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LETTER

Can Habitat Management Mitigate Disease Impacts on Threatened Amphibians?

Geoffrey W. Heard[1,*], Michael P. Scroggie[2], David S. L. Ramsey[2], Nick Clemann[2], Jenny A. Hodgson[3], & Chris D. Thomas[4]

[1] School of BioSciences, University of Melbourne, Parkville, VIC 3010, Australia
[2] Department of Environment, Land, Water and Planning, Arthur Rylah Institute for Environmental Research, P.O. Box 137, Heidelberg, VIC 3084, Australia
[3] Department of Evolution, Ecology and Behaviour, University of Liverpool, Liverpool L69 7ZB, UK
[4] Department of Biology, University of York, Heslington, York YO10 5DD, UK

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Correspondence
Geoffrey W. Heard, School of Environmental Sciences, Charles Sturt University, Albury, NSW 2640, Australia.
Tel: +61 2 6051 9160.
E-mail: gheard@csu.edu.au

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*Current Address: School of Environmental Sciences, Charles Sturt University, Albury, NSW 2640, Australia

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All authors helped design the study and interpret the results. GWH completed the modeling and led the writing. All authors reviewed and contributed to drafts.
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Abstract

Chytridiomycosis has decimated amphibian biodiversity. Management options for the disease are currently limited, but habitat manipulation holds promise due to the thermal and physicochemical sensitivities of chytrid fungi. Here, we quantify the extent to which habitat management could reduce metapopulation extinction risk for an Australian frog susceptible to chytridiomycosis. Our modeling revealed that: (1) habitat management is most effective in climates where hosts are already less susceptible to the disease; (2) creating habitat, particularly habitat with refugial properties adverse to the pathogen, may be substantially more effective than manipulating existing habitat; and (3) increasing metapopulation size and connectivity through strategic habitat creation can greatly reduce extinction risk. Controlling chytridiomycosis is a top priority for conserving amphibians. Our study provides impetus for experiments across a range of species and environments to test the capacity of habitat management to mitigate the impacts of this pervasive disease.

Introduction

Solutions to the amphibian disease crisis have been elusive. Chytridiomycosis, caused by the fungus *Batrachochytrium dendrobatidis* (*Bd*), emerged as a major threat to anuran biodiversity late last century (Berger *et al.* 1998). This century, the congener *Batrachochytrium salamandrivorans* (*Bsal*) has been shown to cause chytridiomycosis in urodeles, with potentially devastating effects (Martel *et al.* 2014; Stegen *et al.* 2017). While the overall threat posed by *Bsal* is not yet clear, around 200 species of anurans are now thought to have perished or suffered significant declines due to chytridiomycosis (Skerratt *et al.* 2007; Berger *et al.* 2016).

Encouragingly, some anurans have stabilized or recovered (Newell *et al.* 2013; Phillott *et al.* 2013; Scheele *et al.* 2014a). However, no broadly applicable management options have emerged. Individuals can be cured with antibiotics, while population-level treatments may include removing reservoir hosts, augmenting habitats with probiotics, biocontrol using microcrustaceans, or wetland draining and fungicidal treatment (Woodhams *et al.* 2011; Scheele *et al.* 2014b; Bosch *et al.* 2015).

An alternative for managing the disease is targeting the abiotic frailties of chytrid fungi (Woodhams *et al.* 2011; Scheele *et al.* 2014b). Temperature regimes are a key determinant of the pathogenicity and virulence of chytrids (Andre *et al.* 2008; Bustamante *et al.* 2010; Richards-Zawacki 2010; Martel *et al.* 2013; Rowley & Alford 2013), and natural thermal refugia have facilitated the persistence of several species that are susceptible to *Bd* (Puschendorf *et al.* 2011; Stevenson *et al.* 2014). Similarly, *Bd* tolerates relatively narrow bands of both salinity and pH (Piotrowski *et al.* 2004; Stockwell *et al.* 2012), resulting in physicochemical refugia from chytridiomycosis for some threatened anurans (Bramwell 2011; Stockwell *et al.* 2015a, b).

Here, we extend our research demonstrating the importance of environmental refugia from chytridiomycosis for growling grass frogs (*Litoria raniformis*) in southern Australia (Heard *et al.* 2015). *Litoria raniformis* is a semi-aquatic hylid frog that declined sharply last century coincident with the spread of *Bd* across eastern Australia (Mahony *et al.* 2013). Our research confirms that chytridiomycosis is an important stressor for remnant populations (Heard *et al.* 2014), but suggests that metapopulations can persist where: (1) relatively warm and saline wetlands provide refuges from the disease; and/or (2) connectivity is sufficient to facilitate a balance between population extinction and recolonization (Heard *et al.* 2015).

We simulated water temperature regimes, infection prevalence, and occupancy dynamics to assess the degree to which increasing wetland microclimates and salinity could enhance metapopulation viability for *L. raniformis*. Simulations included manipulation of existing wetlands and creation of new wetlands with and without refugial properties. We also assessed the influence of climate on the efficacy of this management, running simulations for lowland and upland regions where *L. raniformis* persists, plus colder highlands from which the species has disappeared.

Materials and methods

Study system

This study focuses on four small metapopulations of *L. raniformis* from Melbourne, Victoria, Australia (metapopulations 1, 2, 3, and 6 in Heard *et al.* 2015, with between 5 and 12 patches; Appendix S1). Habitat networks consist of pools along streams, swamps, ponds, and flooded quarries embedded within a lowland volcanic plain (≤290 m above sea level).

Litoria raniformis displays recurrent population extinction and colonization in these networks. Colonization rate depends on geographic isolation from extant populations, as most dispersal occurs over distances <1 km (Heard *et al.* 2012; Hale *et al.* 2013). The prevalence of *Bd* infections is an important predictor of population extinction risk (Heard *et al.* 2015); however, infection rate varies substantially between sites, declining with increasing water temperatures and salinity (Heard *et al.* 2014). Warmer sites occur at lower elevations, are larger and deeper (conferring thermal inertia), and have less shading from emergent and riparian vegetation. Saline sites are generally fed by groundwater, with electrical conductivity up to 13,000 μS/cm (~8 ppt; Heard *et al.* 2015).

Our previous research parameterized statistical models of these dynamics (Heard *et al.* 2015; Figure 1; Appendix S2). During a given active season t for *L. raniformis* (October–April), water surface temperature at each site on each night is determined by a quadratic effect of days since September 1, positive effects of maximum daily air temperature and site size (surface area × depth), and negative effects of elevation and shading vegetation cover. Monthly water temperature regimes and salinity then become predictors in a model of *Bd* infection probability for *L. raniformis* (both having negative effects), which gives estimates of the seasonal prevalence of infections at each site (the proportion of frogs testing positive with random sampling across the season). From season t to $t + 1$, the probability of frog population persistence declines sigmoidally with infection prevalence in season t, while the probability of colonization of vacant sites increases sigmoidally with connectivity to neighboring populations. Connectivity of site i for the period t to $t + 1$ is defined as $\log_e(\text{sum}_j(z_{jt} \times (0.1 \times d_{ij})^{-0.72})) + 1)$, where d_{ij} is the edge-to-edge distance between site i and each neighbor j within 1 km, and z_{jt} is the occupancy status of each neighbor j in season t.

Our framework does not include changes in pathogen virulence or host resistance through time, as there is no evidence of either for *L. raniformis* since *Bd* arrived in Australia. Similarly, contagion is unrelated to host connectivity, as *Bd* is endemic in this system with widespread reservoir hosts and environmental transmission (Heard *et al.* 2015).

Scenarios and simulations

We simulated water temperature regimes, infection prevalence, and the occupancy dynamics of *L. raniformis* under four management options: (1) retain existing conditions; (2) manipulate existing sites to reduce the prevalence of infections (increasing wetland size, depth, and salinity, and reducing shading vegetation); (3) build new, nonrefugial wetlands using current protocols; or (4) build new wetlands with refugial properties. Building

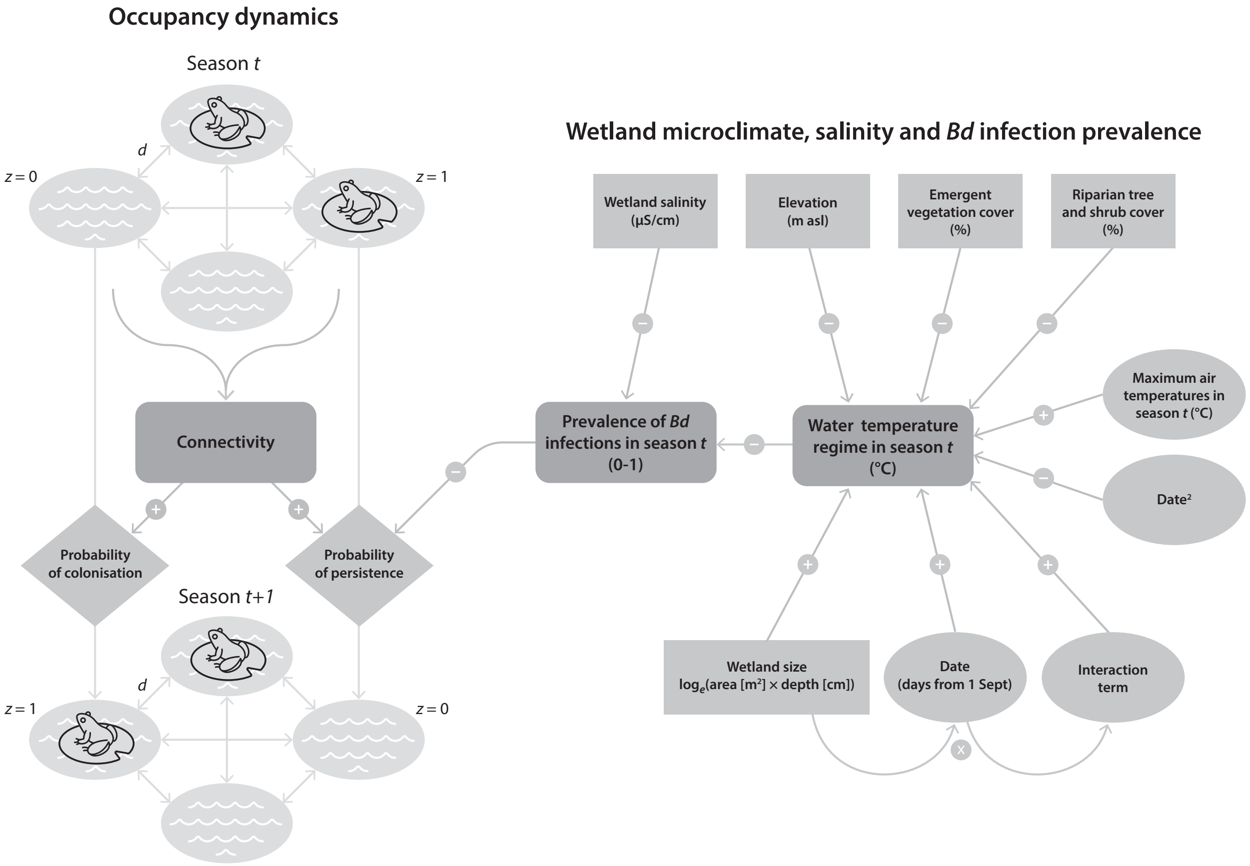

Figure 1 Conceptual diagram of the modeling framework. The left-hand panel depicts the occupancy dynamics of *Litoria raniformis* resulting from population extinction and colonization, and the effects of connectivity on these two processes. "Connectivity" is the distance-weighted sum of surrounding occupied wetlands, where *d* is edge-to-edge wetland distance and *z* is a binary variable indicating wetland occupancy. The right-hand panel shows the effects of wetland attributes (rectangles) and temporal variables (ovals) on seasonal water temperature regime, and in turn the effects of water temperature regime and salinity on the seasonal prevalence of *Bd* infections among *L. raniformis*. The two panels are linked by the effect of infection prevalence on frog population persistence.

habitat is a realistic option for this species, which readily colonizes constructed wetlands (Heard *et al*. 2012, 2013). Our approach is briefly described here, with further details in Appendices S2–S4.

For existing sites, the type and extent of manipulations were based on field measurements of the relevant variables (Heard *et al*. 2015) and a set of practical and regulatory constraints (Appendix S3). Adhering to environmental regulations will be an important consideration for such programs, ensuring impacts on other biota are minimized. We assumed that: (1) altering the surface area and depth of artificial wetlands would be possible, but natural wetlands could only be deepened (protecting their margins) and pools along streams could not be physically altered; (2) salinity could be increased at lentic wetlands by tapping the nearest aquifer, but this would not be possible at lotic sites; and (3) increasing insolation could only be achieved by removing exotic trees and shrubs, and lopping emergent vegetation down to 10% cover (emergent vegetation being an important microhabitat for *L. raniformis*).

Wetland construction scenarios were based on mapping of potential new wetlands for *L. raniformis* completed by the Victorian Government for an offsetting scheme (Appendix S1; DEPI 2013). We first ran simulations in which these wetlands were given the average depth, salinity, and shading vegetation cover of existing artificial wetlands in the study area, mimicking current wetland construction protocols. In subsequent simulations, we imposed refugial properties on these wetlands, giving them a standard maximum depth of 300 cm, zero tree and shrub cover, minimum emergent vegetation cover (10%), and salinity of the nearest ground-water fed site. Surface area remained at the mapped size.

We allowed for up to five manipulations of existing wetlands or five new wetlands per metapopulation (costing ~\$AUD 2.5 M and 3.5 M per metapopulation, respectively; Rose *et al.* 2016). Simulations were run by iteratively adding sites to manipulate or build up to this budget, with site selection based on rankings of infection prevalence and connectivity under the relevant scenario (lower prevalence and higher connectivity preferred).

We repeated these simulations assuming climate matched that on the edge of the species' current elevational range ("upland" scenario), or higher elevations from which the species has disappeared due to chytridiomycosis ("highland" scenario). Ballarat, Victoria, was selected for the upland case (435 m asl) and Cooma, New South Wales, selected for the highland case (778 m asl). Reestimating water temperatures under these scenarios was achieved by adjusting site elevations and replacing daily maximum air temperatures with those from the nearest Australian Bureau of Meteorology station (Appendix S4).

We ran 5,000 simulations of the dynamics of each metapopulation over 30 years for each scenario. Maximum daily temperatures matched those experienced during the 30 seasons preceding 2013. Future climate change was excluded to avoid predicting beyond the data. The probability of metapopulation extinction was the proportion of simulations reaching zero occupied patches. Simulations were run in *R* v. 3.3.1 (R Core Team 2016) using code in Appendix S5.

Results

Disease impacts increased sharply with elevation. Given existing habitat conditions, the average seasonal prevalence of *Bd* infections across all metapopulations was predicted to be 47% higher under the highland climate scenario than the lowland scenario (0.69 vs. 0.45; Figure 2). In turn, the average probability of metapopulation extinction given existing conditions rose by 41% from the lowland to highland scenarios (0.67–0.94; Figure 3).

Habitat management was most effective at low elevation. Manipulation of existing sites reduced predicted infection prevalence by 15% on average for the lowland scenario, 12% for the upland scenario, and 10% for the highland scenario (Figure 2). Similarly, infection prevalence at new refugial wetlands was 34% lower than at existing wetlands under the lowland scenario, 26% lower under the upland scenario, and 20% lower under the highland scenario (infection prevalence at nonrefugial wetlands was always similar to that at existing wetlands; Figure 2). Mitigation of extinction risk by habitat management subsequently declined as elevation increased (Figure 3). Manipulating existing wetlands reduced metapopulation extinction probability by 0.18 (32%) on average under the lowland scenario versus 0.04 (4%) under the highland scenario (Figure 3). Adding five new wetlands reduced metapopulation extinction probability by between 0.49 (72%) and 0.57 (85%) on average under the lowland scenario (adding nonrefugial and refugial wetlands, respectively) versus between 0.28 (30%) and 0.38 (41%) under the highland scenario (Figure 3). Notably, all metapopulations achieved a >80% chance of surviving for 30 years with the addition of five refugial wetlands under lowland conditions, whereas this was the case for only one metapopulation under highland conditions (Figure 3).

Adding wetlands was more effective than manipulating existing wetlands, even when the new wetlands displayed nonrefugial properties (Figure 3). Adding wetlands had two clear benefits. First, it increased metapopulation size, which was negatively correlated with extinction probability (Pearson's r = –0.55 across all metapopulations and scenarios; Figure 4). Second, it increased average connectivity, which drove drastic reductions in extinction risk for some metapopulations. For example, the addition of five closely clustered wetlands to metapopulation 3 increased average connectivity to ≥ 0.4, reducing extinction probability to ≤ 0.23 (Figures 3 and 4). Over all metapopulations and scenarios, there was very strong negative correlation between average connectivity and the probability of metapopulation extinction (Pearson's $r = –0.85$; Figure 4).

Discussion

Chytridiomycosis is a global threat to amphibian biodiversity, yet there remain few options for controlling the disease in the wild (Berger *et al.* 2016). We draw three main conclusions from our modeling of using habitat management to mitigate the impacts of chytridiomycosis in anurans: (1) habitat management is most likely to be effective in climates where hosts are already less susceptible to the disease; (2) creating additional habitat, particularly that with refugial properties, may be substantially more effective than manipulating existing habitat; and (3) increasing metapopulation size and connectivity through strategic habitat creation can greatly reduce extinction risk.

The pathogenicity and virulence of *Bd* is mediated by climate (Bielby *et al.* 2008; Murray *et al.* 2011). In eastern Australia, at least 17 frog species that have declined at higher elevations persist in warmer lowland environments (Skerratt *et al.* 2016). Our study on one of these species, *L. raniformis*, suggests that habitat management to mitigate chytridiomycosis should focus on these

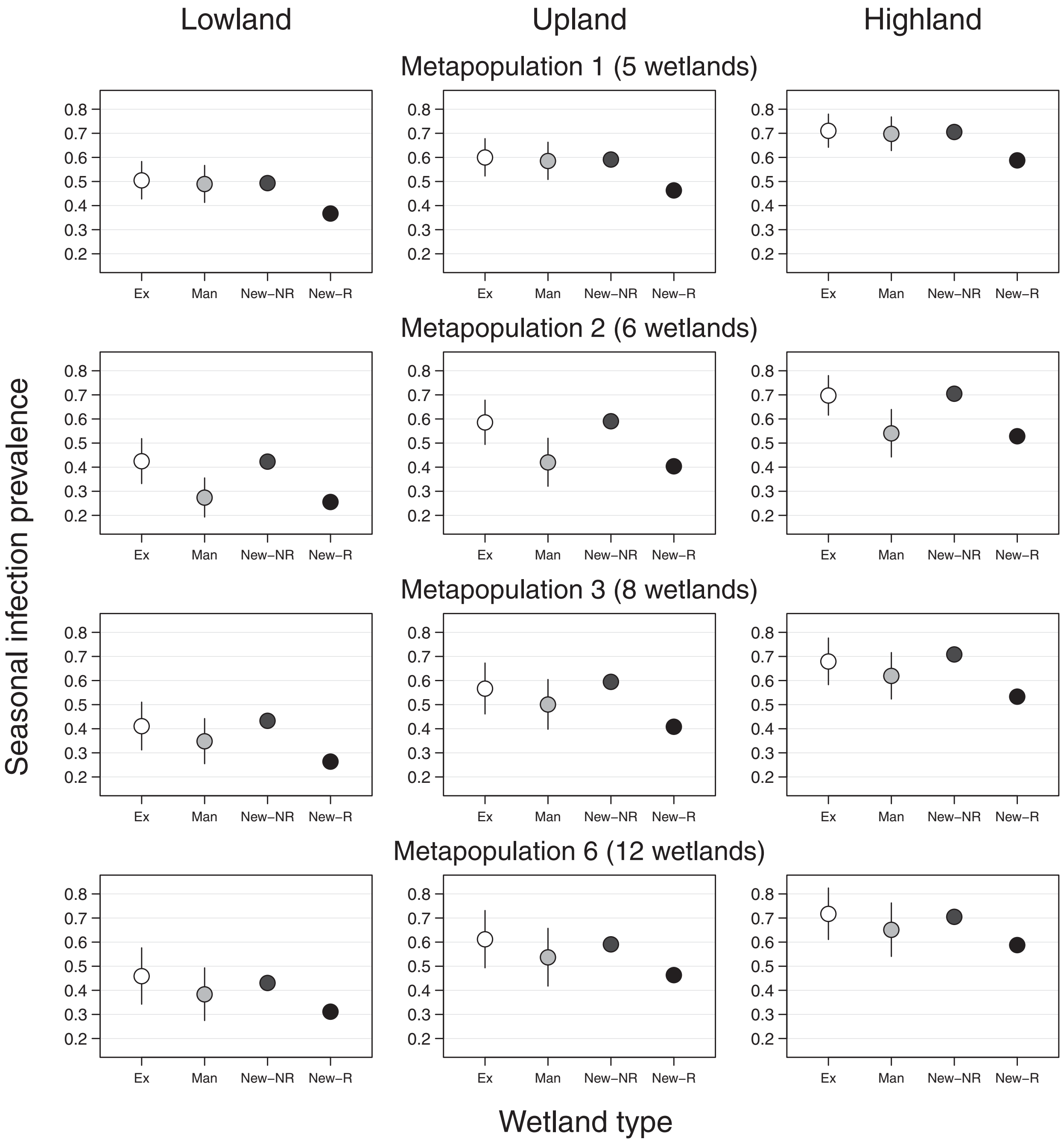

Figure 2 Comparison of the predicted seasonal prevalence of *Bd* infections for each management option under the three elevational scenarios. Management options for each metapopulation are: "Ex," maintain existing conditions at all sites; "Man," manipulate up to five existing wetlands to reduce chytrid prevalence; "New-NR," construct up to five nonrefugial wetlands; or "New-R," construct up to five refugial wetlands. Infection prevalence has been averaged across years for each site in each management category, with dots showing the mean of this figure across sites. Lines are ± one standard deviation among sites in each management category (those not shown are smaller than the dot).

climatic refugia, where adjusting wetland microclimate and physicochemistry has a comparatively greater impact on infection prevalence and host metapopulation viability. As above, all our focal metapopulations achieved a >80% chance of persisting with habitat management under lowland conditions, but this was the case for only

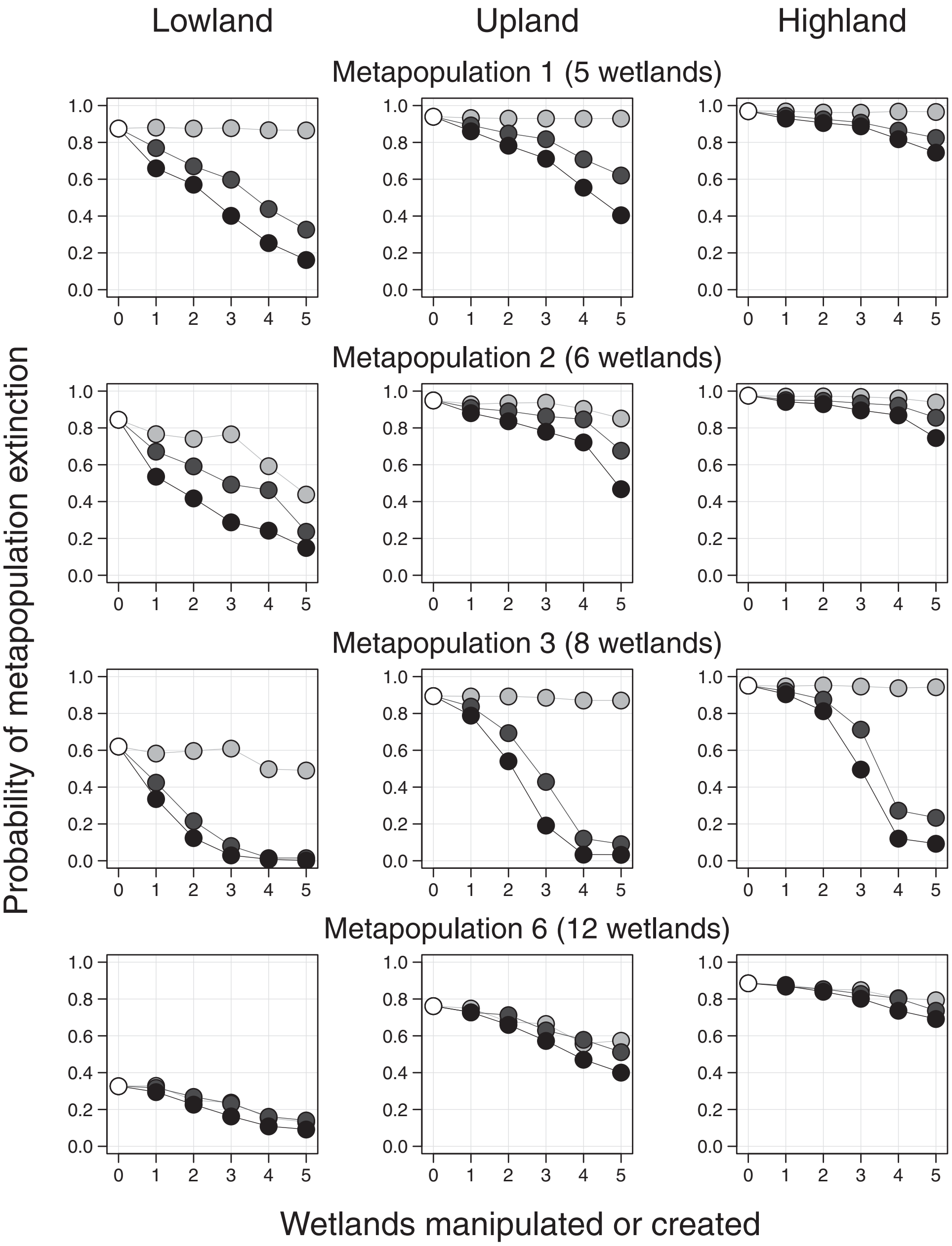

Figure 3 The probability of extinction over 30 years for each metapopulation under the four management options and three elevational scenarios. Colors depict the four management options, matching Figure 2: white dots, maintain existing conditions at all sites ("Ex"); light gray dots, manipulate up to five existing wetlands to reduce chytrid prevalence ("Man"); dark gray dots, construct up to five nonrefugial wetlands ("New-NR"); or black dots, construct up to five refugial wetlands ("New-R").

one metapopulation under colder highland conditions (Figure 3).

In systems for which habitat creation is possible, our simulations suggest that this approach is much more effective than manipulating existing habitat, particularly if created habitat has refugial properties from chytridiomycosis. For example, adding five refugial wetlands to the smallest metapopulation reduced its extinction risk to 16% under lowland conditions (and to 33% if these wetlands displayed nonrefugial properties), whereas extinction risk remained above 80% with only manipulation of existing habitat (Figure 3). The superiority of habitat

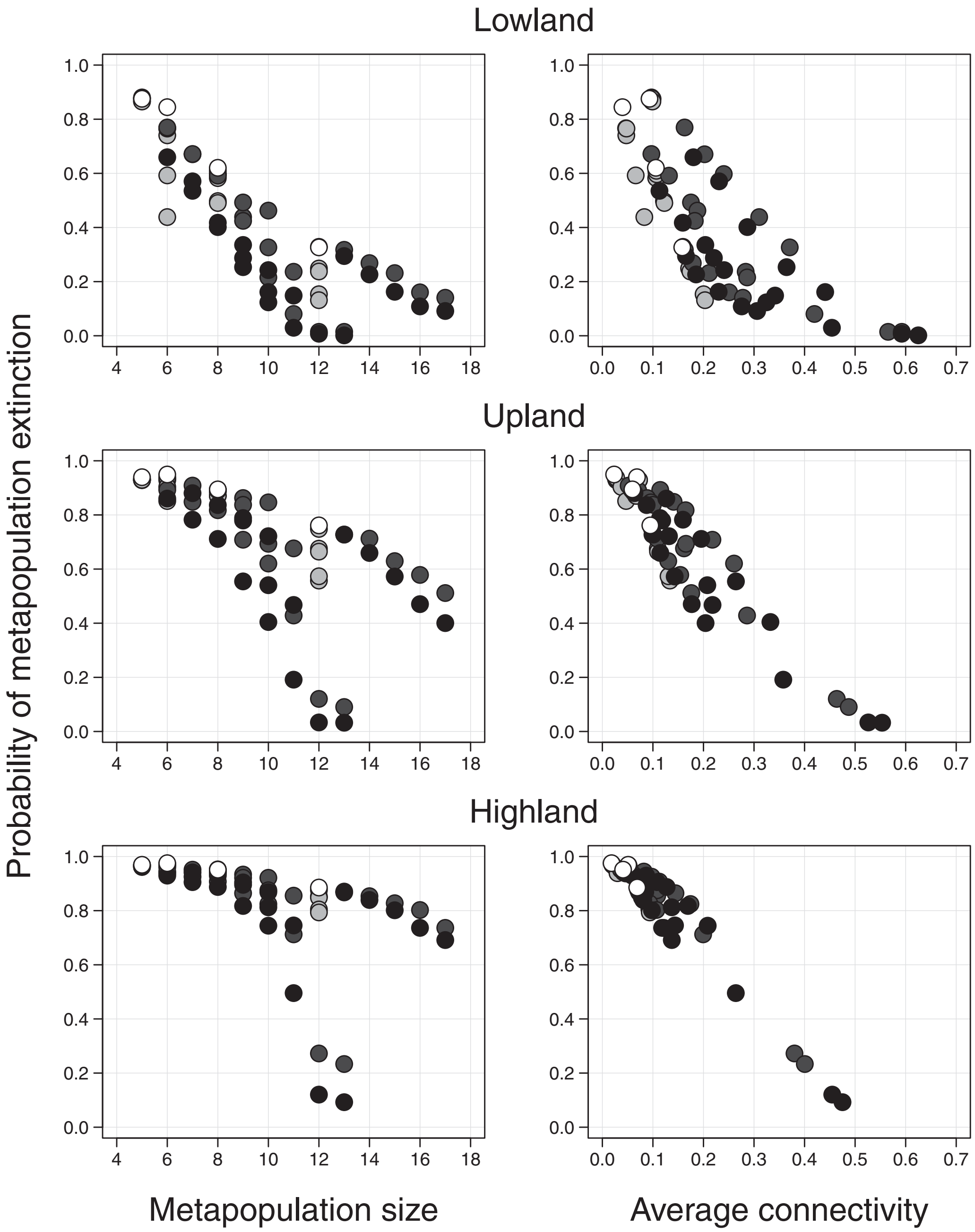

Figure 4 The relationship between the probability of extinction over 30 years and metapopulation size (left panel) and average wetland connectivity (right panel) for each of the three elevational scenarios. Each plot shows the relationship over all management options, with colors depicting the four options, matching Figures 2 and 3: white dots, maintain existing conditions at all sites ("Ex"); light gray dots, manipulate up to five existing wetlands to reduce chytrid prevalence ("Man"); dark gray dots, construct up to five nonrefugial wetlands ("New-NR"); or black dots construct up to five refugial wetlands ("New-R"). Connectivity for an individual wetland is the distance-weighted sum of surrounding occupied wetlands, with average connectivity being the mean across wetlands, years, and simulations for each metapopulation.

creation over habitat manipulation is due, in part, to a fundamental disparity in their contribution to metapopulation viability: habitat creation increases metapopulation size and connectivity, whereas habitat manipulation only increases the quality of existing patches. Nevertheless, the efficacy of wetland creation in our simulations also derives from constraints on manipulating existing habitat. In line with existing environmental regulations, we assumed that altering stream-beds and the margins of natural wetlands would be prohibited, as would inputting saline groundwater to streams and removing native riparian vegetation (Appendix S3). Predicted infection prevalence at manipulated sites was subsequently much higher, on average, than at refugial wetlands where conditions could be dictated *a priori* (Figure 2). Regulatory constraints on manipulating existing habitat are realistic for our study system (Appendix S3), and are an important consideration for habitat-based management of chytridiomycosis more generally (Scheele *et al.* 2014b; Stockwell *et al.* 2015b).

Increasing metapopulation size reduced extinction risk, but the largest reductions were achieved for the second largest metapopulation. Here, proposed wetlands occurred in a dense cluster (Appendix S1), conferring high connectivity and driving extinction risk down sharply as they were added (Figures 3 and 4). Although correlated, network connectivity had a much stronger effect on extinction probability than metapopulation size. These results demonstrate the value of population connectivity for anurans threatened by *Bd* if the pathogen is endemic and migrants are not a major source of disease transmission, as in our study system (Heard *et al.* 2015, Appendix S3). The generality of this conclusion hinges on the generality of this phenomenon. Current evidence suggests that endemic infections are the norm following initial epizootics of *Bd*, with reservoir hosts and environmental transmission becoming the primary drivers of contagion (Beyer *et al.* 2015; Stockwell *et al.* 2015a; Scheele *et al.* 2017; Scheele *et al.* 2017). As such, our conclusions regarding connectivity may hold for many anurans threatened by chytridiomycosis.

Our study system lends itself to using habitat management to mitigate chytridiomycosis, with clear habitat-based mechanisms underlying disease risk (Figure 1), a capacity to influence those mechanisms (Appendix S2), and impetus to pursue habitat-based management through government policy (DEPI 2013). We have shown that creating habitat can enhance the viability of small, extinction-prone metapopulations, in part because this approach may face fewer management constraints. However, in deciding the best approach for any real system, the financial costs of each action need to be taken into account alongside the benefits. We cannot predict costs in general, but in our system habitat creation has the potential to be cost-effective despite being relatively expensive. For example, constructing wetland habitat for *L. raniformis* may be as much as 1.4 times more expensive than enhancing existing habitat ($AUD 0.7 M vs. 0.5 M per site; Rose *et al.* 2016), yet creating habitat was on average five times more effective at reducing metapopulation extinction risk in our simulations than manipulating existing habitat.

It may be impractical or impossible to create habitat for many species afflicted by chytridiomycosis, such as forest-adapted stream frogs in eastern Australia and the Neotropics (Lips *et al.* 2006; Skerratt *et al.* 2016). Manipulating existing habitat, particularly canopy thinning, may be the only practical approach in such environments. While this approach had limited effect in our simulations, riparian vegetation is relatively sparse in our study system and a weak determinant of water temperatures. It is encouraging that canopy cover is a key determinant of frog microclimates in stream environments in Australia (Puschendorf *et al.* 2011; Scheele *et al.* 2014b), and that natural canopy thinning from storm damage has been shown to increase insolation and reduce *Bd* infection prevalence for some susceptible stream frogs (Roznik *et al.* 2015).

We encourage further experimentation on the use of habitat management to mitigate chytridiomycosis. Where there are significant practical, regulatory, or financial constraints, smaller scale technological solutions such as thermal ponds or "hot rocks" could represent a credible alternative to the approaches considered here, and should be considered (Scheele *et al.* 2014b). Be it constructing refugial habitat, manipulating existing habitat, or employing small-scale technological solutions, habitat management targeting the environmental drivers of chytridiomycosis may prove a valuable tool for combating this pervasive disease.

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Supporting Information

Additional Supporting Information may be found in the online version of this article at the publisher's web site:

Appendix S1. Focal metapopulations.
Appendix S2. Modeling framework.
Appendix S3. Manipulating wetland conditions.
Appendix S4. Elevational scenarios.
Figure S1. The four focal metapopulations showing the distribution of existing wetlands (blue shading) and the five proposed wetlands (green shading) included in simulations of metapopulation viability.

Figure S2. Relationships between the nightly water surface temperature and the main effects in the water temperature model of Heard *et al.* (2015).

Figure S3. Relationships between the probability of *Bd* infection of *Litoria raniformis* and water surface temperature and wetland conductivity, from Heard *et al.* (2015).

Figure S4. Relationship between the annual probability of persistence of *Litoria raniformis* populations and predicted *Bd* infection prevalence and connectivity, and between the annual probability of colonisation of vacant wetlands and connectivity.

Figure S5. Average maximum (filled dots) and minimum (open dots) temperatures for northern Melbourne (red), Ballarat (green) and Cooma (blue).

Figure S6. Predicted nightly water surface temperature regime between October 2011 and April 2012 for a site with average conditions located in northern Melbourne (red), Ballarat (green) or Cooma (blue).

Table S1. Parameter estimates for each statistical model.

Table S2. Manipulations applied to existing sites in the four focal metapopulations (red text), in line with the constraints listed above.

Appendix S5. CODE

Appendix S5. DATA

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