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Quantifying the impact of *Gambusia holbrooki* on the extinction risk of the critically endangered red-finned blue-eye

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Abstract. Managing competing endangered and invasive species in spatially structured environments is challenging because it is often difficult to control invasive species without negatively impacting the endangered species. Effective management action requires an understanding of the factors affecting the presence and absence of each species so that promising sites for relocation of endangered species combined with eradication of invasive species can be identified. We investigate competing hypotheses about the factors affecting occupancy of the critically endangered red-finned blue-eye (*Scaturiginichthys vermeilipinnis*; hereafter 'RFBE'), a native Australian fish with a global distribution that is restricted to a group of shallow artesian springs. RFBE are threatened by competition with invasive mosquito fish (*Gambusia holbrooki*), which are steadily colonizing the springs, resulting in local extinctions of RFBE in most cases. While hypotheses about the influences of *Gambusia* on RFBE exist, none have been tested with a quantitative model. We used a spatially-structured two-species occupancy modeling approach to examine the occupancy dynamics of these fish and tested competing hypotheses on how *Gambusia* occupancy affected RFBE. *Gambusia* occupancy had a strong negative effect on RFBE occupancy and colonization potential; increasing the probability of local extinction at a spring and decreasing the persistence probability of RFBE in a spring by 8.0% ± 2.7% (mean ± 1 SE). We found strongest support for the hypotheses that elevation and spring area influence colonization, and that spring area influences patch extinction probability. Using colonization and local extinction estimates for both species, we identify promising sites for eradication of *Gambusia* and relocation of RFBE.

Key words: competition; *Gambusia holbrooki*; Great Artesian Basin; invasive species; Lake Eyre Basin; occupancy modeling; PRESENCE; *Scaturiginichthys vermeilipinnis*; two-species occupancy estimation.

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INTRODUCTION

Invasive species often outcompete local native species due to competitive exclusion—invasive species are fast colonizers, prolific breeders or aggressive competitors for territory and are adapted to a wide range of conditions that afford them advantages over species that have developed within highly specific environments (Lodge 1993, Mooney and Hobbs 2000). Despite this, spatial and temporal structure in populations can allow co-existence between competing species (Levins and Culver 1971, Slatkin 1974, Ritchie 2002). However, if habitat is limited to islands or patches so that species are forced to interact, it may be possible for the stronger competitor to increase the risk of species extinction of the weaker competitor (Slatkin 1974, Bengtsson 1989, Valone and Brown 1995). The negative effects of competition on the native species can be compounded by other factors that also impact its population, especially in the case of critically endangered species. In extreme cases, it may be necessary to artificially separate the two competing species, through management intervention, to prevent extinction of the endangered species (Simons et al. 1989, Laha and Mattingly 2006). Understanding the factors affecting the balance of colonization and local extinction for both species is important for conservation managers seeking to protect the endangered species (Neubert and Caswell 2000), yet these parameters are often confounded by multiple hypotheses about how the system functions and the species interact (Soulé et al. 1988, Marsh and Trenham 2001, Gurevitch and Padilla 2004, Krabbe 2004).

Two-species occupancy modeling provides one means to test hypotheses about systems of competing species. Numerous methods to parameterize spatially structured two-species occupancy models have been developed (MacKenzie et al. 2004, Richmond et al. 2010, Waddle et al. 2010, Miller et al. 2012). These models can be used to infer the transition probabilities of patch colonization and extinction. The level of complexity with which these models parameterize the transition probabilities varies. The most complex models are state-based models, known as susceptible-infected-susceptible (SIS) models (Hethcote 1989) or heterogeneous stochastic patch occupancy models (SPOMS) (Hanski and Ovaskainen 2003). These models require an understanding of how the occupancy states of individual neighboring patches contribute to transition dynamics. However, because these models require parameters for the contribution of each patch in the neighborhood (Yackulic et al. 2013), they require records of many colonization and local extinction events to obtain parameter estimates. A compromise is to assume that the number of occupied neighboring patches can be used to capture the dynamics, which is useful where transition data are scarce (Bled et al. 2010, Yackulic et al. 2012, Yackulic et al. 2013). The approach that requires the fewest parameters is the patch-based occupancy model, which assumes each site is independent of its neighboring patches (Hanski 1994, Miller et al. 2012, Haynes et al. 2014). These models return patch-based parameter estimates and require fewer recorded transition events because there are fewer parameters in the model. This approach enables comparison of different hypotheses about how the model works and an estimate of the dynamics of individual patches that can be used to target management intervention.

In this paper, we use a two-species, multi-season occupancy model (Miller et al. 2012) to investigate a number of competing hypotheses about the factors affecting occupancy of the critically endangered red-finned blue-eye (*Scaturiginichthys vermeilipinnis*; hereafter RFBE) (Wager and Unmack 2004). RFBE is a native Australian fish whose tiny global distribution combined with colonization by invasive mosquito fish (*Gambusia holbrooki;* hereafter *Gambusia*) has led to the RFBE being placed on the IUCN list of the 100 most endangered species on the planet (Baillie and Butcher 2012). The RFBE has a global distribution that is restricted to a group of shallow artesian springs at Edgbaston Reserve in Queensland, Australia (Fig. 1). Although other threats to the species exist, evidence suggests that the presence of *Gambusia* is the most likely factor leading to local extinctions of RFBE (Fairfax et al. 2007, Kerezsy and Fensham 2013). The two closely-related species of *Gambusia* (*G. affinis* and *G. holbrooki*) are collectively the world's most widely distributed freshwater fish (Pyke 2008) and are considered among the world's 100 worst invasive species (Lowe et al. 2000), having been implicated in declines and local extinctions of fish species of similar size and with similar habitat preferences (Courtenay and Meffe 1989, Arthington 1991). *Gambusia* have been steadily colonizing the habitat of the RFBE (Fairfax et al. 2007), and the invasion of *Gambusia* has corresponded to local extinctions of RFBE. RFBE is now restricted to just eight springs, despite a

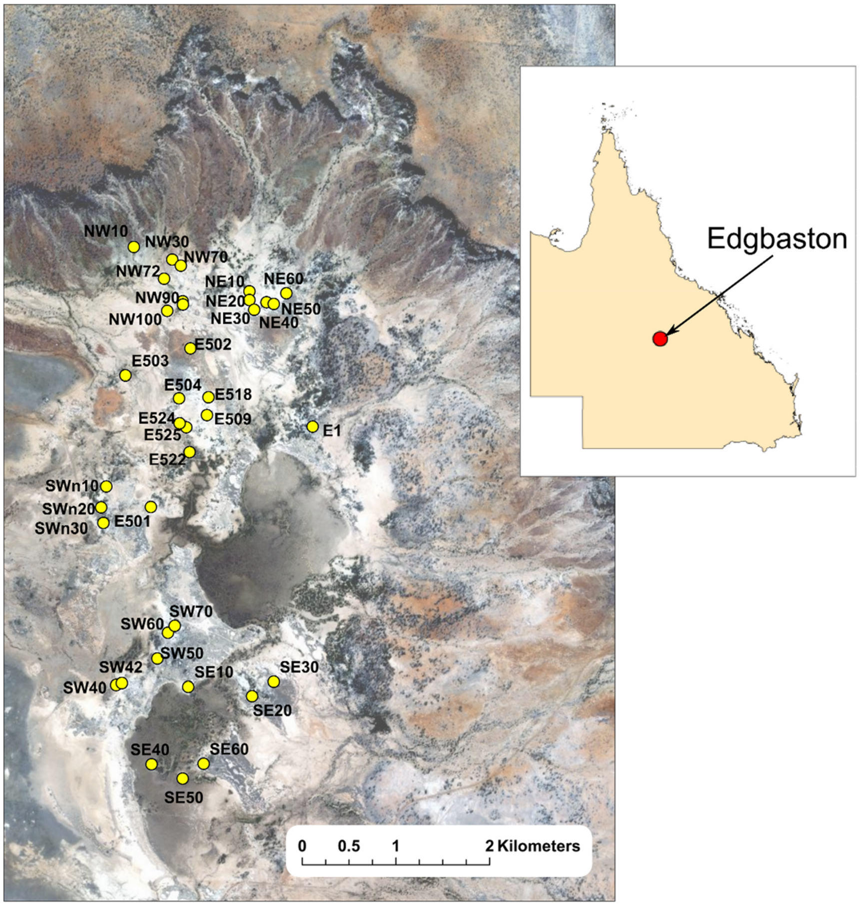

Fig. 1. Locations of modeled springs and Edgbaston Reserve in Queensland, Australia.

number of successful reintroductions and a program of applying the piscicide rotenone to springs occupied by *Gambusia* (Kerezsy and Fensham 2013). Although a key aspect of the recovery program has been to prevent the spread of *Gambusia* into springs occupied by RFBE (Fensham et al. 2010), the mechanisms of competition, colonization and local extinction are not well understood. It is hypothesized that *Gambusia* suppress RFBE (Fairfax et al. 2007), but the extent of the competition between the two species has not yet been quantified. For example, there is at least one spring (spring NE60) where the two species co-existed for at least 15 years before RFBE became locally extinct (Fairfax et al. 2007). The leading hypothesis is that *Gambusia* spread during episodic flood events via local ephemeral creeks and overland flows, so that springs with higher elevation are less likely to be colonized by *Gambusia* (Fairfax et al. 2007). Other hypotheses are that *Gambusia* spread from a source population to the south (i.e., downstream) of Edgbaston, the distance between springs affects colonization success, and spring area is an indicator of spring quality. However, none of these hypotheses have been tested with quantitative models. Here we test these competing hypotheses about the effect of *Gambusia* on RFBE occupancy dynamics and identify the most plausible model structure, including the covariates that influence colonization and local extinction probabilities of both species within the complex of springs at Edgbaston Reserve. We then use our model to identify promising sites for eradication of *Gambusia* and relocation of RFBE.

METHODS

Edgbaston Reserve

The Great Artesian Basin springs at Edgbaston Reserve in semiarid central-western Queensland, Australia, are a complex of up to 100 springs that contain the known global habitat of the critically endangered RFBE. Forty-four of the springs at Edgbaston have been surveyed for RFBE and *Gambusia* since the discovery of the endangered species in 1990 (Fairfax et al. 2007, Kerezsy and Fensham 2013). Spring areas, elevation and coordinates have also been mapped. Since its discovery in 1990, the number of springs continually occupied by the RFBE has declined from eight naturally occupied springs to three springs (RFBE has also been observed intermittently at two additional springs). Managers relocated the RFBE to a further 10 springs, of which five currently contain RFBE.

Edgbaston Reserve forms a basin, encircled to the north, east and west by a low plateau, but it is open to the south, where it forms the headwaters of Pelican Creek, an ephemeral waterway that flows into the Thomson River catchment (Fig. 1). The topography is flat (~5.7 m elevation difference between the northernmost and southernmost springs at Edgbaston, which are 5.6 km apart), and Pelican Creek is usually dry, only flowing during large summer rainfall events. The springs occur in five spatial groupings, which we refer to as the SE, SW, E, NE and NW complexes. RFBE occur naturally in the NW complex, and have been successfully translocated into the E complex. Because *Gambusia* is common in the Thomson River and in the southern complexes of Edgbaston, it is hypothesized that *Gambusia* arrived at Edgbaston via this southern route, and is colonizing the spring complexes during floods.

Data formatting

Occupancy data were available from November 1990-September 2006 (Fairfax et al. 2007) and March 2009–October 2013 (see Supplement). A total of 50 surveys were completed during these two periods over 37 springs. The clear and shallow springs permitted active visual surveys conducted by wading through each spring for a period of up to 30 minutes with species identification confirmed by dip-netting a sample of observed animals. During the survey periods, five colonization and five local extinctions were recorded for *Gambusia*; and 14 colonization events and 13 local extinction events were recorded for RFBE. Additional transitions occurred but were preceded by missing data so the timing of the transition could not be determined exactly. Of the RFBE colonization events, 11 were assisted relocations, four of which were removed from the data set because they occurred in the first timestep of the second data set (i.e., March–May 2009 data was removed to prevent the artificial relocations from biasing parameter estimation). Two of the local extinctions of *Gambusia* were exterminations completed by managers. To use data from sites with artificial colonization and extinctions during the sample period, we split the data for each of the seven affected springs into two separate 'sites', one spanning the period before the artificial transition event; and the other spanning from the transition event until October 2013.

Survey data were not replicated, but we assumed that colonization and local extinction events could not occur during the dry winter season (June–September) when flooding is unlikely and the system is most stable. Because there were no more than three months of survey data in one dry season, we used three as the replication. Wet season data were generally treated as individual 'seasons', but were grouped where they occurred within two months of each other. Grouping the wet season data was done to reduce the number of 'seasons' and reduce the amount of missing data. By grouping data into 'seasons', we assume that transitions in occupancy within a season are caused by detection failures rather than by true transitions. While site closure is an assumption of occupancy modeling, a lack of closure may not bias estimates as long as changes in occupancy are random (MacKenzie 2005, MacKenzie et al. 2006). After reformatting the data to include 'seasons' and replicates, the data set contained 35 'seasons', 3 replicates and 44 sites.

Model selection

Managers need to know which strategies will be effective for protecting RFBE and eradicating *Gambusia*. In particular, the colonization and local extinction probabilities can be used to predict where the species are likely to spread and also where the species is vulnerable to local extinction. This information can be used to direct management to target springs for relocation that have high probabilities of RFBE occupancy and low chance of *Gambusia* colonization; and also to target springs for rotenone treatment that have high local extinction probabilities for *Gambusia*.

Although competition has been observed, there are many possible hypotheses about how *Gambusia* affects RFBE (Kerezsy and Fensham 2013). We used the occupancy model to test seven different hypotheses about how covariates affect the probabilities of colonization and local extinction of both *Gambusia* and RFBE.

We used published data (Fairfax et al. 2007, Kerezsy and Fensham 2013) together with the most recent data collected from the site to test a range of hypotheses about the factors predicting occupancies of both RFBE and *Gambusia* using generalized linear occupancy modeling. In all hypotheses covariates were species-specific. The seven hypotheses about habitat dynamics and species interactions are:

- *Hypothesis 1:* Gambusia have a higher probability of colonizing springs that are further south, due to lower elevation and closer proximity to the source of invasion.
- *Hypothesis 2:* Colonization probability for both species depends on spring area, as larger springs represent larger targets for colonizers and are therefore more likely to receive colonists, increasing the likelihood of successful colonization.
- *Hypothesis 3:* Local extinction probability for both species depends on spring area, as larger springs are less likely to dry out and also contain more individuals, reducing the likelihood of local extinction.
- *Hypothesis 4:* Colonization and local extinction probabilities for both species depend on spring area (a combination of hypotheses 2 and 3).
- *Hypothesis 5:* As average inter-patch distance increases, springs are more isolated, which decreases the probability of colonization.
- *Hypothesis 6:* Spring complexes differ in some unspecified way, and therefore springs from different complexes have different probabilities of transition.
- *Hypothesis 7:* Springs at higher elevation are connected less frequently by floods, and therefore have lower probabilities of colonization.

We employed a two-species, multi-season occupancy model (Richmond et al. 2010, Miller et al. 2012) to model detection probabilities, occupancy, and transition dynamics, including the influences of the 4 covariates identified by the hypotheses (i.e., southness, spring area, average inter-patch distance, and elevation). This model is parameterized assuming that one species dominates the other. In our case, data suggests that the presence of *Gambusia* negatively influences RFBE (Kerezsy and Fensham 2013), so we assumed that *Gambusia* was the dominant competitor. Model parameters include the probabilities of detection (p), occupancy (Ψ), local extinction (ε) and colonization (γ) parameters for both species (Richmond et al. 2010). The model also finds parameters for the probabilities that RFBE is present and is detected, conditional on the presence and detection of *Gambusia*. We denote conditional probabilities with a two-species subscript, where the first subscript denotes the subject species; capital letters in the subscript denote present species; and lowercase letters denote absent species. For example, $\gamma_{A,B}$, denotes the probability of colonization by species A, given species B is present. Alternatively, $\varepsilon_{A,b}$ denotes the probability of local extinction of species A, given that species b is absent.

All models were implemented using program PRESENCE version 6.4 (Hines 2006). Competing models were evaluated using the Akaike Information Criterion corrected for small sample sizes (AIC_c) (Burnham and Anderson 2002). Because the set of candidate models for a conditional two-species parameterization including covariates is potentially very large, we used a two-step process for model selection (Richmond et al. 2010).

In the first step, we selected the best detection models for each species by evaluating alternative model structures with and without a covariate (12 candidate models tested), assuming our best understanding of structure and covariates affecting the transition and occupancy parameters. For these models we assumed that colonization and local extinction were site-dependent (based on site area), and that initial occupancy was non-conditional ($\Psi(.)$). We further assumed that the probability of colonization and local extinction of *Gambusia* were not affected by the presence of RFBE (i.e., $\gamma_{\mathrm{G}} = \gamma_{\mathrm{G,RF}}$ and $\varepsilon_{\mathrm{G}} = \varepsilon_{\mathrm{G,RF}}$). Detection probabilities were allowed to vary by spring complex (E, NE, NW, SE or SW). We also tested whether detection of either *Gambusia* or RFBE depended on the presence of the other species.

After selecting the best structure for the detection model, we developed and tested a set of models of transition parameters based on the identified hypotheses about transition dynamics. With four covariates, the number of models to be tested was large even after selecting the best detection model. To reduce the number of models, we made the following simplifying assumptions:

1. The probabilities of colonization and local extinction of either species were determined by the occupancy of the other species in the current season, and were not affected by the occupancy of the species in the season before (i.e., $\gamma_{\mathrm{G(t),RF|G(t-1)}} = \gamma_{\mathrm{G(t),RF|g(t-1)}} = \gamma_{\mathrm{G,RF}}$, and $\gamma_{\mathrm{G(t),rf|G(t-1)}} = \gamma_{\mathrm{G(t),rf|g(t-1)}} = \gamma_{\mathrm{G,rf}}$; $\varepsilon_{\mathrm{G(t),RF|G(t-1)}} = \varepsilon_{\mathrm{G(t),RF|g(t-1)}} = \varepsilon_{\mathrm{G,RF}}$, and $\varepsilon_{\mathrm{G(t),rf|G(t-1)}} = \varepsilon_{\mathrm{G(t),rf|g(t-1)}} = \varepsilon_{\mathrm{G,rf}}$).
2. The factors affecting colonization and local extinction affected both species in the same way (to different extents). We did not consider models in which factors affect only one species because it would require we test an impractical number of models.
3. All covariates were additive effects only and we did not account for interactions.
4. In our base model used to fit the detection probability, we assumed that *Gambusia* excluded RFBE, and RFBE did not affect *Gambusia* colonization or local extinction. The transition parameters for *Gambusia* did not depend on the occupancy state of RFBE (i.e., $\gamma_{\mathrm{G,RF}} = \gamma_{\mathrm{G,rf}} = \gamma_{\mathrm{G}}$, and $\varepsilon_{\mathrm{G,RF}} = \varepsilon_{\mathrm{G,rf}} = \varepsilon_{\mathrm{G}}$). We tested this assumption without covariates using the best-fit detectability model (see Appendix A). Contrary to our initial expectation, the data suggested that the presence of RFBE affected *Gambusia*. When fitting transition dynamics models, we assumed that the transition parameters for *Gambusia* were affected by the presence of RFBE.

Under these assumptions, we then tested each of the seven hypotheses in isolation and removed the least supported hypotheses (see Appendix A for details). All 16 model combinations of the remaining four hypotheses were then tested and the best model was selected using the $\mathrm{AIC_c}$ value. Determining sample size for occupancy models remains a topic of debate (MacKenzie et al. 2012). An upper limit is the total number of completed surveys (44 sites × 35 timesteps × 3 repeats = 4620) and a lower limit is the number of surveys without accounting for repeat visits (44 sites × 35 timesteps = 1540) (MacKenzie et al. 2012). We used a sample size of 3080 surveys, which is the midpoint between these two values.

Competition between invasive and endemic species

We used estimates from the top ranked model to determine the species interaction factor, or SIF (MacKenzie et al. 2004, MacKenzie et al. 2006, Richmond et al. 2010). The SIF is a ratio that estimates whether species are likely to co-occur compared to a hypothesis of independence. If the species occur independently, the SIF is equal to 1. SIF values less than one suggest that the species are less likely to co-occur together than expected if the species were independent, while SIF values greater than 1 suggest that the species are more likely to co-occur. Given the apparent competition between RFBE and *Gambusia*, we hypothesize that the SIF should be less than 1. The species interaction factor is given by (Richmond et al. 2010):

$$\frac{\Psi_G \Psi_{RF,G}}{\Psi_G(\Psi_G \Psi_{RF,G} + (1 - \Psi_G)\Psi_{RF,g})}.$$

In our model, the objective is to understand the transition dynamics of the species, and the initial occupancy was not the focus of any hypothesis and was not modeled with any covariates. To further understand the effect of *Gambusia* on RFBE, we used the colonization and local extinction parameters to estimate the reduction in RFBE presence probability caused by the presence of *Gambusia*.

The transition parameters allow us to estimate the probability that the RFBE population in a spring occupied by RFBE survives until the next timestep, in both the presence and absence of *Gambusia*. If RFBE are present, then the probability that they remain present depends on two events. Either (1) RBFE don't go extinct; or (2) RFBE go extinct, but the spring is re-colonized by RFBE in the same time step. These probabilities differ in the presence and absence of *Gambusia*:

A. In the absence of *Gambusia*, RFBE remain present with probability $(1 - \varepsilon_{\mathrm{RF,g}}) + \varepsilon_{\mathrm{RF,g}}\gamma_{\mathrm{RF,g}}$.
B. In the presence of *Gambusia*, RFBE remain present with probability $(1 - \varepsilon_{\mathrm{RF,G}}) + \varepsilon_{\mathrm{RF,G}}\gamma_{\mathrm{RF,G}}$.

If $A > B$, then RFBE are more likely to remain present in the absence of *Gambusia*. The difference between A and B gives us a measure of the reduction in the probability of presence of RFBE caused by the co-occurrence of *Gambusia* in each spring considered.

Spring extinction probabilities

Although RFBE data have been collected for 23 years, relatively few unassisted transitions have been observed between occupancy states, so parameterization of models with many parameters is unlikely to provide robust estimates. We fit a patch-based occupancy model that treated each spring independently. The two-species occupancy model that we applied can be used to predict the local extinction probabilities of fish from individual springs, but not the long-term dynamics of fish from all springs, as the correlation between springs is unknown.

We used the stationary state distribution (Norris 2008) of each spring to examine the equilibrium dynamics of the two species in the reserve, and computed the local extinction probabilities of both species in each spring (see Appendix B). The stationary local extinction probabilities may be used to identify the most promising springs for management action—springs with a high local extinction probability for *Gambusia* are likely good management targets for *Gambusia* removal, and springs with low local extinction probability for RFBE may be good targets for RFBE reintroduction. Model estimates are presented ± 1 SE unless otherwise specified.

RESULTS

The model for detection with the lowest $\mathrm{AIC_c}$ was independent of spring complex and suggested that the probability of detection of each species was different if one species was present, but was equivalent if both species were present (Table 1). While the $\mathrm{AIC_c}$ values for detection differed, the transformed probabilities of detection for the three top-ranked models were all very high (e.g., for the top-ranked model; $p_{\mathrm{G}} = 0.99 \pm 0.00$, $p_{\mathrm{RF}} = 1.00 \pm 0.00$ and $r = 0.93 \pm 0.0.02$). Consequently, it was likely that the reduction in $\mathrm{AIC_c}$ of the top-ranked model compared to the two next-highest ranked models came from the reduced number of parameters rather than an improved fit to the data. The probability of detection of either species was high, regardless of the occupancy of the other species.

The top ranked model for transition parameters was strongly supported relative to the other models ($\mathrm{AIC_c}$ weight of 0.71, compared to a weight of 0.11 for the second-ranked and more complex model), so this model was selected without applying model averaging (Table 2). For both species, spring area was positively related to colonization (logit $\beta_{\mathrm{area}} = 1.45 \pm 0.47$) and negatively related to local extinction (logit $\beta_{\mathrm{area}} = -0.43 \pm 0.27$). The influence of elevation on colonization probability varied by species. The probability of colonization by *Gambusia* decreased with elevation of the spring (logit $\beta_{\mathrm{elevation}}$ for *Gambusia* $= -0.42 \pm 0.26$), while the probability of colonization by RFBE increased with elevation (logit $\beta_{\mathrm{elevation}}$ for RFBE $= 1.14 \pm 0.43$). The relative proportion of explained variance in colonization probability explained by spring area for different parameters ranged from 6% to 10% for RFBE and from 14% to 21% for *Gambusia* (Table 3). Elevation accounted for a similar proportion of the explained variance in colonization probability (11–20% for RFBE and 11–16% for *Gambusia*). Area explained 11–14% of the variance for RFBE and 6–8% for *Gambusia*.

Gambusia occupied about half the sites ($\Psi_{\mathrm{G}} = 0.52 \pm 0.12$). The occupancy probability of RFBE was lower at springs with *Gambusia* present ($\Psi_{\mathrm{RF,G}} = 0.45 \pm 0.20$) compared with those with *Gambusia* absent ($\Psi_{\mathrm{RF,g}} = 0.66 \pm 0.21$). While colonization between springs was possible for

Table 1. Rankings of models examining detection probabilities for *Gambusia* and RFBE. The best fitting model was selected based on the Akaike's Information Criterion modified for small sample size (AIC_c), the difference in AIC_c (ΔAIC_c), AIC_c model weights, and model likelihood, given the number of parameters (K). All models assume that (1) colonization and local extinction depend on site area, (2) that initial occupancy was non-conditional ($\Psi(.)$); and (3) that the probability of colonization and local extinction of *Gambusia* are not affected by the presence of RFBEs (i.e., $\gamma_G = \gamma_{G,RF}$ and $\varepsilon_G = \varepsilon_{G,RF}$).

Model name	Model description	AIC_c	ΔAIC_c	AIC_c weight	Model likelihood	K
$p_G(.)$, $p_{RF}(.)$, $r_G(.) = r_{RF,G}(.) = r_{RF,g}(.)$	Probability of detection different if one species present, equivalent if there are two species	539.21	0	0.59	1	14
$p_G(.)$ $p_{RF}(.)$ $r_G(.)$,$r_{RF,G}(.) = r_{RF,g}(.)$	Species dependent, but RFBE detection independent of detection of *Gambusia*	541.04	1.83	0.24	0.40	15
$p_G(.)p_{RF}(.)r_G(.)r_{RF,G}(.)r_{RF,g}(.)$	Non-conditional detection model	541.96	2.75	0.15	0.25	16
$p_G(.) = p_{RF}(.)$, $r_G(.) = r_{RF,G}(.) = r_{RF,g}(.)$	Probability of detection depends on presence/absence of one species	547.06	7.85	0.01	0.02	13
$p_G(\text{complex}) = p_{RF}(\text{complex})$, $r_G(\text{complex}) = r_{RF,G}(\text{complex}) = r_{RF,g}(\text{complex})$	Probability of detection depends on presence/absence of one species and complex	548.94	9.73	0.00	0.01	15
$p_G(\text{complex})$, $p_{RF}(\text{complex})$, $r_G(\text{complex}) = r_{RF,G}(\text{complex}) = r_{RF,g}(\text{complex})$	Probability of detection different if one species present, equivalent if there are two species, detection parameters depend on complex	552.98	13.77	0.00	0.00	17
$p_G(\text{complex})p_{RF}(\text{complex})r_G(\text{complex})$ $r_{RF,G}(\text{complex})r_{RF,g}(\text{complex})$	Complex-dependent detection	555.01	15.8	0.00	0.00	21
$p_G(\text{complex})$ $p_{RF}(\text{complex})$ $r_G(\text{complex})$,$r_{RF,G}(\text{complex}) = r_{RF,g}(\text{complex})$	Species and complex dependent, but RF detection independent of detection of *Gambusia*	557.47	18.26	0.00	0.00	19
$p_G(.) = p_{RF}(.) = r_G(.) = r_{RF,G}(.) = r_{RF,g}(.)$	Species independent detection	563.47	24.26	0	0	12
$p_G(.) = r_G(.)$, $p_{RF}(.) = r_{RF,G}(.) = r_{RF,g}(.)$	Species dependent, occupancy of other species independent	564.8	25.59	0	0	13
Complex	Complex dependent, species independent	564.99	25.78	0	0	13
$p_G(\text{complex}) = r_G(\text{complex})$, $p_{RF}(\text{complex}) = r_{RF,G}(\text{complex}) = r_{RF,g}(\text{complex})$	Complex and species dependent, occupancy of other species independent	567.94	28.73	0	0	15

Note: Initial (non-conditional model) used when testing detection models: Occupancy: $\Psi_G(.)$, $\Psi_{RF,G}(.)$,$\Psi_{RF,g}(.)$; Colonization: $\gamma_G(\text{area})$, $\gamma_{RF,G}(\text{area})$, $\gamma_{RF,g}(\text{area})$; Local extinction: $\varepsilon_G(\text{area})$, $\varepsilon_{RF,G}(\text{area})$, $\varepsilon_{RF,g}(\text{area})$.

Gambusia, especially in the absence of RFBE ($\gamma_{G,RF} = 0.01 \pm 0.01$; $\gamma_{G,rf} = 0.09 \pm 0.03$), colonization by RFBE was negligible ($\gamma_{RF,G} = 0.61 \times 10^{-6} \pm 1.61 \times 10^{-6}$; $\gamma_{RF,g} = 4.00 \times 10^{-3} \pm 5.01 \times 10^{-3}$). Local extinction for both species was rare in the absence of the other fish, but highly likely for RFBE in the presence of *Gambusia* ($\varepsilon_{G,RF} = 0.05 \pm 0.05$; $\varepsilon_{G,rf} = 0.01 \pm 0.01$; $\varepsilon_{RF,G} = 0.19 \pm 0.0.08$; $\varepsilon_{RF,g} = 0.03 \pm 0.01$).

For the best-fitting model, the SIF (Richmond et al. 2010) was 0.83, suggesting that the occupancy of *Gambusia* negatively impacts the occupancy probability of RFBE. In all springs, the one-timestep probability of RFBE persistence was reduced in the presence of *Gambusia* with an average reduction of 7.97% ± 2.68% (Fig. 2).

The stationary local extinction probability in each spring was greater for RFBE than for *Gambusia* in all springs except NW30, NW70, and NW90s (Fig. 3). RFBE stationary local extinction probability ranged from 0.29 to 0.99, with a mean of 0.85 ± 0.20 (1 SD). RFBE stationary local extinction probabilities were >0.9 for all springs in the NE and SE complexes, but in the other complexes there were springs where local extinction probability was lower. For *Gambusia*, the stationary local extinction probability ranged from 0.00 to 0.84, with a mean of

Table 2. Rankings of models examining colonization and local extinction probabilities for *Gambusia* and RFBE. We present only the results for the top four ranked hypotheses—other tests can be found in Appendix A. The best fitting model was selected based on the Akaike's Information Criterion modified for sample size (AIC$_c$), the difference in AIC$_c$, AIC$_c$ model weights, and model likelihood, given the number of parameters (K). Occupancy was modeled with no structure ($\Psi(.)$). Detection probabilities were modeled using the best model from Table 1. Hypotheses with aserisks are those for which there was a single parameter for both species, rather than a separate influence of the covariate on each species.

Hypotheses	Model	AIC$_c$	ΔAIC$_c$	AIC$_c$ weight	Model likelihood	K
4*, 7	γ(area,elev)ε(area)	521.50	0	0.71	1.00	18
4*, 7, 1	γ (area,elev,sth)ε(area)	525.31	3.81	0.11	0.15	20
4*, 7, 5	γ(area,elev,dist)ε(area)	525.34	3.84	0.10	0.15	20
4*, 1	γ(area,sth)ε(area)	527.04	5.54	0.04	0.06	18
4*, 7, 1, 5	γ(area,elev,sth,dist)ε(area)	529.30	7.80	0.01	0.02	22
4*, 5	γ(area,dist)ε(area)	530.56	9.06	0.01	0.01	18
4*, 1, 5	γ(area,sth,dist)ε(area)	530.98	9.48	0.01	0.01	20
4*	γ(area)ε(area)	531.91	10.41	0.00	0.01	16
7	γ(elev)ε(.)	533.25	11.75	0.00	0.00	16
7, 5	γ(elev,dist)ε(.)	535.80	14.3	0.00	0.00	18
7, 1	γ(elev,sth)ε(.)	536.09	14.59	0.00	0.00	18
1	γ(sth)ε(.)	537.46	15.96	0.00	0.00	16
7, 1, 5	γ(elev,sth,dist)ε(.)	539.79	18.29	0.00	0.00	20
5	γ(dist)ε(.)	539.98	18.48	0.00	0.00	16
1, 5	γ(sth,dist)ε(.)	541.04	19.54	0.00	0.00	18
None	γ(.)ε(.)	549.05	27.55	0.00	0.00	14

0.34 ± 0.22 (1 SD).

Of the sites known to be occupied by RFBE, the springs with the lowest stationary probabilities of local extinction for RFBE were in the NW complex (NW30, NW70 and NW90s). These springs had local extinction probabilities that were less than 50%. The other four occupied sites in the east complex (E501, E504, E518 and E524) had high stationary probabilities of local extinction (>0.7) (Fig. 3).

DISCUSSION

Competition between species was clearly identified by our model, with all springs showing a reduction in RFBE persistence in the presence of *Gambusia*. The suppression effect is substantial considering the high stationary probabilities of local extinction of RFBE in most patches at Edgbaston (on average the patch local extinction probability was 0.84). RFBE local extinction stationary probability was lowest in three patches (NW30, NW70 and NW90s), all of which are currently occupied with RFBE. The springs occupied by RFBE in the east complex all have high risks of local extinction in the stationary distribution. Using the stationary distribution as a metric suggests that the probability of persistence of RFBE in any spring other than those already occupied in the NW complex is low. The probability of persistence of *Gambusia* in all but four springs is much higher than the probability of persistence of RFBE. While the population as a whole may survive longer than individual patches, it is likely that in the long term, RFBE will become extinct in all but three springs, and *Gambusia* will continue to occupy the complex

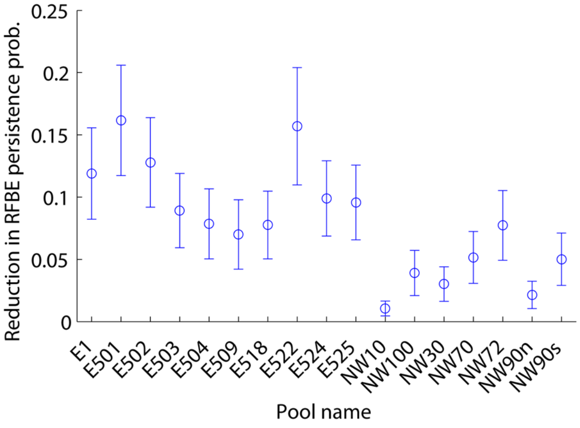

Fig. 2. Reduction in RFBE persistence probability in the presence of *Gambusia*. Reductions in persistence probabilities are shown for the complexes currently occupied by the RFBE (E and NW spring complexes). Error bars depict one standard error.

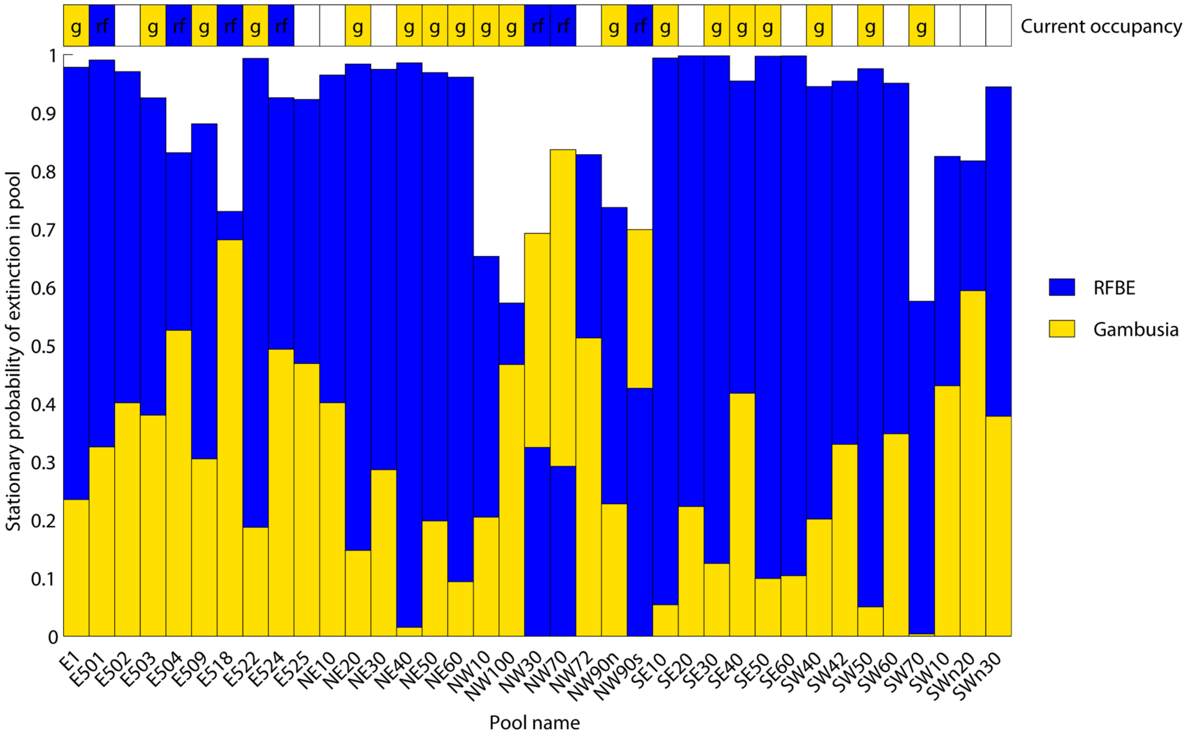

Fig. 3. Stationary probabilities of local extinction of RBFE (blue bars) and *Gambusia* (yellow bars) in each spring at Edgbaston reserve. In many springs, the RFBE has a stationary probability of local extinction that is close to 1. *Gambusia* has a lower probability of local extinction than RFBE in all springs except NW30, NW70, and NW90s. The species known to occupy each spring during the latest survey are indicated in the strip above the bar chart; blank sites in the strip indicate sites that were unoccupied by both species.

unless management intervention can alter the transition dynamics. These results suggest that the continuation of management efforts to improve the probability of persistence of the RFBE will be necessary to prevent global extinction.

Protecting the RFBE requires understanding the factors affecting local extinction and colonization. Of the seven hypotheses tested in this study, we found strongest support for the hypotheses that elevation and spring area influence colonization, and that spring area influences patch extinction probability. This finding is consistent with the existing leading hypothesis about the dispersal of *Gambusia*, which predicts that colonization occurs during episodic flood events. Higher elevation springs are subjected to fewer floods large enough to connect them, and therefore to lower propagation pressure from *Gambusia* (Fairfax et al. 2007). This result is also supported by the literature on *Gambusia* dispersal, which suggests *Gambusia* preferentially disperse downstream during floods (Chapman and Kramer 1991, Congdon 1995, Chapman and Warburton 2006). The current distribution of RFBE provides additional support for the hypothesis, as the springs where RFBE is extant are in the higher elevation areas of Edgbaston (although the elevation difference between the highest and lowest springs is only 5.7 m over a horizontal distance of 5.6 km).

While identifying support for the elevation hypothesis is appealing and will be useful for managers, the effect of elevation accounts for only 10–20% of the variance depending on the spring. This effect was comparable to the spring area, and considerably smaller than the variance explained by the intercept term. Spatial heterogeneity among the springs accounted for considerably more variation than elevation. Managers should not base their relocation decisions solely on selecting high-elevation springs. If a high-elevation spring has other characteristics that leads to low quality, RFBE may still have a high probability of local extinction. For example, a high elevation spring that is connected by a drainage channel is more vulnerable to *Gambusia* colonization than a lower elevation spring occurring on a terrace that is isolated from drainage channels (Alemadi and Jenkins 2008). Further, there are aeolian deposits that form barriers to overland flow across the floodplain which may reduce the colonization of *Gambusia* (Alemadi and Jenkins 2008). The manipulation of these barriers, or the establishment of similar barriers for the best RFBE refuges, could decrease the local extinction probability for RFBE by reducing the probability of colonization of *Gambusia* during high floods.

Given the support for the elevation hypothesis, it would be useful to understand the flood frequencies that cause the springs to connect. This covariate would provide an upper estimate of the frequency that each spring is subject to *Gambusia* invasion given spring elevation. We took preliminary steps to understand this covariate, but the low differences in elevations between the springs and the large areas of non-channel flow combined with low-resolution elevation models and an ungauged basin caused us to abandon this approach. While the project was beyond our current capabilities, this approach should be possible given the right expertise in hydrological modeling.

The relatively large amount of variance explained by the intercept term suggests that spatial heterogeneity is a major factor. While our model is able to determine the transition parameters for a spring and therefore aid with selection of springs for management, the intercept term does not provide much explanation of why springs differ. Factors such as spring and groundwater chemistry, temperature, depth and water quality, the impact of herbivore grazing on springs and weed colonization are all factors hypothesized to contribute to RFBE occurrence (Fairfax et al. 2007). We could not examine these factors because there is no published data on these factors for all springs. It would be valuable to explore additional covariates to better understand other factors driving RFBE and *Gambusia* occurrence.

Table 3. Relative mean contributions (%) of explained variance from covariates for transition parameters, averaged over all Edgbaston springs.

Parameter	Intercept (%)	Area (%)	Elevation (%)
$\gamma_{G,RF}$	75	14	11
$\gamma_{G,rf}$	63	21	16
$\gamma_{RF,G}$	83	6	11
$\gamma_{RF,g}$	70	10	20
$\varepsilon_{G,RF}$	92	8	…
$\varepsilon_{G,rf}$	94	6	…
$\varepsilon_{RF,G}$	86	14	…
$\varepsilon_{RF,g}$	93	7	…

Southness and average inter-patch distance both featured amongst the top three models, suggesting that there could be some merit to these hypotheses, but these models had relatively low weight compared to the elevation hypothesis. Studies have found that *Gambusia* dispersal is reduced with increased inter-patch distance, but other factors were of similar importance (Congdon 1995, Chapman and Warburton 2006). In this system southness is quite strongly correlated with elevation (correlation coefficient 0.62; Appendix C) as elevation at Edgbaston increases from south to north, so it is likely that elevation and southness will explain similar components of the variance.

Neither average inter-patch distance nor spring complex were selected in the top model for colonization or local extinction. This could be evidence of a system where most springs are connected by the same flood events, so that all springs can be colonized with equal likelihood regardless of the distance between them. The relatively flat topography of most of Edgbaston supports this hypothesis (although the support for the elevation hypothesis suggests that there must be some differentiation by elevation, if not by distance). If the spring complex is not a key factor in prediction, this further supports the idea that the springs are highly spatially heterogeneous. Spring depth is a possible driver of habitat choice and/or persistence that was not included in this modeling (Chapman and Warburton 2006). RFBE can live in extremely shallow water (<2 cm) for their entire life cycle but it is likely that adult *Gambusia* require slightly deeper habitat (Fairfax et al. 2007). However, shallow springs tend to be small, and these are vulnerable to intermittent drying out during extended periods of high temperatures and evaporation.

It will be important to secure some springs of at least medium size as RFBE habitat.

Detection probabilities for both species were very high, both when a single species was present and when both species were present. While few published estimates of detection probabilities for freshwater fish exist, at least one other study found low rates of false detection when fish are confined to distinct pools (Broadhurst et al. 2012). Detection probability did not vary by spring complex, probably because detection estimates were so high for all spring complexes. Given the small size and shallow depth of most of the springs, this result is not surprising. However this may be positive for management, because it means that failing to observe a species is likely to mean that the species is truly not present (Chadès et al. 2008). This is most critical for RFBE relocation, as relocating RFBE to a spring where *Gambusia* are present but not detected could reduce the chances of successful RFBE establishment in the spring. Similarly, declaring a spring treated with rotenone to be clear of *Gambusia* would be difficult if detection probability was low (Cacho et al. 2006, Regan et al. 2006).

Our model provides some answers for managers seeking to control *Gambusia* and conserve RFBE. However more transition data would improve model estimates. In our current model, the state of neighboring patches is ignored and patches can always be colonized from a 'source' population. Given additional data on transitions, the model parameters could be estimated with a model that includes the occupancy of neighboring patches (Bled et al. 2010, Yackulic et al. 2012, Yackulic et al. 2013). The advantage of a neighborhood-based occupancy model is that it allows estimation of colonization probability based on the existing state of the population. This means that patches can only be colonized if their neighbors are occupied. This approach allows simulation of the whole population over time (as opposed to individual patch dynamics) to gain an estimate of the probability of and time until population extinction (Akçakaya and Ginzburg 1991, Palmqvist and Lundberg 1998). The state-based neighborhood approach also allows for optimal management strategies to be developed (Mangel and Clark 1988, Possingham 1996, Nicol et al. 2010). Although neighborhood models provide greater inference, our model is a useful contribution because it is able to quantify the suppression effect of *Gambusia* on RFBE, as well as determine the best individual patches for management attention.

Gambusia negatively affect populations of similarly sized native fish that use similar habitat, particularly in North American deserts (Meffe and Snelson 1989, Pyke 2008). Species restricted to spring systems seem particularly vulnerable (Unmack and Minckley 2008). In other studies involving freshwater fish that rely on a few discrete desert springs in a similar way to RFBE, *Gambusia affinis* have been observed to prey directly on the juveniles and also negatively affect individuals of all size levels through aggressive behavior (Meffe et al. 1983, Ayala et al. 2007). Competition with *Gambusia* forces weaker competitors to use parts of the springs that are undesirable for *Gambusia* (Ayala et al. 2007). Similar aggressive behavior by *Gambusia* and spatial stratification of the two species has been observed for the RBFE (Fairfax et al. 2007). Our study quantified the strength of these competitive interactions between *Gambusia* and RFBE, providing a first estimate of the negative impact imposed by *Gambusia* on the unique biodiversity of spring species worldwide.

Competition and invasion dynamics are highly complex, yet conservation managers need to quantify these processes to act effectively. As expected, colonization and local extinction of RFBE is strongly affected by *Gambusia* occupancy dynamics. Managers can use this study to refine conservation measures and increase the probability of persistence for RFBE. Although *Gambusia* appears to have a competitive advantage, we identified sites where RFBE have a higher potential to persist compared with *Gambusia* (NW30, NW70 and NW90s). Springs with the least probability of *Gambusia* colonization (NW70, E518, E504, and NW90s) have high elevations or other barriers to dispersal (the five highest elevation springs are in the NW complex, followed by E518, SWn20 and E504). Springs with these characteristics may be the best focus for complete *Gambusia* removal and RFBE reintroductions, as well as management measures to prevent *Gambusia* recolonization. Although conservation planning for a critically endangered species such as the RFBE is a difficult task, understanding the occupancy dynamics of the system will allow managers to proceed with conservation measures using a more focused and informed approach.

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SUPPLEMENTAL MATERIAL

APPENDIX A

SELECTING COLONIZATION AND EXTINCTION MODELS

To select the best transition model, we tested models using four covariates: pool area, average inter-patch distance, southness, pool complex and elevation. Because of the large number of potential models, we tested specific hypotheses rather than attempting to test all combinations. We also made the following simplifying assumptions:

1. The probability of colonization of either species is determined by the current occupancy of the other species, and is not affected by the occupancy of the species in the season before (i.e., $\gamma_{G(t),RF|G(t-1)} = \gamma_{G(t),RF|g(t-1)} = \gamma_{G,RF}$, and $\gamma_{G(t),rf|G(t-1)} = \gamma_{G(t),rf|g(t-1)} = \gamma_{G,rf}$).
2. Similarly, the probability of extinction of either species is determined by the current occupancy of the other species, and is not affected by the occupancy of the species in the season before (i.e., $\varepsilon_{G(t),RF|G(t-1)} = \varepsilon_{G(t),RF|g(t-1)} = \varepsilon_{G,RF}$, and $\varepsilon_{G(t),rf|G(t-1)} = \varepsilon_{G(t),rf|g(t-1)} = \varepsilon_{G,rf}$).
3. The factors affecting colonization and extinction affect both species in the same way (to different extents). We do not test models where factors affect only one species. Although this may potentially reduce the number of parameters in the model and improve the fit, it also greatly increases the number of models that we need to test, making model testing vastly more difficult.
4. We assume all covariates are additive effects only and do not account for interactions.

In our base model used to fit the detection probability, we assumed that Gambusia excluded RFBE, and RFBE did not affect Gambusia migration or extinction. The transition parameters for Gambusia did not depend on the occupancy state of RFBE (i.e., $\gamma_{G,RF} = \gamma_{G,rf} = \gamma_G$, and $\varepsilon_{G,RF} = \varepsilon_{G,rf} = \varepsilon_G$). We tested this assumption without covariates using the best-fit detectability model. The results of the two fits are in Table A1. Contrary to our initial expectation, the data suggests that the presence of RFBE affects Gambusia. When fitting model covariates (see below), we assume that the transition parameters for Gambusia are affected by the presence of RFBE.

We first define a set of model hypotheses about the influences of covariates:

- Hypothesis 1: Gambusia have a higher probability of colonizing pools that are further south, due to lower elevation and closer proximity to the source of invasion: $\gamma_{G,RF}$(southness), $\gamma_{G,rf}$(southness).
- Hypothesis 2: Colonization probability for both species depends on pool area, as larger

Table A1. Comparison of a model that assumes transition probabilities for Gambusia are affected by the presence of RFBE with a model that assumes that transition probabilities for Gambusia are not affected by the presence of RFBE.

Model	AIC$_c$	ΔAIC$_c$
Ψ_G, Ψ_{RFG}, Ψ_{RFg},p_G,p_{RF},r,γ_{GRF}(area), γ_{Grf}(area), γ_{RFG}(area), γ_{RFg}(area),ε_{GRF}(area), ε_{Grf}(area), ε_{RFG}(area), ε_{RFg}(area)	531.91	0
Ψ_G, Ψ_{RFG}, Ψ_{RFg},p_G,p_{RF},r, γ_G(area), γ_{RFG}(area), γ_{RFg}(area), ε_G(area), ε_{RFG}(area), ε_{RFg}(area)	539.21	7.30

pools contain more individuals, increasing the likelihood of successful colonization: γ_G(area), γ_{RF}(area).

- Hypothesis 3: Extinction probability for both species depends on pool area, as larger pools are less likely to dry out and also contain more individuals, reducing the likelihood of extinction: ε_G(area), ε_{RF}(area).
- Hypothesis 4: Both colonization and extinction probability for both species depends on pool area (a combination of hypotheses 2 and 3): γ_G(area), γ_{RF}(area), ε_G(area), ε_{RF}(area).
- Hypothesis 5: Greater average inter-patch distances mean that pools are more isolated, which means that the probability of colonization for these pools is decreased: γ_G(inter-patch distance), γ_{RF}(inter-patch distance).
- Hypothesis 6: Pool complexes differ in some unspecified way, and therefore pools from different complexes have different probabilities of transition: γ_G(complex), γ_{RF}(complex), ε_G(complex), ε_{RF}(complex).
- Hypothesis 7: Pools at higher elevation are connected less frequently by floods, and therefore have lower probabilities of colonization: γ_G(elevation), γ_{RF}(elevation).

Testing all seven hypotheses would require evaluating $2^7 = 128$ models, which is a formidable task. We first test each hypothesis using our best model for detectability and test each hypothesis in isolation, with the hope of removing the least plausible hypotheses after the first set of tests. The results of this first-pass of fitting are in Table A2.

Based on Table A2, there is very little support for a model with no covariates. There is also little support for the influence of pool complex (hypothesis 6). Because hypothesis 4 is a combination of hypotheses 2 and 3, and the combined effect has lower AIC$_c$ than either individual covariate, we reject hypotheses 2 and 3 in favor of hypothesis 4. Our next step is to remove hypotheses 2, 3 and 6 from the model set, as well as remove the least-supported model from each hypothesis (i.e., select the best model from either

Table A2. Rankings of models assuming individual covariates. The best fitting model was selected based on the Akaike's Information Criterion modified for sample size (AIC$_c$), the difference in AIC$_c$, AIC$_c$ model weights, and model likelihood, given the number of parameters (K). Asterisked values imply that there is a single parameter for both species, rather than a separate influence of the covariate on each species.

Hypothesis	AIC$_c$	ΔAIC$_c$	AIC$_c$ weight	Model likelihood	K
4*	531.91	0	0.36	1	16
4	532.81	0.9	0.24	0.64	18
7	533.25	1.34	0.19	0.51	16
2*	534.55	2.64	0.10	0.27	15
2	536.11	4.2	0.04	0.12	16
3*	537.28	5.37	0.02	0.07	15
1	537.46	5.55	0.02	0.06	16
1*	539.47	7.56	0.01	0.02	15
5	539.98	8.07	0.01	0.02	16
3	540.61	8.7	0.00	0.01	16
5*	542.59	10.68	0.00	0.00	15
7*	542.95	11.04	0.00	0.00	15
Baseline (no covariates)	549.05	17.14	0.00	0.00	14
6*	578.12	46.21	0.00	0	16
6	674.64	142.73	0.00	0	18

Table A3. Rankings of models assuming individual covariates, with models for hypotheses 2, 3, 6 and the baseline model removed. The best fitting model was selected based on the Akaike's Information Criterion modified for sample size (AIC_c), the difference in AIC_c, AIC_c model weights, and model likelihood, given the number of parameters (K). Asterisked values imply that there is a single parameter for both species, rather than a separate influence of the covariate on each species.

Hypothesis	AIC_c	ΔAIC_c	AIC_c weight	Model likelihood	K
4*	531.91	0	0.63	1	16
7	533.25	1.34	0.32	0.51	16
1	537.46	5.55	0.04	0.06	16
5	539.98	8.07	0.01	0.02	16

Table A4. Rankings of all combinations of most likely individual covariates. The best fitting model was selected based on the Akaike's Information Criterion modified for sample size (AIC_c), the difference in AIC_c, AIC_c model weights, and model likelihood, given the number of parameters (K). Asterisked values imply that there is a single parameter for both species, rather than a separate influence of the covariate on each species.

Hypotheses	Model	AIC_c	ΔAIC_c	AIC_c weight	Model likelihood	K
4*, 7	γ(area,elev)ε(area)	521.50	0	0.71	1.00	18
4*, 7, 1	γ (area,elev,sth)ε(area)	525.31	3.81	0.11	0.15	20
4*, 7, 5	γ(area,elev,dist)ε(area)	525.34	3.84	0.10	0.15	20
4*, 1	γ(area,sth)ε(area)	527.04	5.54	0.04	0.06	18
4*, 7, 1, 5	γ(area,elev,sth,dist)ε(area)	529.30	7.80	0.01	0.02	22
4*, 5	γ(area,dist)ε(area)	530.56	9.06	0.01	0.01	18
4*, 1, 5	γ(area,sth,dist)ε(area)	530.98	9.48	0.01	0.01	20
4*	γ(area)ε(area)	531.91	10.41	0.00	0.01	16
7	γ(elev)ε(.)	533.25	11.75	0.00	0.00	16
7, 5	γ(elev,dist)ε(.)	535.80	14.30	0.00	0.00	18
7, 1	γ(elev,sth)ε(.)	536.09	14.59	0.00	0.00	18
1	γ(sth)ε(.)	537.46	15.96	0.00	0.00	16
7, 1, 5	γ(elev,sth,dist)ε(.)	539.79	18.29	0.00	0.00	20
5	γ(dist)ε(.)	539.98	18.48	0.00	0.00	16
1, 5	γ(sth,dist)ε(.)	541.04	19.54	0.00	0.00	18
None	γ(.)ε(.)	549.05	27.55	0.00	0.00	14

a single parameter for both species or a parameter for each species). After these alterations we are left with the following models and AIC_c weights (Table A3).

Based on this preliminary testing, we are left with hypotheses 4* (γ and ε depend on pool area, species-independent), 7 (γ depends on elevation, species-dependent), 1 (γ depends on southness, species-dependent), and 5 (γ depends on interpatch distance, species-dependent).

Testing all combinations of these hypotheses leaves us with 16 models (Table A4).

The top-ranked model suggests that colonization probability is a function of area (species independent) and elevation (species dependent). Extinction probability is a function of area (species independent). The model is strongly supported relative to the other models (AIC_c weight of 0.71, compared to the next-highest weighted model which has weight 0.11), so we

Table A5. Untransformed parameter estimates for the top ranked (i.e., lowest AIC_c) model. Estimates can be converted back to the original measurement scale using the logit transformation: $e^{\theta}/(1 + e^{\theta})$.

Parameter	Untransformed (θ)
Ψ_G	0.094
$\Psi_{RF,G}$	−0.193
$\Psi_{RF,g}(.)$	0.647
p_G (.)	5.576
$P_{RF}(.)$	57.922
r(.)	2.553
$\gamma_{G,RF}$(area,elev)	$-4.211 + 1.454 \times$ ZArea $- 0.418 \times$ (Elev-280m)
$\gamma_{G,rf}$(area,elev)	$-2.286 + 1.454 \times$ ZArea $- 0.418 \times$ (Elev-280m)
$\gamma_{RF,G}$(area,elev)	$-12.002 + 1.454 \times$ ZArea $+ 1.139 \times$ (Elev-280m)
$\gamma_{RF,g}$(area,elev)	$-5.583 + 1.454 \times$ ZArea $+ 1.139 \times$ (Elev-280m)
$\varepsilon_{G,RF}$(area)	$-2.866 - 0.434 \times$ ZArea
$\varepsilon_{G,rf}$(area)	$-4.322 - 0.434 \times$ ZArea
$\varepsilon_{RF,G}$(area)	$-1.434 - 0.434 \times$ ZArea
$\varepsilon_{RF,g}$(area)	$-3.575 - 0.434 \times$ ZArea

choose to use this model without applying model averaging. This choice also has the advantage of removing two covariates (southness and distance, which feature in the next two highest models) and maintaining a simpler model.

In full, the best model is given in Table A5.

APPENDIX B

SIMULATING THE STATIONARY DISTRIBUTION

The parameters of colonization and extinction define the transition matrix of a Markov chain. We simulate the Markov chain to obtain the probability of extinction of the two fish species over 50 years. We do this by using a random starting occupancy values and running 1000 simulations from each random start point. We then count the number of times the Markov chain reached the absorbing state (extinction) and compute the probability of extinction by dividing the number of chains that reached the absorbing state by 1000.

We also compute the stationary distribution of the system. We do this by running the chain for a 'burn in' period of 1000 timesteps. The results of the initial 'burn in' are discarded. After 1000 timesteps we sample 1000 points and store the distribution of states. The resulting state distribution is the stationary distribution. We check this by re-starting the chain from different values and checking whether the resulting distributions are the same.

APPENDIX C

CORRELATION BETWEEN COVARIATES

We created a correlation matrix to check the degree of collinearity between covariates in the model (Table C1). The highest degree of correlation between variables was between the average inter-patch distance and the southness variable. This negative correlation is not unexpected as springs are clustered to the north of Edgbaston. Southness was also quite strongly positively correlated (0.62) with elevation. Spring complex and average distance were also quite strongly correlated (0.58). We expect that models containing two highly correlated covariates should be penalized in by the AIC_c, which penalizes models that add additional variables without offering a corresponding increase in explanatory power. The covariates selected in the top-ranking model (area and elevation) are weakly correlated (0.13).

Table C1. Correlation matrix for hypothesized model covariates. Covariates that are more strongly related have correlation coefficients closer to 1. Uncorrelated (independent) covariates have correlation coefficients close to 0.

Covariates	Area	Average distance	Southness	Complex	Elevation
Area	1				
Average distance	0.14	1			
Southness	0.00	−0.71	1		
Complex	0.26	0.58	−0.56	1	
Elevation	0.13	−0.38	0.62	−0.06	1

SUPPLEMENT

Data files used to generate occupancy models in the main text (*Ecological Archives* http://dx.doi.org/10.1890/ES14-00412.1.sm).