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Habitat connectivity and resident shared predators determine the impact of invasive bullfrogs on native frogs in farm ponds

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Habitat connectivity is considered to have an important role on the persistence of populations in the face of habitat fragmentation, in particular, for species with conservation concern. However, it can also impose indirect negative effects on native species through the spread of invasive species. Here, we investigated direct and indirect effects of habitat connectivity on populations of invasive bullfrogs and native wrinkled frogs and how these effects are modified by the presence of common carp, a resident shared predator, in a farm pond system in Japan. The distribution pattern analysis using a hierarchical Bayesian modelling indicated that bullfrogs had negative effects on wrinkled frogs, and that these negative effects were enhanced with increasing habitat connectivity owing to the metapopulation structure of bullfrogs. The analysis also suggested that common carp mitigated these impacts, presumably owing to a top-down trophic cascade through preferential predation on bullfrog tadpoles. These presumed interspecific interactions were supported by evidence from laboratory experiments, i.e. predation by carp was more intense on bullfrog tadpoles than on wrinkled frog tadpoles owing to the difference in refuge use. Our results indicate that metacommunity perspectives could provide useful insights for establishing effective management strategies of invasive species living in patchy habitats.

1. Introduction

Anthropogenic habitat fragmentation is a major threat to native biodiversity worldwide [1]. Habitat fragmentation leads to increased stochastic extinction of local populations [2], decreased rescue effects [3], reduced mutualistic interactions with pollinators or seed dispersers [4,5] and decreased genetic diversity of populations [6]. To ameliorate these negative effects of habitat fragmentation, enhancement of habitat connectivity has been repeatedly recommended [7,8].

However, habitat connectivity can also facilitate biological invasions across a wide range of taxa (e.g. plants, fishes, birds and mammals) [9–13]. A recent synthetic review has noted that habitat connectivity and invader dispersal ability are important elements in biological invasions [14]. In the face of rapid biodiversity loss owing to biological invasions on a global scale [15], it is important to consider whether habitat connectivity may impose indirect negative effects on native species by facilitating the spread of invasive species. Yet, these effects have rarely been demonstrated in the field.

Additional interactions with other species make it difficult to predict the effect of habitat connectivity on native species. In particular, the presence of a shared predator of both invasive and native species could lead to different outcomes, depending on the relative magnitude of underlying indirect effects, such as trophic cascade or hyperpredation [16]. When trophic cascade is stronger

than hyperpredation as the underlying indirect effect, the shared predator decreases invasive species populations, which, in turn, increases native species populations. Conversely, invasive species could indirectly enhance predation pressure on native species if invasive species improve survival or reproduction of the shared predator. Because complex interspecific interactions are common in nature, untangling the indirect effects of the species in a community containing both invasive and native species is essential to understanding how habitat connectivity affects native species. In particular, when the shared predator is also non-native, knowledge of indirect effects is crucial for conservation purposes, because the order in which non-native species should be eradicated will probably determine the restoration success of native populations [17].

In this study, we examined a patchy farm pond system in northern Japan to clarify how habitat connectivity and a shared predator affect native species through the spread of non-native species. Farm ponds are widely distributed in East Asia for irrigating paddy fields, and are important habitats for a variety of animals and plants, including many endangered species [18,19]. We focused on the invasive American bullfrog, *Rana catesbeiana*; the native wrinkled frog, *Glandirana rugosa* and predatory non-native common carp, *Cyprinus carpio* (hereinafter bullfrogs, wrinkled frogs and carp, respectively). Bullfrogs are native to the eastern United States, and are known to have negative effects on various native species, including other anurans, in invaded areas [20,21]. Because both bullfrogs and wrinkled frogs appear to prefer similar permanent ponds and spend their whole lives in and near water bodies [22], bullfrogs are likely to have negative effects on wrinkled frogs, mainly through predation (see Methods for details). Non-native carp have been established in Japanese aquatic systems for at least 200 years after their introduction from the Eurasian continent [23]. Carp are efficient predators of tadpoles [24], and as the top predators in ponds may thus limit the distributions of both frog species. Because most of the farm ponds in our system were not connected by aquatic pathways, connectivity among ponds was considered to be important for only frog species, as many adult anurans, including bullfrogs, are known to move among breeding sites through the terrestrial landscape matrix [25–28].

Here, our objectives are to elucidate the direct and indirect effects of habitat connectivity on the distributions of both invasive and native species and to understand how shared resident predators modify these effects in a landscape context. To this end, we analysed distribution data for invasive bullfrogs and native wrinkled frogs obtained from 145 farm ponds. In particular, we sought to identify whether bullfrogs have negative effects on wrinkled frogs, how farm-pond connectivity affects wrinkled frogs directly and indirectly, and how carp modify the negative effects of bullfrogs on wrinkled frogs. We used a hierarchical Bayesian approach to estimate direct and indirect effects simultaneously and account for detectability of frog species. In addition to the above field survey, we conducted two laboratory experiments to evaluate the differential predation pressure of carp on bullfrog and wrinkled frog tadpoles and the underlying mechanisms. We hypothesized that the differential predation pressure of carp is owing to the difference between the two tadpole species in refuge use and/or response to chemical cues from carp.

2. Methods

(a) Study species and site

(i) Study species

The bullfrog is an invasive frog species introduced from the eastern United States to Japan in 1918, and is now widely distributed throughout Japan. Because of its strong negative effect on native fauna through predation or competition, the bullfrog has been listed as one of the world's 100 worst invasive alien species [29]. The wrinkled frog is native to Japan and is much smaller than the bullfrog (approx. 50 mm versus 150 mm in snout–vent length [30]). Although the wrinkled frog is widely distributed in Japan, it is designated as an endangered species in several prefectures. Both the bullfrog and the wrinkled frog reproduce in lentic or slow lotic habitats, and overwinter as tadpoles [22].

The carp is a large freshwater fish distributed from Asia to Eastern Europe. Two different strains of carp inhabit Japan: a native strain and a non-native strain introduced from the Eurasian continent at least 200 years ago [31]. The distribution of the native strain is now highly limited, whereas the non-native strain inhabits most lakes, rivers and ponds in Japan. Our study site contains only non-native carp.

(ii) Study site

We surveyed farm ponds in a hilly region of Ichinoseki City, Iwate Prefecture, northern Japan (38°94′ N, 141°04′ E). Over 500 farm ponds are patchily distributed in this region (5 × 10 km). Because there are only a few rivers in this hilly area, numerous farm ponds were constructed to store water for cultivation of rice fields. The area of each pond varies from 0.01 ha to over 1 ha (0.083 ± 0.15 (s.d.) ha) and the mean maximum depth is 1–2 m. The ponds have relatively low turbidity with muddy sediment overlain by allochthonous detritus and are surrounded to varying degrees by deciduous forests. Because these ponds typically depend on rainfall for their water supply and have only one outlet with fixed flashboards, most of them are not connected by aquatic pathways. Therefore, the farm ponds can be regarded as isolated ecosystems with respect to fully aquatic taxa such as fishes.

Through interviews with local farmers, bullfrogs were revealed to have been established in this region for at least 20 years, and they reproduce almost exclusively in farm ponds. Carp have been introduced into farm ponds for ornamental use, food or control of aquatic plants, and do not appear to reproduce [32]. Because carp seldom move between ponds by themselves [32], they can be regarded as a factor limiting frog abundance at the pond level. Other alien predators, such as largemouth bass, bluegill and red swamp crayfish, are rarely found in the study area. Thus, there are few major aquatic predators, including native species, that are likely to limit population densities of bullfrogs.

Through bullfrog pest control efforts undertaken by volunteers at a local non-profit organization, it was found that adult anurans were the dominant taxa in the stomachs of bullfrogs by frequency of occurrence (35%) in 131 adult bullfrogs captured, followed by Gerridae (30%), Scarabaeidae (18%) and Carabidae (17%; H. Takeda 2010, unpublished data, see appendix S1 in the electronic supplementary material). Native anuran species other than wrinkled frogs either use farm ponds during only the breeding season (*Rhacophorus arboreus*, *Rhacophorus ornativentris*) or mainly inhabit paddy fields (*Rhacophorus porosa*, *Rhacophorus schlegelii*). Thus, most of the anurans found in the stomach of bullfrogs appeared to be either wrinkled frogs or young bullfrogs rather than other native species.

(b) Methods and analyses

(i) Field survey

We selected 145 farm ponds to cover the range of pond areas and neighbouring pond densities in our study area (26.9% of all

Table 1. Description of all variables measured in our study system.

variable names	description	
bullfrog	occupancy	56 out of 145 ponds
	number of individuals	mean: 0.92 (min−max: 0−7)
with wrinkled frog	occupancy	9 out of 145 ponds
wrinkled frog	occupancy	50 out of 145 ponds
	number of individuals	1.17 (0−15)
common carp	occupancy	59 out of 145 ponds
with bullfrog	occupancy	25 out of 145 ponds
with wrinkled frog	occupancy	15 out of 145 ponds
floating plant	coverage (%)	39.7 (0−99)
emergent plant	coverage (%)	2.3 (0−45)
submerged plant	coverage category (absent, low, high)	103, 30, 12 ponds
pH	pH	6.68 (5.33−9.31)
electrical conductivity	(mS m^{-1})	6.42 (2.5−29.5)
forest	area proportion (%)	52.7 (0−100)
paddy field	area proportion (%)	41.7 (0−100)
dry field	area proportion (%)	2.96 (0−100)
pond area	area (m^2)	499.9 (10.6−2485.5)

ponds). In these farm ponds, both adult bullfrogs and wrinkled frogs were counted by call surveys in July and August of 2009 and 2010 (except on rainy days) when the reproductive activities of both frog species were the highest. Call surveys were conducted for 15 min near a pond between 20.00 and 00.00 [33]. To estimate the detectability of calling frogs at the time of each survey, additional surveys were conducted on three consecutive days in 40 ponds in 2010, following the above method. These replicated survey data in each pond enabled us to estimate detectability of calling frogs, using a binomial distribution (see 'Statistical analyses').

In each pond, we also recorded occupancy (presence or absence) of carp, coverage by aquatic plants and water properties (pH and electrical conductivity). The carp occupancy was evaluated by 30 min visual surveys from the pond shore, interviews with pond owners, or both. As the introduced carp were large (mostly more than 50 cm) and swam near the surface of the water during the daytime, they could be detected easily. For aquatic plants, the degree of coverage of floating and emergent plants was determined as the proportion of occupied areas, and that of submerged plants was classified into three categories; absent, low (less than 30%), or high (more than 30%). In addition to these factors, we extracted information on terrestrial environments surrounding each pond, pond area and distance between ponds by using geographical information systems. For surrounding environments, we used area proportions of forests, rice fields and dry crop fields within 10 m from the outer edge of ponds. All data measured in our field survey are summarized in table 1.

(ii) Statistical analyses

We used a hierarchical Bayesian approach to simultaneously explore the direct and indirect effects of pond connectivity, carp occupancy and local environments on the densities of both frog species [34]. The Bayesian approach easily accounts for detectability of call surveys and uncertainties of unknown parameters related to connectivity (figure 1). We used a zero-inflated Poisson model to describe the abundance of bullfrogs

and wrinkled frogs because they exhibited overdispersion to some extent [35]. The logarithm of pond area was always included as an offset term in our analyses to evaluate the effect of environmental variables on frog densities.

Connectivity between ponds was calculated as in earlier studies [36]:

$$S_i = \sum_{i \neq j} \exp(-\alpha d_{ij}) \times A_j^{\beta},$$

where d_{ij} represents the distance between ponds i and j, A_j represents the area of pond j, and α and β are distance- and area-dependent parameters of connectivity. For calculating connectivity, we used pond area as a suitable proxy for long-term average of frog abundance, rather than using snapshot abundance estimates [37,38]. Decreasing α and increasing β, respectively, indicates that more distant ponds and larger ponds contribute to connectivity. The magnitude of these parameters largely depends on species characteristics, such as dispersal ability. We also calculated alternative connectivity to account for permeability of forests surrounding ponds, because forest areas could act as a dispersal barrier for moving non-forest frog species [39,40]. The alternative connectivity is

$$S_i' = NF_i \times S_i,$$

where NF_i is the proportion of non-forested areas within a 10 or 50 m buffer from the outer edge of pond i.

We conducted principal component (PC) analyses to summarize the three subsets of environmental variables (aquatic plants (AP), water properties (WP) and surrounding environments (SE)). For subsequent analyses, we used PC1 and PC2 of aquatic plants, PC1 of water properties, and PC1 of surrounding environment, on the basis of a 60% cumulative contribution to each environmental variable (hereafter AP1, AP2, WP and SE, respectively; see appendix S1 in the electronic supplementary material).

To take into account the detectability of frog calls in surveys, we assumed that the actual frog abundance was constant over three survey days and that detectability was independent of pond and dependent on only frog species. Then, the observed
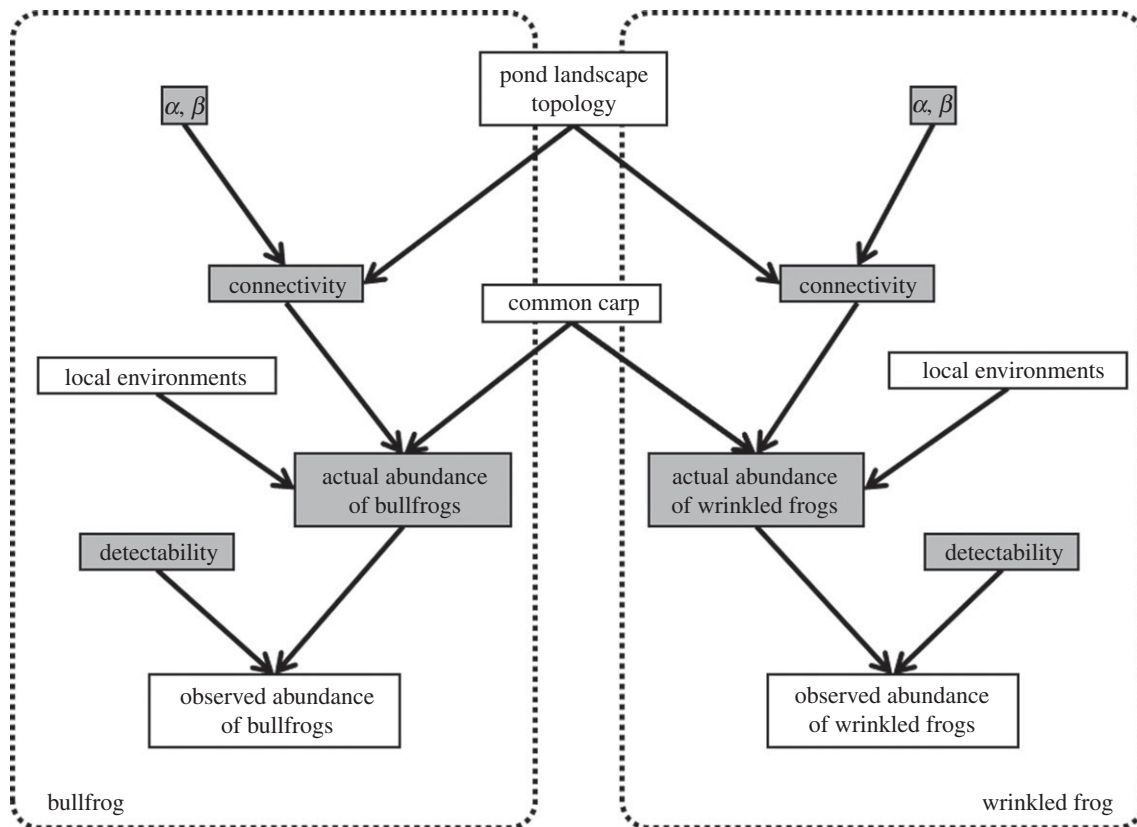
Figure 1. Bayesian analysis diagram for how the abundance of invasive bullfrogs and native wrinkled frogs are directly and indirectly affected by pond connectivity, carp and local environments. Grey boxes represent estimated parameters and white boxes represent data collected from our field surveys and geographical information systems (GIS). Using a Bayesian hierarchical approach, we estimated detectability of call surveys and unknown distance- and area-dependent parameters, α and β, for connectivity, rather than we fixed them a priori.

count $Y_{s,i,k}$ of frog species s in focal pond i on the kth survey was modelled as a binomial distribution [41]:

$$Y_{s,i,k} \,|\, N_{S,i},\, p_s \sim \text{Binomial}(N_{s,i},\, p_s),$$

where $N_{s,i}$ represents the actual frog number and p_s is the detectability of an individual in our calling surveys.

Prior to performing a Bayesian analysis, we conducted a preliminary analysis to narrow down explanatory variables for Bayesian modelling because using all the variables is extremely time-consuming. In this analysis, the explanatory variables used were two types of connectivity (S_i or S_i'), carp occupancy, bullfrog abundance (only for wrinkled frogs), AP1, AP2, WP, SE, pond area and year. Here, bullfrog abundance was log-transformed after adding 0.5 to make it easy to calculate indirect effects. All explanatory variables other than categorical data (carp occupancy and year) were standardized. Unlike in the Bayesian analysis detailed below, the density of each frog species was evaluated separately without taking detectability into account. We first calculated the corrected Akaike information criterion (AICc) for models with all possible combinations of explanatory variables. As α and β in connectivity measures are unknown, we set these parameters to various values ($\alpha = 1, 2, \ldots, 10$ and $\beta = 0.4, 0.6, \ldots, 1.6$). Second, we chose a set of models with ΔAICc < 2 (the difference in AICc between the best model and the focal model), and selected explanatory variables that appeared frequently (more than 60%) in these models. As a result, five variables were selected as explanatory variables for bullfrogs: connectivity without forest buffer (S_i), carp occupancy, WP, pond area and year. In addition, seven variables were selected for wrinkled frogs: connectivity without forest buffer (S_i), carp occupancy, bullfrog abundance, AP1, AP2, SE and pond area (see appendix S1 in the electronic supplementary material).

We assigned vague priors for the detectability and coefficients of explanatory variables: uniform distributions on [0, 1] and normal distributions with mean 0 and variance 10 000. We also set the prior of connectivity parameters α and β to uniform distributions on [0.1, 12.0] and [0.1, 2.0], respectively. The number of iterations for Markov chain Monte Carlo simulations was 200 000, the number of burn-ins was 100 000 and the thinning interval was 100. We confirmed convergence by assessing whether $\hat{R}$ of all estimates were smaller than 1.1 [42]. All of the analyses were conducted using R v. 3.0.0 [43] and JUST ANOTHER GIBBS SAMPLER v. 3.3.0 [44]. Our field survey dataset is available in appendix S2 of the electronic supplementary material.

(iii) Laboratory experiments

In addition to the above-mentioned field surveys, we conducted two different laboratory experiments to confirm the differential predation pressure of carp on bullfrog and wrinkled frog tadpoles and to infer the underlying mechanisms. All tadpoles of both the frog species used in the experiments had been raised in the laboratory from eggs, with no previous experience of encountering fish predators. The body sizes of both tadpole species used for the experiments were similar, approximately 20 mm in total length (developmental stage 26–30 [45]). Non-native carp (249 ± 19 mm) were purchased from a fish farm. They had no experience in consuming tadpoles prior to the trials. They were fed commercial flake food (10 g) daily, but not given flake food 24 h before trials to standardize the motivation of carp to feed among trials. All animals were kept on a 16 L : 8 D h photoperiod at 25 ± 2°C.

In experiment 1, we aimed to evaluate differential predation pressure of carp on the two species of tadpoles. Trials were conducted in a plastic tub ($67 \times 40 \times 32$ cm) containing 70 l of aged tap water. To mimic natural habitat structures along a
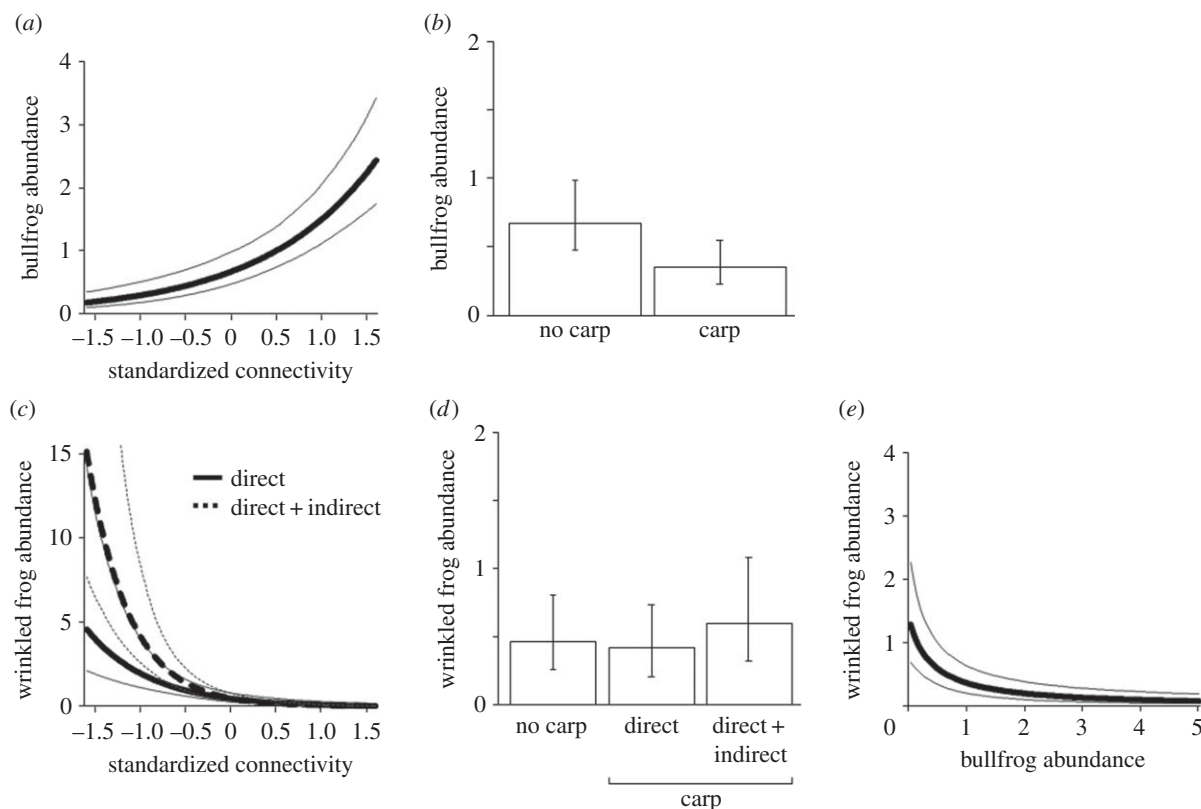
Figure 2. The effect of connectivity and species interactions on the abundance of wrinkled frogs and bullfrogs: the effects of (*a*) connectivity and (*b*) carp on bullfrogs, and the effects of (*c*) connectivity, (*d*) carp and (*e*) bullfrogs on wrinkled frogs. In (*c,d*), we described not only the direct effect, but also the indirect effect on wrinkled frogs through bullfrogs. The abundance of two frog species in figures represents values when variables other than the interests were fixed to their averages. Each figure represents estimate (bold lines or rectangles) and 95% credible interval (thin lines or error bars).

pond shore, we placed plastic aquarium plants (density: 200 stems m^{-2}; height: 10 cm) in one half of the tub to serve as refuge for tadpoles whereas the other half of the tub was an open water space with no plants [46]. For each trial, one carp was placed in the tub for 1 h for acclimatization. Just before the introduction of tadpoles, a hand net was gently set in the open space to divide the space between carp side and tadpole side, to prevent attacks by the carp on tadpoles immediately after their introduction. Then, five tadpoles of either bullfrog or wrinkled frog were introduced to the tub and allowed to acclimatize for 15 min [46,47]. The hand net was then removed carefully from the tub, allowing the carp to prey on the tadpoles. The number of tadpoles that had survived was counted 1 h later. We used a total of 10 carp and each carp was used twice, once for each frog species. The order of the trials of the two frog species presented to each carp was randomly assigned. The number of tadpoles consumed by carp was analysed using a generalized linear mixed model (GLMM) with a logit link function and a binomial error distribution. Frog species and carp identifier were included in the model as fixed and random effects, respectively. Note that we did not introduce the two species of tadpoles together, because we expected an absolute rather than relative difference in predation by carp.

Furthermore, we conducted experiment 2 to test the hypothesis that the differential predation pressure of carp is owing to the difference in refuge use and/or response to chemical cues from carp. We used a small plastic tub (37 × 25 × 14 cm) containing either treatment or control water (10 l) in this experiment to observe refuge use by tadpoles in the absence of carp. The treatment water was prepared by keeping two carp for 24 h in a tub with 70 l of aged tap water and then filtering the water through a filter net (mesh size less than 500 μm). As in experiment 1, we placed plastic aquarium plants in half of the tub to serve as a refuge. As tadpoles are known to increase the frequency of refuge use when exposed to the chemical cues from predatory

fish [47,48], we expected that the tadpoles would frequently take refuge in the plastic aquarium plants when exposed to the treatment water. Five tadpoles (bullfrog or wrinkled frog) were placed in the tub and acclimatized to the experimental conditions for 15 min. Then, we counted the tadpoles' positions in the tub (in refuge or out of refuge) at 1 min intervals for 15 min. Each of the four different trials (two treatments × two frog species) was performed 10 times. The number of individuals in refuge at each interval was analysed using GLMM with a logit link function and a binomial error distribution. We used frog species and water treatment as fixed effects and trial identifier as a random effect. Our experimental dataset is available in appendix S2 of the electronic supplementary material.

3. Results

(a) Field survey

Here, we describe the results of the Bayesian analysis with regard to direct effects on bullfrogs, direct effects on wrinkled frogs and indirect effects on wrinkled frogs through bullfrogs (figure 2 and table 2).

(i) Direct effects on bullfrogs

Bullfrog densities increased with increasing pond connectivity, and this relationship was clearly positive (figure 2*a*): the 95% credible interval (CI) did not include zero. The presence of carp decreased bullfrog densities, and this relationship was clearly negative (figure 2*b*). Bullfrog density was correlated negatively with pond area and positively with WP (high pH and electrical conductivity). Connectivity parameters α and β were estimated to be 0.70 (95%

Table 2. The results from our Bayesian analysis: (a) direct effects on the densities of bullfrogs and (b) direct and indirect effects on the densities of wrinkled frogs. (WP, AP1 and AP2 are principal components of water properties and aquatic plants. We represented median and 95% credible interval (CI) for each parameter. Italics parameters indicates that 95% CI did not overlap with zero. Note that α, β and detectability must be positive.)

	median	95% CI
(a) bullfrogs		
direct effects		
intercept	-6.02	$(-6.39, -5.63)$
connectivity without forest buffer	0.80	$(0.59, 1.02)$
carp	-0.65	$(-1.10, -0.24)$
WP (high pH and EC)	0.19	$(0.02, 0.39)$
pond area	-0.20	$(-0.32, -0.10)$
year	0.06	$(-0.35, 0.42)$
α (distance-dependent parameter in connectivity)	0.70	$(0.15, 1.43)$
β (area-dependent parameter in connectivity)	1.08	$(0.62, 1.38)$
detectability	0.83	$(0.69, 0.90)$
(b) wrinkled frogs		
direct effects		
intercept	-5.88	$(-6.50, -5.33)$
connectivity without forest buffer	-1.42	$(-2.26, -0.89)$
carp	-0.12	$(-0.50, 0.24)$
bullfrog	-1.15	$(-1.61, -0.74)$
AP1 (floating and submerged plants)	0.19	$(0.05, 0.32)$
AP2 (emerged plants)	0.18	$(0.02, 0.32)$
SE (few forest and abundant paddy field)	0.12	$(-0.01, 0.32)$
pond area	-0.36	$(-0.51, -0.22)$
indirect effects		
connectivity $\rightarrow$ bullfrogs	-0.74	$(-1.13, -0.45)$
carp $\rightarrow$ bullfrogs	0.37	$(0.15, 0.65)$
α (distance-dependent parameter in connectivity)	1.22	$(0.49, 1.86)$
β (area-dependent parameter in connectivity)	1.83	$(1.52, 1.99)$
detectability	0.54	$(0.38, 0.67)$

CI: 0.15–1.43) and 1.08 (0.62–1.38), and the detectability of bullfrogs was estimated to be 0.83 (0.69–0.90).

(ii) Direct effects on wrinkled frogs
In contrast to bullfrogs, wrinkled frog densities decreased with increasing pond connectivity (figure 2c). Furthermore, the presence of carp appeared to have little effect on wrinkled frog densities: the 95% CI overlapped with zero (figure 2d). As we expected, wrinkled frog densities clearly decreased with increasing bullfrog abundance (figure 2e). Wrinkled frog densities correlated negatively with pond area and positively with AP1 (high coverage by floating and submerged plants) and AP2 (high coverage by emergent plants). Connectivity parameters α and β were estimated to be 1.22 (95% CI: 0.49–1.86) and 1.83 (1.52–1.99), and the detectability of wrinkled frogs was estimated to be 0.54 (0.38–0.67).

(iii) Indirect effect on wrinkled frogs through bullfrogs
Pond connectivity was estimated to have an indirect negative effect on wrinkled frog densities through increased bullfrog

densities (figure 2c). Furthermore, the presence of carp was estimated to have an indirect positive effect on wrinkled frogs (figure 2d).

(b) Laboratory experiments
In experiment 1, bullfrog tadpoles were consumed by carp threefold more frequently than wrinkled frog tadpoles (figure 3a), and the difference was highly significant ($\chi_1^2 = 10.85$, $p < 0.001$). In experiment 2, the rate of refuge use by bullfrog tadpoles was lower than that by wrinkled frog tadpoles, regardless of whether the water in the experimental tub contained chemical cues from carp (figure 3b). The effect of frog species was highly significant ($\chi_1^2 = 27.77$, $p < 0.0001$), whereas that of chemical cues was not ($\chi_1^2 = 0.34$, $p = 0.56$).

4. Discussion
Our spatial distribution analysis yielded three main findings: (i) bullfrogs had negative effects on wrinkled frog densities,
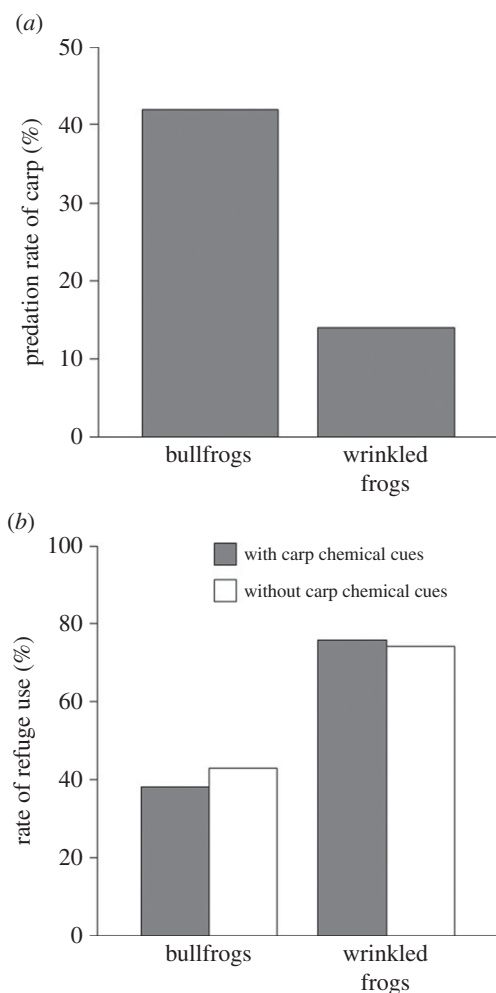
Figure 3. The results from our laboratory experiments: (*a*) predation rate of common carp on tadpoles and (*b*) frequency of refuge use by tadpoles. Grey bars in (*b*) represent the experimental tub with chemical cues of carp, and white bars represent the tub without chemical cues.

(ii) connectivity between farm ponds increased the bullfrog densities and indirectly decreased wrinkled frog densities, and (iii) the presence of carp decreased bullfrog densities and indirectly increased wrinkled frog densities. The advantage of our analysis is that it accounts for multiple sources of uncertainty, including frog detectability and connectivity parameters, by using a hierarchical Bayesian approach. The above-mentioned inferences from the field surveys were further supported by laboratory experiments on the predation pressure of carp on the two frog species. These lines of evidence indicate that our study system was a metacommunity system consisting of carp as a resident top predator, bullfrogs as an intermediate predator and wrinkled frogs as a prey species. Although there are many experimental studies on metacommunities [49–51], only a few field studies had been conducted thus far [52,53]. To the best of our knowledge, there are no field studies on a metacommunity of three trophic levels. In the following, we detail the metacommunity structure that gave rise to the above-described field patterns, and we discuss the implications for conservation of invaded ecosystems.

(a) Metacommunity structure in our system

Around the world, invasive bullfrogs are known to have negative impacts on native species, mainly through predation

[20,21]. As in previous studies, populations of native wrinkled frogs in our study appear to have been decreased by bullfrog predation, because wrinkled frog densities in farm ponds decreased with increasing numbers of bullfrogs, and anurans were most common in the stomach contents of bullfrogs. In addition to predation, bullfrogs might have negatively affected wrinkled frogs though interspecific competition for resources, but this does not seem to have played a major role. First, as our experiment showed, larvae of the two species are likely to exhibit microhabitat segregation to some degree, as wrinkled frogs do not prefer open water. Second, adult wrinkled frogs consume primarily ants [54], which bullfrogs rarely consumed in our study site (see appendix S1 in the electronic supplementary material). Interspecific predation in the larval stage is also unlikely to be important, as anuran larvae are primarily algophagous or detritivorous [55,56] and thus predation events at larval stages may be uncommon in the wild.

We found a positive correlation between habitat connectivity and bullfrog abundance in farm ponds. This suggests that high pond connectivity may promote migration of bullfrogs and decrease the risk of local extinction or enhance local population size, that is, bullfrogs can occur in a metapopulation structure. In our analysis, the spatial scale of connectivity affecting bullfrog abundance was estimated to be about 1.4 km ($=1/\alpha$). Because bullfrogs are known to move up to a few kilometres between ponds [26], our connectivity estimate agrees well with the earlier finding on bullfrog movements. The analysis of our field surveys also revealed that pond connectivity had an indirect negative effect on the abundance of wrinkled frogs through increased numbers of bullfrogs. Many previous studies have encouraged enhancement of connectivity, for example, by creating corridors and fishways [7,8,57]. However, when invasive species have become established, it is necessary to evaluate the effect of habitat connectivity on both invasive and native species in advance.

Surprisingly, our results revealed a direct negative effect of connectivity on wrinkled frog densities. Several reasons can be considered, but it is most likely that reduced colonization of wrinkled frogs from neighbouring ponds played a role. This is because increasing connectivity had a positive effect on bullfrog densities both in focal and neighbouring ponds and thus reduced the abundance of wrinkled frogs at the metapopulation level. This may be partly supported by the finding that the spatial scale of connectivity of wrinkled frogs (0.8 km) was about half that of bullfrogs (1.4 km). Wrinkled frogs were expected from their small body size to have low movement ability, so this spatial scale also appears to be biologically reasonable. Further research is necessary to confirm the mechanisms by which connectivity has a direct negative effect on native species.

Our field survey further suggested that carp decreased bullfrog densities, but that their negative effect on wrinkled frogs was insignificant. Our laboratory experiments confirmed that this pattern may be owing to the difference in predation pressure of carp between the two tadpole species (experiment 1) and this difference may result from a difference in refuge use (experiment 2). We should acknowledge some limitations of this study, namely small volume and short-term laboratory experiments. Nevertheless, these lines of evidence suggested that the presence of carp induced a

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top-down trophic cascade, rather than hyperpredation, in which they had positive indirect effect on wrinkled frogs through predation on bullfrog larvae.

Our experiment also revealed that bullfrog tadpoles did not exhibit behavioural plasticity in response to chemical cues from carp. Earlier studies showed that bullfrogs respond to chemical cues from fish predators, for example, largemouth bass (*Micropterus salmoides*), bluegill (*Lepomis macrochirus*) and green sunfish (*Lepomis cyanellus*), all of which share native distribution ranges with bullfrogs [46,48], but they do not respond to chemical cues from mosquitofish (*Gambusia affinis*), which does not overlap in distribution range with bullfrogs [58]. Because only a relatively short amount of time has passed since bullfrogs in Japan were exposed to predation by carp, they cannot respond adaptively to chemical cues from carp. Wrinkled frog tadpoles also did not exhibit behavioural plasticity, but they preferred to use microhabitats with refuge irrespective of chemical cues from carp. It appears that wrinkled frog tadpoles might have developed an innate, not plastic, anti-predatory behaviour.

In freshwater systems, introduction of non-native fishes often has negative effects on native organisms [59,60], but occasionally has positive effects via trophic cascades [61,62]. It is important to note that such a cascading effect occurring at the pond level could spread across surrounding landscapes by suppressing bullfrog abundance at the metapopulation level.

(b) Conservation implications

Habitat connectivity is widely known to play an important role in metapopulation persistence [36,63]. By the same token, depression of connectivity is effective for controlling invasive species that have metapopulation structures. For conservation of native species in this context, two approaches for connectivity management can be considered; one is to manage links connecting habitat patches and the other is to manage habitat patches themselves [64]. For link management, introduction of barriers to invasive fishes in rivers [65] and alteration of the landscape matrix for invasive plants to prevent seed dispersal [66] have been proposed. However, reducing the quality of habitat patches has received little attention in the landscape context. We have shown that habitat connectivity increases negative effects of bullfrogs on native species, but that predatory carp depresses local densities of bullfrogs, thus ameliorating their negative effects. Because bullfrogs appear to disperse between ponds mainly through the terrestrial matrix, link management that could prevent or reduce their colonization rate is unrealistic. In this situation, reducing the quality of habitat patches may be promising. In our system, introduction of carp into farm ponds may thus be an effective way to manage bullfrogs in both local and landscape contexts. However, introduction of top predators occasionally leads to unintended negative outcomes for native species [67]. The carp inhabiting farm ponds in Japan is a non-native strain, and is known to have negative effects on native submerged plants through bioturbation [32,68]. Therefore, it is essential to minimize these negative effects when carp are to be introduced into ponds. For instance, carp should not be introduced into ponds with submerged aquatic plants of high conservation priority. However, deliberate introduction of carp may be allowable into ponds with a high connectivity for bullfrogs or that contain endangered organisms highly vulnerable to bullfrog predation (e.g. anurans and some aquatic insects).

Finally, our study may bring to mind metapopulation dynamics of non-native pathogens driven by the complex relationships between habitat connectivity and species interactions [69,70]. Although there are some differences between prey–predator and host–pathogen systems, there appear to be fundamental similarities between the two systems, implying that management implications derived from host–pathogen systems may be useful for the management of invasive species in a metacommunity context. However, it should also be kept in mind that the effectiveness of connectivity management for invasive species is likely to depend on the system of interest. For example, how does connectivity affect the abundance of invasive and native species? Is there any difference in the spatial scale of connectivity between these species? Are species interactions and habitat environments likely to modify the effects of connectivity? In any case, we need to have deeper knowledge of the mechanisms determining the distributions of native and invasive species in a landscape context, and metacommunity perspectives could provide useful insights for establishing effective strategies for management of invasive species living in patchy habitats.

References

1. Fahrig L. 2003 Effects of habitat fragmentation on biodiversity. *Annu. Rev. Ecol. Syst.* **34**, 487–515. (doi:10.1146/annurev.ecolsys.34.011802.132419)

2. Gonzalez A, Lawton JH, Gilbert FS, Blackburn TM, Evans-Freke I. 1998 Metapopulation dynamics, abundance, and distribution in a microecosystem. *Science* **281**, 2045–2047. (doi:10.1126/science.281.5385.2045)

3. Gilbert-Norton L, Wilson R, Stevens JR, Beard KH. 2010 A meta-analytic review of corridor effectiveness. *Conserv. Biol.* **24**, 660–668. (doi:10.1111/j.1523-1739.2010.01450.x)

4. Tewksbury JJ et al. 2002 Corridors affect plants, animals, and their interactions in fragmented landscapes. *Proc. Natl Acad. Sci. USA* **99**, 12 923–12 926. (doi:10.1073/pnas.202242699)

5. Van Geert A, Van Rossum F, Triest L. 2010 Do linear landscape elements in farmland act as biological

corridors for pollen dispersal? *J. Ecol.* **98**, 178–187. (doi:10.1111/j.1365-2745.2009.01600.x)

6. Cascante A, Quesada M, Lobo JJ, Fuchs EA. 2002 Effects of dry tropical forest fragmentation on the reproductive success and genetic structure of the tree *Samanea saman*. *Conserv. Biol.* **16**, 137–147. (doi:10.1046/j.1523-1739.2002.00317.x)

7. Bennett AF. 1990 Habitat corridors and the conservation of small mammals in a fragmented forest environment. *Landsc. Ecol.* **4**, 109–122. (doi:10.1007/bf00132855)

8. Noss RF. 2003 A checklist for wildlands network designs. *Conserv. Biol.* **17**, 1270–1275. (doi:10.1046/j.1523-1739.2003.02489.x)

9. Puth LM, Allen TFH. 2005 Potential corridors for the rusty crayfish, *Orconectes rusticus*, in northern Wisconsin (USA) lakes: lessons for exotic invasions. *Landsc. Ecol.* **20**, 567–577. (doi:10.1007/s10980-004-5649-y)

10. Alofs KM, Fowler NL. 2010 Habitat fragmentation caused by woody plant encroachment inhibits the spread of an invasive grass. *J. Appl. Ecol.* **47**, 338–347. (doi:10.1111/j.1365-2664.2010.01785.x)

11. Fausch KD. 2008 A paradox of trout invasions in North America. *Biol. Invasions* **10**, 685–701. (doi:10.1007/s10530-007-9162-5)

12. Lenda M, Zagalska-Neubauer M, Neubauer G, Skorka P. 2010 Do invasive species undergo metapopulation dynamics? A case study of the invasive Caspian gull, *Larus cachinnans*, in Poland. *J. Biogeogr.* **37**, 1824–1834. (doi:10.1111/j.1365-2699.2010.02344.x)

13. Bartak V, Vorel A, Simova P, Pus V. 2013 Spatial spread of Eurasian beavers in river networks: a comparison of range expansion rates. *J. Anim. Ecol.* **82**, 587–597. (doi:10.1111/1365-2656.12040)

14. Gurevitch J, Fox GA, Wardle GM, Inderjit W, Taub D. 2011 Emergent insights from the synthesis of conceptual frameworks for biological invasions. *Ecol. Lett.* **14**, 407–418. (doi:10.1111/j.1461-0248.2011.01594.x)

15. Butchart SHM *et al.* 2010 Global biodiversity: indicators of recent declines. *Science* **328**, 1164–1168. (doi:10.1126/science.1187512)

16. Zavaleta ES, Hobbs RJ, Mooney HA. 2001 Viewing invasive species removal in a whole-ecosystem context. *Trends Ecol. Evol.* **16**, 454–459. (doi:10.1016/s0169-5347(01)02194-2)

17. Courchamp F, Langlais M, Sugihara G. 1999 Control of rabbits to protect island birds from cat predation. *Biol. Conserv.* **89**, 219–225. (doi:10.1016/s0006-3207(98)00131-1)

18. Takasaki Y. 1994 Odonata of irrigation pond (in Japanese). In *Introduction to natural history of Irrigation ponds* (ed. The Research Group of Natural Irrigation Ponds), pp. 62–73. Tokyo, Japan: Gogo Shuppan.

19. Kadono Y, Yuma M. 1995 *Nature of wetlands* (in Japanese). Osaka, Japan: Hoikusya.

20. Kiesecker JM, Blaustein AR. 1997 Population differences in responses of red-legged frogs (*Rana aurora*) to introduced bullfrogs. *Ecology* **78**, 1752–1760. (doi:10.1890/0012-9658(1997)078[1752:PDIROR]2.0.CO;2)

21. Pearl CA, Adams MJ, Bury RB, McCreary B. 2004 Asymmetrical effects of introduced bullfrogs (*Rana catesbeiana*) on native ranid frogs in Oregon. *Copeia* **2004**, 11–20. (doi:10.1643/CE-03-010R2)

22. Maeda N, Matsui M. 1989 *Frogs and toads of Japan* (in Japanese). Tokyo, Japan: Bun-ichi Sogo Shuppan.

23. Ikuta K, Hosoya K. 2000 Common carp viewed from the biological perspective (in Japanese). *Biostory* **3**, 52–61.

24. Kloskowski J. 2011 Impact of common carp *Cyprinus carpio* on aquatic communities: direct trophic effects versus habitat deterioration. *Fundam. Appl. Limnol.* **178**, 245–255. (doi:10.1127/1863-9135/2011/0178-0245)

25. Ingram WM, Raney EC. 1943 Additional studies on the movement of tagged bullfrogs, *Rana catesbeiana*. *Am. Midl. Nat.* **29**, 239–241. (doi:10.2307/2420996)

26. Willis YL, Moyle DL, Baskett TS. 1956 Emergence, breeding, hibernation, movements and transformation of the bullfrog, *Rana catesbeiana*, in Missouri. *Copeia* **1956**, 30–41. (doi:10.2307/1439241)

27. Marsh DM, Trenham PC. 2001 Metapopulation dynamics and amphibian conservation. *Conserv. Biol.* **15**, 40–49. (doi:10.1046/j.1523-1739.2001.00129.x)

28. Smith MA, Green DM. 2005 Dispersal and the metapopulation paradigm in amphibian ecology and conservation: are all amphibian populations metapopulations? *Ecography* **28**, 110–128. (doi:10.1111/j.0906-7590.2005.04042.x)

29. Lowe S, Browne M, Boudjelas S, De Poorter M. 2000 *100 of the world's worst invasive alien species: a selection from the global invasive species database*. Auckland, New Zealand: Invasive Species Specialist Group.

30. Sengoku S, Hikida T, Matsui M, Nakaya K. 1996 *The encyclopedia of animals in Japan. vol. 5: amphibians, reptiles, chondrichthyes* (in Japanese). Tokyo, Japan: Heibonsha.

31. Mabuchi K, Senou H, Nishida M. 2008 Mitochondrial DNA analysis reveals cryptic large-scale invasion of non-native genotypes of common carp (*Cyprinus carpio*) in Japan. *Mol. Ecol.* **17**, 796–809. (doi:10.1111/j.1365-294X.2007.03626.x)

32. Miyazaki Y, Matsuzaki SS, Kadoya T, Sekizaki Y, Washitani I. 2010 Impacts of common carp (*Cyprinus carpio*) on aquatic plants at small agricultural ponds in Ichinoseki City, Iwate Prefecture (in Japanese). *Jpn J. Conserv. Ecol.* **15**, 291–295.

33. Pellet J, Schmidt BR. 2005 Monitoring distributions using call surveys: estimating site occupancy, detection probabilities and inferring absence. *Biol. Conserv.* **123**, 27–35. (doi:10.1016/j.biocon.2004.10.005)

34. Mysterud A, Yoccoz NG, Langvatn R, Pettorelli N, Stenseth NC. 2008 Hierarchical path analysis of deer responses to direct and indirect effects of climate in northern forest. *Phil. Trans. R. Soc. B* **363**, 2359–2368. (doi:10.1098/rstb.2007.2206)

35. Martin TG, Wintle BA, Rhodes JR, Kuhnert PM, Field SA, Low-Choy SJ, Tyre AJ, Possingham HP. 2005 Zero tolerance ecology: improving ecological inference by modelling the source of zero observations. *Ecol. Lett.* **8**, 1235–1246. (doi:10.1111/j.1461-0248.2005.00826.x)

36. Hanski I. 1994 A practical model of metapopulation dynamics. *J. Anim. Ecol.* **63**, 151–162. (doi:10.2307/5591)

37. Pellet J, Fleishman E, Dobkin DS, Gander A, Murphy DD. 2007 An empirical evaluation of the area and isolation paradigm of metapopulation dynamics. *Biol. Conserv.* **136**, 483–495. (doi:10.1016/j.biocon.2006.12.020)

38. Hartel T, Nemes S, Ollerer K, Cogalniceanu D, Moga C, Arntzen JW. 2010 Using connectivity metrics and niche modelling to explore the occurrence of the northern crested newt *Triturus cristatus* (Amphibia, Caudata) in a traditionally managed landscape. *Environ. Conserv.* **37**, 195–200. (doi:10.1017/s037689291000055x)

39. Stevens VM, Polus E, Wesselingh RA, Schtickzelle N, Baguette M. 2004 Quantifying functional connectivity: experimental evidence for patch-specific resistance in the natterjack toad (*Bufo calamita*). *Landsc. Ecol.* **19**, 829–842. (doi:10.1007/s10980-004-0166-6)

40. Goldberg CS, Waits LP. 2010 Comparative landscape genetics of two pond-breeding amphibian species in a highly modified agricultural landscape. *Mol. Ecol.* **19**, 3650–3663. (doi:10.1111/j.1365-294X.2010.04673.x)

41. Royle JA, Dorazio RM. 2008 *Hierarchical modeling and inference in ecology: the analysis of data from populations, metapopulations and communities*. Amsterdam, The Netherlands: Academic Press.

42. Gelman A, Carlin JB, Stern HS, Rubin DB. 2003 *Bayesian data analysis*. Boca Raton, FL: Chapman and Hall/CRC Press.

43. R Development Core Team. 2013 *R: a language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. (http://www.R-project.org/)

44. Plummer M. 2003 JAGS: a program for analysis of Bayesian graphical models using Gibbs sampling. In *Proc. Third Int. Workshop on Distributed Statistical Computing* (eds K Hornik, F Leisch, A Zeileis). Viono hoikuenna. (http://www.ci.tuwien.ac.at/Conferences/DSC-2003/Proceedings/)

45. Gosner KL. 1960 A simplified table for staging anuran embryos and larvae with notes on identification. *Herpetologica* **16**, 183–190.

46. Smith GR, Burgett AA, Temple KG, Sparks KA, Winter KE. 2008 The ability of three species of tadpoles to differentiate among potential fish predators. *Ethology* **114**, 701–710. (doi:10.1111/j.1439-0310.2008.01505.x)

47. Pearl CA, Adams MJ, Schuytema GS, Nebeker AV. 2003 Behavioral responses of anuran larvae to chemical cues of native and introduced predators in

the Pacific Northwestern United States. *J. Herpetol.* **37**, 572 – 576. (doi:10.1670/134-02n)

48. Kats LB, Petranka JW, Sih A. 1988 Antipredator defenses and the persistence of amphibian larvae with fishes. *Ecology* **69**, 1865 – 1870. (doi:10.2307/1941163)

49. Kneitel JM, Miller TE. 2003 Dispersal rates affect species composition in metacommunities of *Sarracenia purpurea* inquilines. *Am. Nat.* **162**, 165 – 171. (doi:10.1086/376585)

50. Chase JM, Bergett AA, Biro EG. 2010 Habitat isolation moderates the strength of top-down control in experimental pond food webs. *Ecology* **91**, 637 – 643. (doi:10.1890/09-0262.1)

51. Limberger R, Wickham SA. 2011 Predator dispersal determines the effect of connectivity on prey diversity. *PLoS ONE* **6**, e29071. (doi:10.1371/journal.pone.0029071)

52. Briers RA, Biggs J. 2005 Spatial patterns in pond invertebrate communities: separating environmental and distance effects. *Aquat. Conserv. Mar. Freshwat. Ecosyst.* **15**, 549 – 557. (doi:10.1002/aqc.742)

53. Hamasaki K, Yamanaka T, Tanaka K, Nakatani Y, Iwasaki N, Sprague DS. 2009 Relative importance of within-habitat environment, land use and spatial autocorrelations for determining odonate assemblages in rural reservoir ponds in Japan. *Ecol. Res.* **24**, 597 – 605. (doi:10.1007/s11284-008-0531-z)

54. Hirai T, Matsui M. 2000 Myrmecophagy in a ranid frog *Rana rugosa*: specialization or weak avoidance to ant eating? *Zool. Sci.* **17**, 459 – 466. (doi:10.2108/0289-0003(2000)17[459:miarfr]2.0.co;2)

55. Wassersug RJ. 1980 Internal oral features of larvae from eight anuran families: functional, systematic, evolutionary and ecological considerations.

Misc. Publ. Univ. Kans. Mus. Nat. Hist. **68**, 1 – 146.

56. Duellman WE, Trueb L. 1986 *Biology of amphibians*. New York, NY: Johns Hopkins University Press.

57. Calles O, Greenberg L. 2009 Connectivity is a two-way street: the need for a holistic approach to fish passage problems in regulated rivers. *River Res. Appl.* **25**, 1268 – 1286. (doi:10.1002/rra.1228)

58. Smith GR, Boyd A, Dayer CB, Winter KE. 2008 Behavioral responses of American toad and bullfrog tadpoles to the presence of cues from the invasive fish, *Gambusia affinis*. *Biol. Invasions* **10**, 743 – 748. (doi:10.1007/s10530-007-9166-1)

59. Witte F, Goldschmidt T, Wanink J, Van Oijen MJP, Goudswaard K, Wittemaas E, Bouton N. 1992 The destruction of an endemic species flock: quantitative data on the decline of the haplochromine cichlids of Lake Victoria. *Environ. Biol. Fish.* **34**, 1 – 28. (doi:10.1007/bf00004782)

60. Knapp RA, Boiano DM, Vredenburg VT. 2007 Removal of nonnative fish results in population expansion of a declining amphibian (mountain yellow-legged frog, *Rana muscosa*). *Biol. Conserv.* **135**, 11 – 20. (doi:10.1016/j.biocon.2006.09.013)

61. Maezono Y, Miyashita T. 2004 Impact of exotic fish removal on native communities in farm ponds. *Ecol. Res.* **19**, 263 – 267. (doi:10.1111/j.1440-1703.2004.00634.x)

62. Miyake M, Miyashita T. 2011 Identification of alien predators that should not be removed for controlling invasive crayfish threatening endangered odonates. *Aquat. Conserv.: Mar. Freshwat. Ecosyst.* **21**, 292 – 298. (doi:10.1002/aqc.1178)

63. Fahrig L, Merriam G. 1985 Habitat patch connectivity and population survival. *Ecology* **66**, 1762 – 1768. (doi:10.2307/2937372)

64. Bunn AG, Urban DL, Keitt TH. 2000 Landscape connectivity: a conservation application of graph theory. *J. Environ. Manage.* **59**, 265 – 278. (doi:10.1006/jema.2000.0373)

65. Fausch KD, Rieman BE, Dunham JB, Young MK, Peterson DP. 2009 Invasion versus isolation: trade-offs in managing native salmonids with barriers to upstream movement. *Conserv. Biol.* **23**, 859 – 870. (doi:10.1111/j.1523-1739.2008.01159.x)

66. Donald PF, Evans AD. 2006 Habitat connectivity and matrix restoration: the wider implications of agri-environment schemes. *J. Appl. Ecol.* **43**, 209 – 218. (doi:10.1111/j.1365-2664.2006.01146.x)

67. Watari Y, Takatsuki S, Miyashita T. 2008 Effects of exotic mongoose (*Herpestes javanicus*) on the native fauna of Amami-Oshima Island, southern Japan, estimated by distribution patterns along the historical gradient of mongoose invasion. *Biol. Invasions* **10**, 7 – 17. (doi:10.1007/s10530-007-9100-6)

68. Matsuzaki SS, Usio N, Takamura N, Washitani I. 2009 Contrasting impacts of invasive engineers on freshwater ecosystems: an experiment and meta-analysis. *Oecologia* **158**, 673 – 686. (doi:10.1007/s00442-008-1180-1)

69. Hess G. 1996 Disease in metapopulation models: implications for conservation. *Ecology* **77**, 1617 – 1632. (doi:10.2307/2265556)

70. Cronin JT, Reeve JD. 2005 Host-parasitoid spatial ecology: a plea for landscape-level synthesis. *Proc. R. Soc. B* **272**, 2225 – 2235. (doi:10.1098/rspb.2005.3286)