM function in S-Plus 2000 (Anonymous 1999) to produce such a model. To test the significance ($\alpha = 0.05$) of the main effect of fish, the main effect of aeshnids and the interaction, we evaluated the deviance explained by each factor (McCullagh & Nelder 1989). To compensate for overdispersion (residual error > residual df), we used an F statistic rather than chi-square to test significance (Crawley 1993). The number of tadpoles or aeshnids originally stocked in each enclosure was the binomial denominator.

RESULTS

Field surveys

Four models were necessary to reach $w_{cum} \geq 0.9$ when the response variable was presence of a breeding population of bullfrogs: FISH + SHALLOW ($w = 0.45$), NNFISH + SHALLOW ($w = 0.22$), FISH \times SHALLOW ($w = 0.15$), and NNFISH \times SHALLOW ($w = 0.10$) (Table 1). Bullfrogs were most common in relatively deep ponds where non-native fish were detected (bullfrogs occupied 86% of such ponds). The probability that bullfrogs would be present increased from 0.13 at ponds where fish were not detected to 0.67 when fish were detected or from 0.20 at ponds where non-native fish were not detected to 0.74 when non-native fish were detected. The interactions were only weakly supported, but are apparently because of a small increase in the positive effect of FISH or NNFISH as SHALLOW increased (Fig. 1). As all four models contain SHALLOW and a term for some type of fish, this analysis provides strong evidence that the effects of fish in general and the bathymetry of ponds are the best predictors of bullfrog presence given the data. However, because four models were necessary to reach $w_{cum} \geq 0.9$ and because these models differed with respect to the fish variable, the analysis does not conclusively indicate whether the type of fish is important.

The best predictors of the abundance of bullfrogs were NNFISH and SHALLOW, with the model that included both main effects and the interaction being strongly favoured over all others ($w = 0.99$; Table 2). The trap rate of bullfrogs increased from 0.1/trap-night in ponds where non-native fish were not detected to 0.9/trap-night in ponds where non-native fish were detected. The interaction was because of an increase in the positive effect of NNFISH as SHALLOW increased (Fig. 2). The abundance of bullfrogs had a positive association with SHALLOW when non-native fish were detected and a negative association with SHALLOW when non-native fish were not detected.

A total of 45 of 85 ponds had at least one species of fish. The non-native fish found were (with number of ponds in parentheses) *Gambusia affinis* (Baird and Girard 1853) (25), *Lepomis* spp. (20) (*L. gibbosus* (Linnaeus 1758); *L. macrochirus* Rafinesque, 1819; and apparent hybrids), *Micropterus salmoides* (Lacepede 1802) (6), *Ictalurus* spp. (3), *Perca flavescens* (Mitchill 1814) (1) and *Pomoxis* sp. (1). Native fish were *Gasterosteus aculeatus* (22), *Cottus* spp. (7), *Richardsonius balteatus* (4), unknown salmonids (3) and *Rhinichthys* sp. (1). Of the 45 ponds with fish, 34 ponds had at least one species of non-native fish present, and 18 had only non-native fish. A total of 26 ponds had at least one native fish present, and 10 had only native fish. One pond had only an unidentified fish.

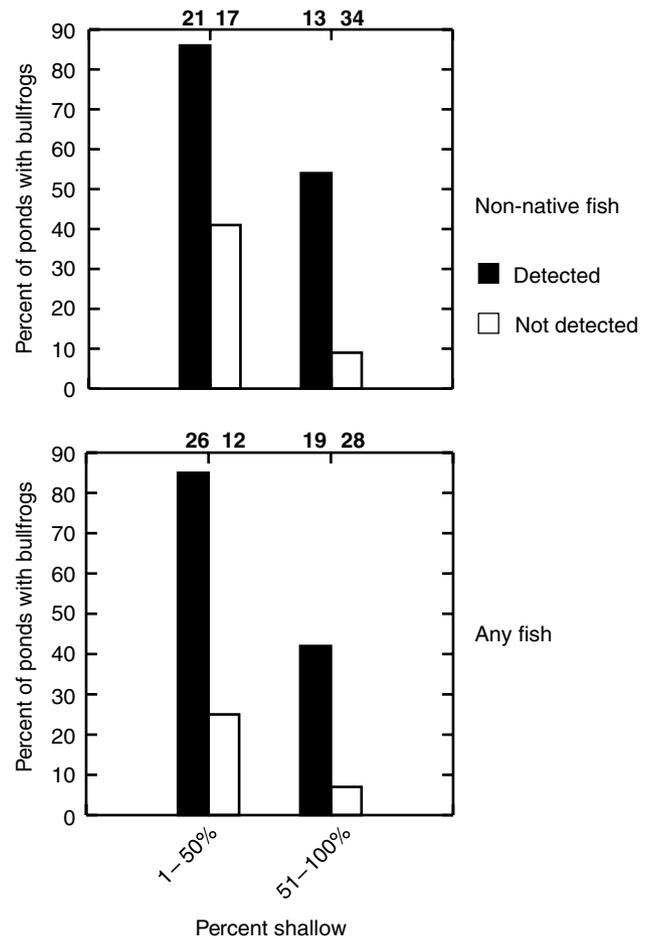


Figure 1 Comparison of pond occupancy by breeding populations of bullfrogs at 85 ponds in the Willamette Valley, OR, USA. The Y-axis is the percentage of ponds in the indicated category where we detected breeding populations of bullfrogs. Sample size is shown above each column.

Field experiment

The field experiment supported the hypothesis that non-native bluegill facilitate bullfrog survival by decreasing the abundance of native aeshnid dragonfly nymphs. Survival of bullfrogs decreased from 57% in the no-aeshnid treatments to 10% in the aeshnid treatments ($F_{1,9} = 96.96$, $P < 0.001$; Fig. 3). The main effect of fish was not significant ($F_{1,9} = 1.49$, $P = 0.253$) but a significant interaction with aeshnids indicated that fish decreased the negative effect of aeshnids on bullfrog survival ($F_{1,9} = 20.82$, $P = 0.001$; Fig. 3). Aeshnid survival decreased from 85% in the control treatments to 13% in the bluegill treatment ($F_{2,9} = 70.95$, $P < 0.001$; Fig. 3). Bluegill presence explained 88% of the total deviance in aeshnid survival, and aeshnid presence explained 76% of the total deviance in bullfrog survival.

Table 2 The top five Poisson regression models describing the trap rate of bullfrogs for the Willamette Valley, OR, USA. Ranking of models is based on the small sample version of Akaike's Information Criterion (AIC_c). The null model, containing only the intercept, is shown for comparison. The weight (w) is the probability that a model is the best of the candidate models given the data, and w_{cum} is the cumulative sum of the w 's. df are shown as model, residual

Model	df	Residual deviance	AIC_c	w	w_{cum}
NNFISH \times SHALLOW	4, 81	100.50	111.26	0.998	0.998
FISH \times SHALLOW	4, 81	114.74	125.50	0.001	0.998
NNFISH + ORIGIN	4, 81	115.24	126.00	0.001	0.999
NFISH \times SHALLOW	4, 81	115.30	126.06	0.001	1.000
PERM + ORIGIN	4, 81	118.46	129.22	<0.001	1.000
Null	1, 84	163.11	167.25	<0.001	1.000

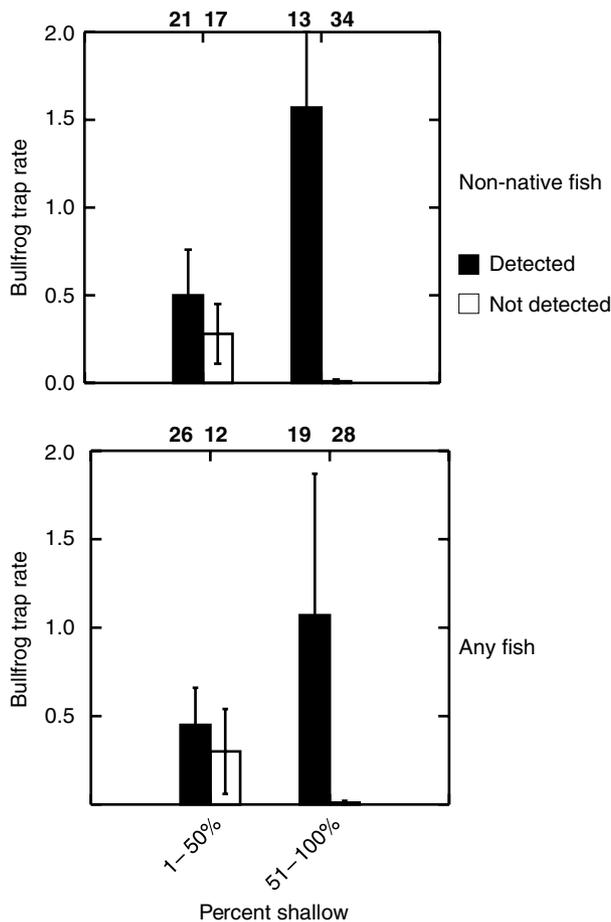


Figure 2 A comparison of bullfrog relative abundance (number caught per trap-night) at 85 ponds in the Willamette Valley, OR, USA. Data are mean and standard error (SE). Sample size is shown above each column.

DISCUSSION

The 'invasional meltdown' hypothesis (Simberloff & Von Holle 1999) suggests that positive interactions among non-

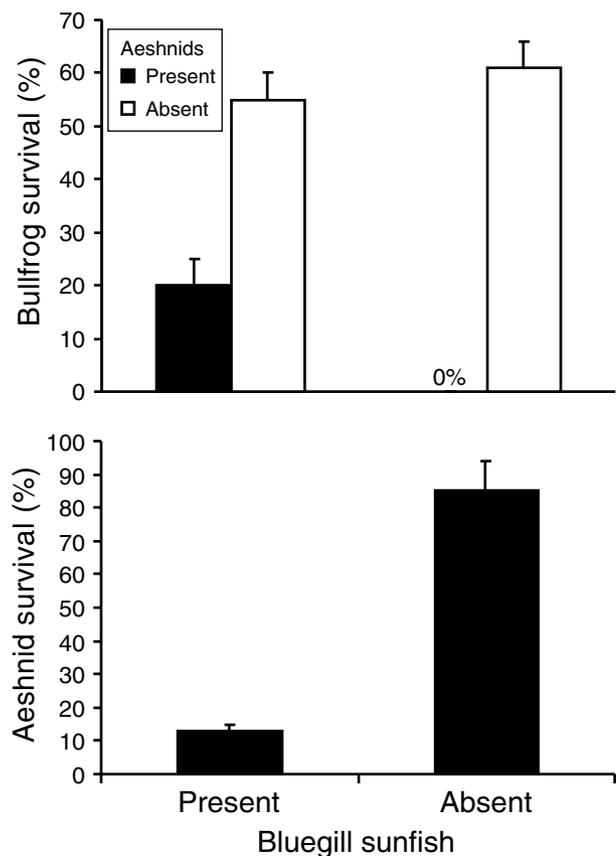


Figure 3 Results of a manipulative field experiment conducted in 2000. Data are mean and standard error (SE) of survival of bullfrog and aeshnid larvae in field enclosures.

native species are prevalent and that establishment of non-native species can increase the probability of further invasion. This runs counter to the biotic resistance theory, but has gained some support from observations in the Great Lakes and in San Francisco Bay showing an accelerating rate of invasion (Cohen & Carlton 1998; Ricciardi 2001) and

from numerous comparative studies suggesting positive interactions among invaders (Simberloff & Von Holle 1999). More rare has been the coupling of manipulative experiments with comparative studies to test suspected positive interactions among non-native species (Simberloff & Von Holle 1999). Positive interactions among non-native vertebrates have not, to our knowledge, been experimentally documented prior to our study.

Our experiment shows that an indirect, positive interaction between bluegill sunfish and bullfrogs facilitates the survival of bullfrog tadpoles. Moreover, presence of non-native fish coupled with the percentage of a pond <0.75 m deep, explains bullfrog abundance in the Willamette Valley ponds we sampled decidedly better than any of the other models we examined. However, when the presence of a breeding population of bullfrogs was the response variable, our analysis of field surveys did not lead to a clear distinction between non-native fish and a general variable indicating the presence of any species of fish. Ten of the 51 sites we surveyed that lacked non-native fish hosted breeding populations of bullfrogs. Native fish do not explain this pattern as six of the 10 ponds lacked fish completely. Bullfrogs are known to sometimes persist in the absence of fish in other parts of their native (Werner & McPeck 1994) and introduced range (Schwalbe & Rosen 1988). We hypothesize that natural variation in the size or density of predaceous macroinvertebrates could explain this pattern.

Our analysis of bullfrog abundance at ponds in the Willamette Valley strongly supports the hypothesis that non-native, rather than native, fish facilitate bullfrogs. However, the ambiguity in our analysis of bullfrog presence leaves open some possibility that native fish could have a similar effect. We suggest that native fish are unlikely to have an important effect on the distribution of bullfrogs because: (1) native fish are strongly gape limited, and available information suggests they do not ingest many predaceous macroinvertebrates (e.g. Hynes 1950), (2) native fish are comparatively rare in lentic habitats in the Willamette Valley (natives occupied 31% of the ponds we surveyed compared with 53% for non-native fish), and (3) native fish were not an important predictor of bullfrog distribution and abundance compared with other variables. Thus, our study suggests that the introduction of bluegill and perhaps other centrarchids in the Willamette Valley is facilitating the invasion of bullfrogs. However, further research is needed to conclusively demonstrate whether this effect is because of a difference in the feeding habits of native and non-native fish or whether it is simply because of an increase in the proportion of ponds occupied by fish.

Facilitation between non-native species can fall into a number of categories, but the most commonly suspected examples involve plant-pollinator interaction or dispersal-

related cases (Simberloff 1986). In the case of bullfrogs and centrarchids, the facilitation stemmed from a co-evolved, commensal relationship. The positive effect of bluegill sunfish on bullfrogs results from fish predation on macroinvertebrates that prey on bullfrog larvae in both their native (Werner & McPeck 1994) and introduced range (this study). The macroinvertebrate species involved differed between the native and non-native range of the bullfrog.

The variable SHALLOW was included in every model of field surveys with $w_{cum} \geq 0.9$ for both response variables, but its effect was mixed. Bullfrogs were less likely to breed in SHALLOW ponds whether or not fish were present, but also reached their highest abundance in relatively shallow ponds with non-native fish present (Fig. 1). This suggests that shallow ponds can be productive bullfrog breeding sites if non-native fish are present, but that bullfrogs are unlikely to be found at such ponds. Shallow ponds are less likely to be permanent (in our study, 28% of shallow ponds were classified as permanent compared with 76% of deep ponds) and bullfrogs may avoid them for that reason. Given that we assessed permanence for some ponds during drought conditions, the variable SHALLOW may have been a better indicator than PERM of the probability that surface water will persist through a more average year (see below). Shallow ponds also tend to have more aquatic vegetation, which provides cover, oviposition sites and hunting perches for aeshnids (Corbet 1999). We do not know if the effect of SHALLOW is related to macroinvertebrate densities, but this could explain the increase in the effect of non-native fish on abundance in shallow compared with deeper ponds.

General descriptions of bullfrog preferences for large, altered or constructed lentic habitats were not well-supported in our analysis and have not been well-documented in other parts of the bullfrog's range (Wright & Wright 1949; Stebbins 1985; Jennings 1988; but see Zapella & Bunnell 2000). Our results gave little support for the effects of pond origin, size or permanence. The low importance of permanence is especially surprising because bullfrogs typically require permanent water for their larvae to overwinter in our area (Stebbins 1985). There was a positive trend (bullfrogs were found breeding in 61% of 42 permanent ponds compared with 20% of 43 temporary ponds), but PERM was not a good predictor compared with NNFISH and SHALLOW. As we did not observe the success of breeding we do not know if recruitment in temporary and permanent ponds was comparable. Our study overlapped a drought, and many of the ponds that we classified as temporary may be permanent most years.

The invasions of non-native fishes and bullfrogs are both contributing to amphibian declines in western North America (Kupferberg 1997; Adams 1999; Knapp *et al.* 2001; Blaustein & Kiesecker 2002). Hayes & Jennings (1986) argued that effects of non-native fish merit greater concern

than bullfrogs in low elevation habitats. Recent field studies in the Pacific north-west support this argument (Richter & Azous 1995; Adams 1999, 2000). Many invasions, including that of the bullfrog, will be very difficult to control directly, but managing habitats and communities to resist invasion offers hope for progress. We suggest that fish can be viewed as a sort of keystone invader in the formerly fishless ponds, lakes and wetlands that were once common in the west. Organisms must possess special adaptations like small size, low-activity levels, or unpalatability to co-occur with fish, and fish predators alter pond trophic dynamics via a variety of direct and indirect pathways (Kats *et al.* 1988; Wellborn *et al.* 1996; Schindler *et al.* 2001). Our study suggests that reducing the distribution and abundance of bluegill and perhaps other non-native fishes of similar feeding characteristics has potential to reduce the abundance of bullfrogs in their introduced range.

It is increasingly clear that indirect trophic effects, including positive interactions, are critical to the formation of ecological communities (Werner & McPeck 1994; Stachowicz 2001). Positive interactions among non-native species can occur directly or indirectly and are thought to be prevalent in the process of invasion, but have seldom been experimentally demonstrated (Simberloff & Von Holle 1999; Richardson *et al.* 2000). Our findings provide the first experimental evidence of an indirect, facilitatory relationship between two non-native vertebrates and underscore the need for greater attention to positive interactions among non-native species.

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