

Multi-species occupancy modeling provides novel insights into amphibian metacommunity structure and wetland restoration

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Abstract. A fundamental goal of community ecology is to understand species–habitat relationships and how they shape metacommunity structure. Recent advances in occupancy modeling enable habitat relationships to be assessed for both common and rare species within metacommunities using multi-species occupancy models (MSOM). These models account for imperfect species detection and offer considerable advantages over other analytical tools commonly used for community analyses under the elements of metacommunity structure (EMS) framework. Here, we demonstrate that MSOM can be used to infer habitat relationships and test metacommunity theory, using amphibians. Repeated frog surveys were undertaken at 55 wetland sites in southeastern Australia. We detected 11 frog species from three families (Limnodynastidae, Myobatrachidae, and Pelodyadidae). The rarest species was detected at only one site whereas the most common species was detected at 42 sites (naive occupancy rate 0.02–0.76). Two models were assessed representing two competing hypotheses; the best-supported model included the covariates distance to the nearest site (connectivity), wetland area, presence of the non-native eastern mosquitofish (*Gambusia holbrooki*), proportion cover of emergent vegetation, an interaction term between *Gambusia* and emergent vegetation cover, and the proportion canopy cover over a site. Hydroperiod played no detectable role in metacommunity structure. We found species–habitat relationships that fit with current metacommunity theory: occupancy increased with wetland area and connectivity. There was a strong negative relationship between occupancy and the presence of predatory *Gambusia*, and a positive interaction between *Gambusia* and emergent vegetation. The presence of canopy cover strongly increased occupancy for several tree frog species, highlighting the importance of terrestrial habitat for amphibian community structure. We demonstrated how responses by amphibians to environmental covariates at the species level can be linked to occupancy patterns at the metacommunity scale. Our results have clear management implications: wetland restoration projects for amphibians and likely other taxa should maximize wetland area and connectivity, establish partial canopy cover, and eradicate *Gambusia* or provide aquatic vegetation to mitigate the impact of this non-native fish. We strongly advocate the use of MSOM to elucidate the habitat drivers behind animal occupancy patterns and to derive unbiased occupancy estimates for monitoring programs.

Key words: Bayesian modeling; conservation; declining amphibians; frog community; *Gambusia holbrooki*; habitat; metacommunity; species richness; wetland management.

INTRODUCTION

A fundamental goal of community ecology is to understand how environmental and spatial factors drive species–habitat patterns locally and shape metacommunity structure at larger spatial scales (Vellend 2010). Sets of local communities of animal species are frequently distributed across landscapes as metacommunities,

which are linked by dispersal of multiple species (Leibold et al. 2004). Understanding metacommunity theory requires ecologists to often apply complex models that provide insight into how species respond to environmental parameters, and how species responses collectively shape the entire community. Species-specific models of the probability of occupancy, corrected for detection bias, are frequently implemented to determine habitat and landscape relationships within ecological communities (MacKenzie et al. 2002). However, rarity in occurrence may preclude the assessment of species detected at few survey sites in single-species occupancy models due to sparse data sets.

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Multi-species occupancy models (MSOM) can derive inferences regarding habitat relationships for rare species and provide insights into species richness and other biodiversity metrics (Dorazio and Royle 2005, Kéry and Royle 2008). The first explicit description of hierarchical models for estimating species richness and species responses to habitat fragmentation was formulated by Zipkin et al. (2009). The key advantage of using a hierarchical modeling framework over single-species models for estimating species occupancy is that they account for individual species responses to a parameter of interest, as well as the aggregated response by the whole community, which increases precision in estimates for infrequently observed species through the use of collective community data (Kéry and Royle 2008, Zipkin et al. 2009).

Multi-species occupancy models also address the issue of imperfect species detection that often bias the statistics commonly used for community analyses under the elements of metacommunity structure (EMS) framework (Leibold and Mikkelsen 2002). The EMS is a set of analytical tools that uses species occurrence data to identify and classify metacommunity structure and link it to underlying environmental gradients (Mihaljevic et al. 2015). This framework was extended by Mihaljevic et al. (2015) to account for imperfect detection of species at sites under the detection error-corrected EMS (DECEMS) framework, which integrates MSOM into the EMS framework thereby reducing bias in characterizing metacommunity structure by using occupancy models to uncouple species-specific occupancy and detection probabilities. Simulation modeling has also been used to demonstrate that the detection of metacommunity patterns under the EMS framework is prone to Type II error (Schmera et al. 2018), which is analogous to a false negative result due to the failed detection of a species at a site (Guillera-Arroita and Lahoz-Monfort 2012). Multi-species occupancy models can be used to better inform how species-specific responses to environmental covariates can scale up to affect metacommunity-wide patterns of occupancy, thereby addressing a key gap within the EMS framework by improving the ability to link species-level processes to metacommunity structure (Mihaljevic et al. 2015).

Application of MSOM can provide insight into fundamental concepts of metacommunity theory. Spatially explicit multi-species models that test the effect of distance between habitat patches can shed light on the dispersal processes underpinning a metacommunity, such as the mass-effect perspective that focuses on the effect of immigration and emigration on local population dynamics (Leibold et al. 2004). Also, because metacommunity theory is largely an extension of metapopulation theory, which emphasizes greater species persistence with increased patch size and connectivity (Hanski 1994, 1998), larger, less-isolated patches should also support a greater number of species. Models that assess species responses to environmental gradients by including

abiotic and biotic variables relating to local habitat quality essentially test the species-sorting perspective of metacommunity theory. This perspective emphasizes that heterogeneity in local patches instigates strong differences in the local demography of species, which occurs through the dispersal of species tracking local environmental conditions, but also emphasizes that spatial niche separation among species is more important than spatial dynamics (Leibold et al. 2004). The identification of important habitat parameters in MSOM can also guide management actions for individual species and communities (Zipkin et al. 2010, Maphisa et al. 2019).

Ecological concepts such as the response of aquatic communities to freshwater habitat gradients can be examined using MSOM. This hypothesis emphasizes that lentic waterbodies exist along a gradient from ephemeral to permanent ponds, where community structure is determined by abiotic factors (e.g., pond drying) and biotic factors, particularly predation by fish (Wellborn et al. 1996). The distribution of aquatic taxa along the gradient is largely governed by individual species' life-history traits whereby species can have faster development rates in short-lived (ephemeral, typically fish-free) aquatic habitats, but are vulnerable to predation by fish in more permanent waterbodies (Wellborn et al. 1996). Conversely, species with anti-predator defenses but slower development rates may survive well in permanent waterbodies with fish but suffer catastrophic losses in more ephemeral ponds when they dry out (e.g., amphibians; Kats et al. 1988, Semlitsch 2000). The net result of these patterns in species adaptability is distinct patterns in community composition along the permanence gradient (Wellborn et al. 1996, Snodgrass et al. 2000a). Moreover, pond drying should be viewed as an environmental disturbance or perturbation, which results in radical changes to the abiotic and biotic conditions of the waterbody (Urban 2004). Consideration of wetland hydroperiod and fish predation into metacommunity studies of freshwater ecosystems would provide fundamental insight into community structure and greatly inform conservation management.

Amphibian communities are inherently suited to test ideas surrounding metacommunity theory as aquatic-breeding species are restricted to breeding in freshwater ponds and wetlands embedded in a mosaic of terrestrial (non-breeding) habitat, and have complex life histories with larvae that metamorphose to a terrestrial stage and juveniles and adults that often disperse widely (Wilbur 1987). Accordingly, amphibian communities hold great potential for advancing a synthesis of local and regional processes in metacommunity ecology (Werner et al. 2007, 2009).

Globally, amphibian species have been declining and there is an urgent need to implement effective monitoring and management programs if we are to identify trends in occupancy patterns, to elucidate the proximate drivers of declines such as habitat change, and to

implement habitat restoration that halts or reverses decreases in the proportion of sites occupied (Adams and Muths 2019, Sterrett et al. 2019). MSOM have been integrated into a structured decision-making approach to inform the management of amphibian communities, based on the inclusion of key habitat variables (hydroperiod, area, and connectivity) linked to important management decisions (Grant et al. 2013). These models have also been used to evaluate anthropogenic impacts to amphibian communities and management practices (Muncy et al. 2014, Guzy et al. 2018, 2019). Rare amphibian species require sufficient data to inform management practices underpinned by clear inferences, yet these data are hard to obtain due to their rarity (MacKenzie et al. 2005). This constraint may be overcome by using MSOM to essentially borrow information from more frequently detected species to improve the precision of parameter estimates for these data-poor species (Zipkin et al. 2009).

Here, we used MSOM to elucidate the spatial, biotic and abiotic factors driving community structure in a frog metacommunity, and to provide unbiased estimates of the probability of occupancy for each species inhabiting a coastal wetland system in southeastern Australia. A previous study of the habitat relationships within this metacommunity was constrained because the statistical methods used could not provide inferences for rare and very common species detected at wetland sites (Lane et al. 2007). There has also been extensive research conducted at the site on the endangered green and golden bell frog (*Litoria aurea*) that has examined relationships between occupancy and various habitat and landscape variables (e.g., Hamer et al. 2002a, Hamer and Mahony 2010, Valdez et al. 2015). However, these studies have not considered species occupancy within the entire frog metacommunity. Therefore, we provide a fresh perspective into species-habitat relationships for this site and use our findings to test perspectives of metacommunity theory. We also provide new insight into the relationship between the non-native eastern mosquitofish (*Gambusia holbrooki*; hereafter referred to as *Gambusia*) and patterns in frog occupancy. This small fish has been implicated in the decline of *Lit. aurea* due to predation on eggs and larvae (Pyke and White 2001, Hamer et al. 2002b, Remon et al. 2016) and we examined the interactions between *Gambusia*, aquatic habitat complexity and wetland hydroperiod, in line with the models of freshwater community structure proposed by Wellborn et al. (1996).

We predicted that individual species relationships between both local and landscape variables would shape metacommunity structure, thereby connecting metacommunity patterns to species-level processes and demonstrating how MSOM can test general ecological theories. We also discuss the implications of our findings for wetland restoration projects that can provide land managers with informed guidance on wetland creation and management for amphibians and other wetland-dependent taxa.

METHODS

Study area

We conducted our study at 55 waterbodies on Kooragang Island in southeastern Australia (see Google Earth image, Data S1). Kooragang Island (approximately 2,560 ha) is located in the Hunter River estuary, approximately 5 km northwest of Newcastle, New South Wales (32°50'–32°54' S, 151°42'–151°47' E). Kooragang Island was originally comprised of deltaic islands that were initially used for agriculture. Land reclamation commenced after 1950 to consolidate the southeastern portion of the island into an industrial area, which is used for disposal of industrial waste and supports infrastructure associated with a large coal-loading terminal. The northwestern (agricultural) end of the island was formerly grazing land but was managed as the Kooragang Wetland Rehabilitation Project at the time of the study. This area is now managed as the Hunter Wetlands National Park. The industrial and agricultural areas support a mosaic of freshwater wetlands varying in size and hydroperiod, interspersed with brackish wetlands in estuarine areas (Hamer et al. 2008). Thirteen frog species have been previously recorded from the study area (Lane et al. 2007). Further recent descriptions of the study area are in Valdez et al. (2015).

Frog surveys

Frog surveys were conducted at 55 waterbodies over two breeding seasons, September–April in 2000–2001 and 2001–2002. This survey period covers the breeding season for spring- and summer-breeding frog species. Thirty-two sites were included in a mark–recapture study for *Litoria aurea* focusing on waterbodies inhabited by the core of the population in the industrial and estuarine areas. The mark–recapture study comprised a maximum of 28 standardized nocturnal surveys at 32 sites, divided into 14 surveys at each site per year (for survey details see Hamer and Mahony 2007, 2010). Surveys at the remaining 23 sites were conducted mostly five times, two surveys in 2000–2001 and three surveys in 2001–2002. Seventeen sites were situated in the industrial area, and 38 sites were located in the agricultural and estuarine areas. Site selection included a range of waterbody types so that the 55 sites were considered to be representative of the heterogeneity present in the wetland system.

Nocturnal surveys comprised quiet listening at each waterbody for approximately 10 minutes to detect calling male frogs (Scott and Woodward 1994). Frog species present in the local region have distinct mating calls and so there was minimal risk of misidentifications (i.e., false positive detections). Searches for frogs were then conducted in waterbodies with a head-mounted light using a standard visual encounter survey technique (Crump and Scott 1994). The surrounding terrestrial habitat

including trees and shrubs within 10 m of the waterbody was also searched. Surveys were mostly done by one person (A. J. Hamer), with survey effort for visual searches conducted in proportion to waterbody area and vegetation complexity. Air temperature and water levels were measured at the start of each survey, because detectability of amphibians is often affected by ambient temperature (Weir et al. 2005) and the availability of water at a site (Alford and Richards 1999). In limited instances when air temperature was not recorded during a survey, the mean temperature recorded from other sites on that same night was used, or when temperature was not recorded on a survey night, we used the minimum temperature recorded that night at the nearest weather station, within 5 km of the study area (University of Newcastle).

Habitat variables

Wetland area was recorded for each site using digitized maps and a Geographical Information System (MapInfo 4.5, MapInfo Corp., Troy, New York, USA) and Google Earth imagery (dated 10 January 2007 to account for the historical nature of the data set). The distance to the nearest wetland site was also measured using these methods; however, we excluded sites where no frog species were detected or highly ephemeral sites, as these sites are unlikely to contribute to population persistence. We used water levels recorded at a site to determine hydroperiod: permanent waterbodies were not observed to dry out over the two seasons; ephemeral waterbodies dried out on one or more occasions. Wetland ephemerality was scored as a binary variable (permanent wetlands, 0; ephemeral wetlands, 1). The proportion of the waterbody surface area covered by emergent vegetation and canopy overstory was recorded. Emergent vegetation included aquatic plants that extended above the water surface, whereas canopy overstory included trees and shrubs (>5 m in height; live or dead) around the wetland perimeter. The presence of *Gambusia* was recorded by visual examination of the water column and dip-netting during diurnal site visits (see Hamer et al. 2008, Hamer and Mahony 2010). Descriptive statistics of habitat variables recorded in the study area are in Appendix S1: Table S1.

Data analysis and modeling

We used hierarchical Bayesian modeling to estimate community-level and species-specific responses to six habitat covariates: distance to the nearest wetland site (Distsite), wetland area (Area), presence/absence of *Gambusia* (Fish), proportion emergent vegetation cover (Emergveg), wetland ephemerality (Ephemerality), and proportion canopy cover (Canopy). There is widespread evidence that all six covariates are important determinants of amphibian occupancy, and the inclusion of each covariate examined six different components of

metacommunity or ecological theory (Appendix S2: Table S1). Hydroperiod and fish presence are strong structuring forces of amphibian communities and so should be included in any model of expected amphibian community structure (Pechmann et al. 1989, Wellborn et al. 1996, Snodgrass et al. 2000a).

We also included survey-specific covariates to jointly estimate the probability of detection: number of days since 1 September (Days) to capture detection since the start of the field surveys and corresponding to the beginning of the activity season for spring-breeding frogs, including a quadratic term (Days²) to potentially capture the window of activity for each species; air temperature (Temp); whether a site had standing water during a survey or was otherwise dry (Wetness: 0, dry; 1, wet); and survey year (Year: 1, 2000–2001; 2, 2001–2002). We assumed that the frog metacommunity was closed over the 2 yr during the study (i.e., the species pool remained constant), but added a year effect to account for potential variation in frog activity (detection) between the two seasons due to annual fluctuations in seasonality (see Zipkin et al. 2009). Survey date (time since September) has been shown to influence detection probabilities for several frog species in southeastern Australia (Canessa et al. 2012, Heard et al. 2015). High water levels and higher temperatures have been shown to increase the probability of detection for *Lit. aurea* in the study area (Hamer and Mahony 2010).

We implemented the original species richness hierarchical model developed by Zipkin et al. (2009) as modified by others for examining responses by reptile and amphibian communities to anthropogenic impacts (Guzy et al. 2013, 2018, Hunt et al. 2013, Muncy et al. 2014). This hierarchical model links species-specific detection and occupancy, and is a much more informative extension of the single-species hierarchical linear models used to estimate site occupancy rates of species with imperfect detection probabilities (Dorazio and Royle 2005, Dorazio et al. 2006, Kéry and Royle 2008). Hierarchical multi-species models consider all occupancy and detection parameters as random effects rather than deterministic relations among parameters and processes, which improves estimation of individual parameters for individual species by considering each within the context of a group of related variables (Link 1999, Link et al. 2002). This approach increases the precision of estimates for rare or elusive species by also considering each within the context of the broader community (Sauer and Link 2002, Russell et al. 2009). Therefore, by generating separate estimates for species-specific occupancy and detection probabilities and then relating each to species richness, species-level and community-level information is combined into the same modeling framework (Dorazio and Royle 2005, Zipkin et al. 2009, Hunt et al. 2013). Essentially, models of data-poor species borrow information from more frequently detected or data-rich species in order to improve precision and predictive ability for parameter estimates of rare species (Zipkin

et al. 2009). Therefore, estimates for these rarely observed species are drawn towards group averages (“Bayesian shrinkage” toward the mean; Link 1999).

The statistics underpinning the multi-species hierarchical model we used have been described by others (e.g., Guzy et al. 2013, 2018, Hunt et al. 2013, Muncy et al. 2014) but are summarized here. The first level of the model assumed a true (but only partially observed) presence-absence matrix $z_{i,j}$ for species $i = 1, 2, \dots, N$ at site $j = 1, 2, \dots, J$, where $z_{i,j} = 1$ if species i was present at site j , and $z_{i,j} = 0$ if the species was absent. Because $z_{i,j}$ was uncertain, an occurrence model was specified where $z_{i,j} \sim \text{Bern}(\Psi_{i,j})$, and $\Psi_{i,j}$ is the probability that species i occurs at site j . The state variable $z_{i,j}$ is usually not known with certainty; instead, we observed data $x_{i,j,k}$ for species i at site j during sampling period k , which are also assumed to be Bernoulli random variables if species i is present (Zipkin et al. 2009). Based on the survey data collected, we generated species-specific observance matrices for up to 28 sampling occasions at each of 55 sites where detection was represented as 1, and non-detection was represented as 0. Thus, the data provided a three-dimensional matrix $x_{i,j,k}$ for species i at site j for the k th sampling occasion. The second level of the model (observation model) specified that $x_{i,j,k} \sim \text{Bern}(\theta_{i,j,k} \times z_{i,j})$ where $z_{i,j}$ is the true occurrence matrix described above, and $\theta_{i,j,k}$ is the detection probability for species i at site j for the k th sampling occasion.

Prior to modeling, multicollinearity was assessed among the habitat variables using Pearson correlation coefficients (r) for pairwise comparisons of continuous variables, and Spearman rank correlation coefficients for binary variables (r_s ; Appendix S3: Table S1). There was a strong correlation between emergent vegetation cover and wetland ephemerality ($r_s = 0.58$); therefore, these two variables were not included in the same model. There was no strong correlation between the presence of *Gambusia* at a site and ephemerality ($r_s = -0.11$), or the other four variables (Appendix S3). Accordingly, we assessed two competing metacommunity hypotheses relating primarily to the effects of *Gambusia*, emergent vegetation cover and ephemerality on the frog metacommunity. Model 1 included the following equations to relate species-specific covariate parameters (α and β values), and occupancy and detection probabilities ($\Psi_{i,j}$ and $\theta_{i,j,k}$, respectively) to the hierarchical models previously described

$$\begin{aligned} \text{Model 1: } \text{logit}(\Psi_{i,j}) &= u_i + \alpha_{1i}(\text{Distsite}_j) + \alpha_{2i}(\text{Area}_j) + \alpha_{3i}(\text{Fish}_j) \\ &+ \alpha_{4i}(\text{Emergveg}_j) + \alpha_{5i}(\text{Fish}_j \times \text{Emergveg}_j) + \alpha_{6i}(\text{Canopy}_j) \\ \text{logit}(\theta_{i,j,k}) &= v_i + \beta_{1i}(\text{Days}_{j,k}) + \beta_{2i}(\text{Days}_{j,k}^2) + \beta_{3i}(\text{Temp}_{j,k}) \\ &+ \beta_{4i}(\text{Wetness}_{j,k}) + \beta_{5i}(\text{Year}_{j,k}) \end{aligned}$$

where u_i and v_i are species-level effects and α_j and β_j are site-level effects on occupancy and detection, respectively. Model 1 tested for a potential interaction between

the presence of *Gambusia* at a site and emergent vegetation cover, because aquatic vegetation may ameliorate *Gambusia* predation on amphibians by providing habitat complexity as refugia (Baber and Babbitt 2004). Model 2 included the following equation for the species-specific occupancy parameters, while retaining the same parameters for detection probabilities as in Model 1

$$\begin{aligned} \text{Model 2: } \text{logit}(\Psi_{i,j}) &= u_i + \alpha_{1i}(\text{Distsite}_j) + \alpha_{2i}(\text{Area}_j) + \alpha_{3i}(\text{Fish}_j) \\ &+ \alpha_{4i}(\text{Ephemerality}_j) + \alpha_{5i}(\text{Fish}_j \times \text{Ephemerality}_j) + \alpha_{6i}(\text{Canopy}_j) \end{aligned}$$

Model 2 tested for a potential interaction between the presence of *Gambusia* at a site and wetland ephemerality, because *Gambusia* occupancy may be lower in ephemeral wetlands (Pyke 2008) and hydroperiod can have a strong influence in shaping amphibian communities in wetlands (Wellborn et al. 1996). The covariate Distsite was included in both models to account for spatial non-independence among sites. One frog species has a spatially aggregated distribution in the study area (*Lit. aurea*; Hamer et al. 2002a) indicating potential spatial autocorrelation among sites. Failing to account for spatial autocorrelation can lead to biased parameter estimates (Wintle and Bardos 2006) and should be an important consideration in amphibian occupancy studies (Ficetola 2015). However, there are no apparent barriers to frog movement in the study area and microchipped *Lit. aurea* have been detected moving between the industrial and estuarine areas (Hamer et al. 2008). The variables Area and Distsite were $\log_{10}(x)$ -transformed prior to analysis. Continuous variables were standardized prior to analysis by converting to z scores (i.e., the mean was subtracted from each value and then divided by the standard deviation). Standardized covariates allowed direct comparison of model coefficients so that the relative importance of each covariate could be determined according to the magnitude of the coefficient. Missing values for survey-specific (detection) covariates at sites were replaced by the mean for that variable.

Both models therefore contained 13 species-specific parameters ($u_i, \alpha_{1i}, \alpha_{2i}, \alpha_{3i}, \alpha_{4i}, \alpha_{5i}, \alpha_{6i}, v_i, \beta_{1i}, \beta_{2i}, \beta_{3i}, \beta_{4i}, \beta_{5i}$). An additional hierarchical component of the model was added by estimating community summaries (μ), which assume that the species-level parameters are random effects, each governed by a community-level hyperparameter (Zipkin et al. 2009). For example, $\alpha_{1i} \sim N(\mu_{\alpha 1}, \sigma_{\alpha 1})$ where $\mu_{\alpha 1}$ is the mean community response (across species) to the Distsite covariate, and $\sigma_{\alpha 1}$ is the standard deviation in α_1 among species.

We estimated model parameters and community summaries using a Bayesian analysis of the model with uninformative priors for the hyper-parameters (i.e., $U[-5, 5]$ for α and β , $U[0, 10]$ for σ , and $U[-10, 10]$ for μ parameters), and species-specific model coefficients were truncated at ± 5 from μ to avoid traps (see Guzy et al. 2018). We calculated the mean and standard deviation of the model coefficients, and the 2.5th and 97.5th percentiles

of the posterior distribution, which represents a 95% Bayesian credible interval (BCI). Parameter estimates of covariates with a BCI that did not overlap zero were considered to be clearly more important, whereas estimates with a BCI overlapping zero had greater uncertainty. However, some minor overlap of the BCI with zero was tolerated in inferring relationships (see Cuning and Finch 2005). Species-specific occupancy and detection estimates were derived using the log transformation ($\exp(\alpha)/(1 + \exp(\alpha))$). We estimated species richness (number of species at a site) by summing the estimated probability of occupancy for each species detected at a site. We used Pearson correlation coefficients in post hoc analyses to assess relationships between the mean estimated number of species and the four continuous covariates.

Data analyses were performed in the software program OpenBUGS 3.2.3 (Spiegelhalter et al. 2014) using R2WinBUGS (Sturtz et al. 2005). Each model was run using three replicate Markov chain Monte Carlo (MCMC) iterations to generate 40,000 samples from the posterior distribution of each model after discarding a “burn-in” of 20,000 samples, with a thinning rate of 3. The Gelman-Rubin statistic was checked for all estimated parameters and was found to indicate acceptable convergence (i.e., $\hat{R} < 1.05$; Gelman and Rubin 1992).

The relative fit of Model 1 and Model 2 was assessed using the Deviance Information Criterion (DIC; Spiegelhalter et al. 2002). The use of DIC for ranking hierarchical occupancy models has been recently questioned, mainly because of the models’ latent parameters (Hooten and Hobbs 2015) or because the model is sensitive to parameterization (Gelfand et al. 2006; also see Broms et al. 2016). However, despite the criticisms, DIC remains one of the most frequently used methods for ranking Bayesian hierarchical models (Hooten and Hobbs 2015) and is still advocated by others for ecological prediction (e.g., Stevens and Conway 2019). The best-supported model was the one with the lowest DIC value and greater than two units from the competing model. We also computed Bayesian P values to assess model fit; a model with a good fit to the data has a P value near 0.5 (Gelman et al. 1996).

RESULTS

Frog detections

During the 2000–2001 and 2001–2002 breeding seasons 980 surveys were conducted at 55 wetland sites (mean = 18 surveys per site; range: 4–28). A total of 11 frog species were detected (3.9 ± 1.9 species per site [mean \pm SD], range: 0–8), representing the taxonomic families Limnodynastidae and Myobatrachidae (ground frogs), and Pelodryadidae (tree frogs). No frogs were detected at two sites. The most frequently detected species was the striped marsh frog (*Limnodynastes peronii*; naive occupancy rate = 0.76), followed by the common

eastern froglet (*Crinia signifera*; 0.71) and the eastern dwarf tree frog (*Litoria fallax*; 0.71), whereas the Jervis Bay tree frog (*Lit. jervisiensis*) was detected at only one site (naive occupancy rate = 0.02). A further three species were detected at fewer than five sites: green tree frog (*Lit. caerulea*), broad-palmed frog (*Lit. latopalmata*), and ornate burrowing frog (*Platyplectrum ornatum*). The remaining four species (spotted grass frog *Lim. tasmaniensis*, green and golden bell frog *Lit. aurea*, bleating tree frog *Lit. dentata*, Peron’s tree frog *Lit. peronii*) were detected at 8–34 sites (naive occupancy rates: 0.15–0.62). All species detected are native, reproduce in water and have free-swimming aquatic larvae.

The mean estimated number of frog species (species richness) at a site was 4.7 (4.0–6.2), which is slightly higher than the naive mean species richness. The mean probability of occupancy across all species was 0.549 (95% BCI: 0.193–0.871), whereas the mean probability of detection was 0.092 (0.039–0.175). Mean estimated probabilities of occupancy varied widely among the frog species detected, ranging from 0.039 (95% BCI: 0.008–0.246) for *Lit. jervisiensis* to 0.940 (0.725–0.990) for *Lim. peronii* (Table 1). Mean estimated probabilities of detection were also highly variable among the 11 frog species, ranging from 0.036 (95% BCI: 0.010–0.108) for *Lit. dentata* to 0.283 (0.176–0.410) for *Lit. fallax* (Table 1).

Model inference and fit

The best-supported model included the proportion cover of emergent vegetation (Model 1; DIC = 4605.2). There was no support for the model that included wetland ephemerality (Model 2; DIC = 4658.0). Moreover, there was no clear relationship between ephemerality and the mean estimated probability of occupancy (Appendix S4: Table S1). Bayesian P values for both models were close to 0.5 indicating acceptable model fit (Model 1, $P = 0.428$; Model 2, $P = 0.433$).

Community-level summary

There was a clear negative relationship between the mean estimated probability of occupancy across all frog species and distance to the nearest site ($\mu_{\alpha 1}$; Table 2). Mean occupancy was predicted to decrease from 0.627 at the site nearest to another site to 0.267 at the most distant site (Fig. 1a). There was a clear positive relationship between mean occupancy and wetland area ($\mu_{\alpha 2}$; Table 2). Mean occupancy was predicted to increase from 0.470 to 0.882 at the smallest to largest sites, respectively (Fig. 1b).

There was a clear negative relationship between mean community occupancy and the presence of *Gambusia* and this response was the strongest among the covariates examined ($\mu_{\alpha 3} = -1.223$; Table 2). Mean occupancy was predicted to decrease from 0.555 (95% BCI: 0.194–0.875) at sites with no *Gambusia* present, to 0.210 (0.040–0.545) at sites with *Gambusia* present. There was

TABLE 1. Summary of model-estimated occupancy and detection probabilities for 11 frog species from three families detected on Kooragang Island, Australia.

Species	Occupancy		Detection	
	Occupancy	95% BCI	Detection	95% BCI
Limnodynastidae				
<i>Limnodynastes peronii</i>	0.940	0.725–0.990	0.114	0.062–0.192
<i>Lim. tasmaniensis</i>	0.936	0.749–0.989	0.064	0.028–0.125
<i>Platyplectrum ornatum</i>	0.099	0.015–0.434	0.075	0.022–0.220
Myobatrachidae				
<i>Crinia signifera</i>	0.938	0.770–0.988	0.093	0.045–0.174
Pelodyadidae				
<i>Litoria aurea</i>	0.721	0.374–0.916	0.200	0.099–0.354
<i>Lit. caerulea</i>	0.129	0.016–0.603	0.039	0.009–0.144
<i>Lit. dentata</i>	0.503	0.143–0.901	0.036	0.010–0.108
<i>Lit. fallax</i>	0.936	0.736–0.988	0.283	0.176–0.410
<i>Lit. jervisiensis</i>	0.039	0.008–0.246	0.066	0.014–0.244
<i>Lit. latopalmeta</i>	0.065	0.009–0.345	0.065	0.017–0.211
<i>Lit. peronii</i>	0.707	0.321–0.945	0.038	0.012–0.101

Notes: Estimates were extracted from Model 1. Estimates include 95% Bayesian credible intervals (BCI).

TABLE 2. Summary of hyper-parameters for occupancy (α) and detection (β) covariates across all 11 frog species detected on Kooragang Island.

Community-level hyper-parameter				
Variable	Definition	Mean	SD	95% BCI
$\mu_{\alpha 1}$	Distsite	-0.463	0.221	-0.923 to -0.047
$\sigma_{\alpha 1}$	Distsite	0.281	0.230	0.008 to 0.844
$\mu_{\alpha 2}$	Area	0.497	0.249	0.008 to 0.996
$\sigma_{\alpha 2}$	Area	0.461	0.298	0.030 to 1.163
$\mu_{\alpha 3}$	Fish	-1.223	0.577	-2.381 to -0.128
$\sigma_{\alpha 3}$	Fish	0.740	0.551	0.029 to 2.050
$\mu_{\alpha 4}$	Emergveg	-0.871	0.469	-1.816 to 0.030
$\sigma_{\alpha 4}$	Emergveg	0.915	0.419	0.221 to 1.897
$\mu_{\alpha 5}$	Fish \times Emergveg	1.183	0.478	0.269 to 2.162
$\sigma_{\alpha 5}$	Fish \times Emergveg	0.673	0.457	0.041 to 1.760
$\mu_{\alpha 6}$	Canopy	0.823	0.826	-0.771 to 2.518
$\sigma_{\alpha 6}$	Canopy	2.188	0.864	0.794 to 4.198
$\mu_{\beta 1}$	Days	-0.712	0.201	-1.090 to -0.297
$\sigma_{\beta 1}$	Days	0.198	0.184	0.008 to 0.677
$\mu_{\beta 2}$	Days ²	0.678	0.228	0.204 to 1.097
$\sigma_{\beta 2}$	Days ²	0.394	0.193	0.157 to 0.892
$\mu_{\beta 3}$	Temp	0.136	0.077	0.000 to 0.305
$\sigma_{\beta 3}$	Temp	0.151	0.089	0.020 to 0.369
$\mu_{\beta 4}$	Wetness	0.612	0.296	0.023 to 1.197
$\sigma_{\beta 4}$	Wetness	0.609	0.272	0.191 to 1.262
$\mu_{\beta 5}$	Year	-0.170	0.106	-0.387 to 0.031
$\sigma_{\beta 5}$	Year	0.145	0.112	0.006 to 0.420

Notes: Hyper-parameter estimates were extracted from Model 1. Estimates include 95% Bayesian credible intervals (BCI). Variables are μ , mean community response; σ , standard deviation in the response to the covariate across species; SD, standard deviation. Abbreviations are Distsite, distance to the nearest site; Area, wetland area; Fish, presence (1) or absence (0) of *Gambusia holbrooki*; Emergveg, proportion cover of emergent vegetation; Canopy, proportion canopy cover; Days, number of days since 1 September; Days², quadratic effect of Days; Temp, air temperature; Wetness, presence of standing water during a survey; Year, survey year (2000–2001, 1; 2001–2002, 2).

also a negative relationship between mean occupancy and emergent vegetation cover ($\mu_{\alpha 4}$; Fig. 1c), although the 95% BCI overlapped zero slightly (Table 2).

There was a strong positive interaction between the presence of *Gambusia* and emergent vegetation cover ($\mu_{\alpha 5} = 1.183$, 95% BCI: 0.269–2.162; Table 2).

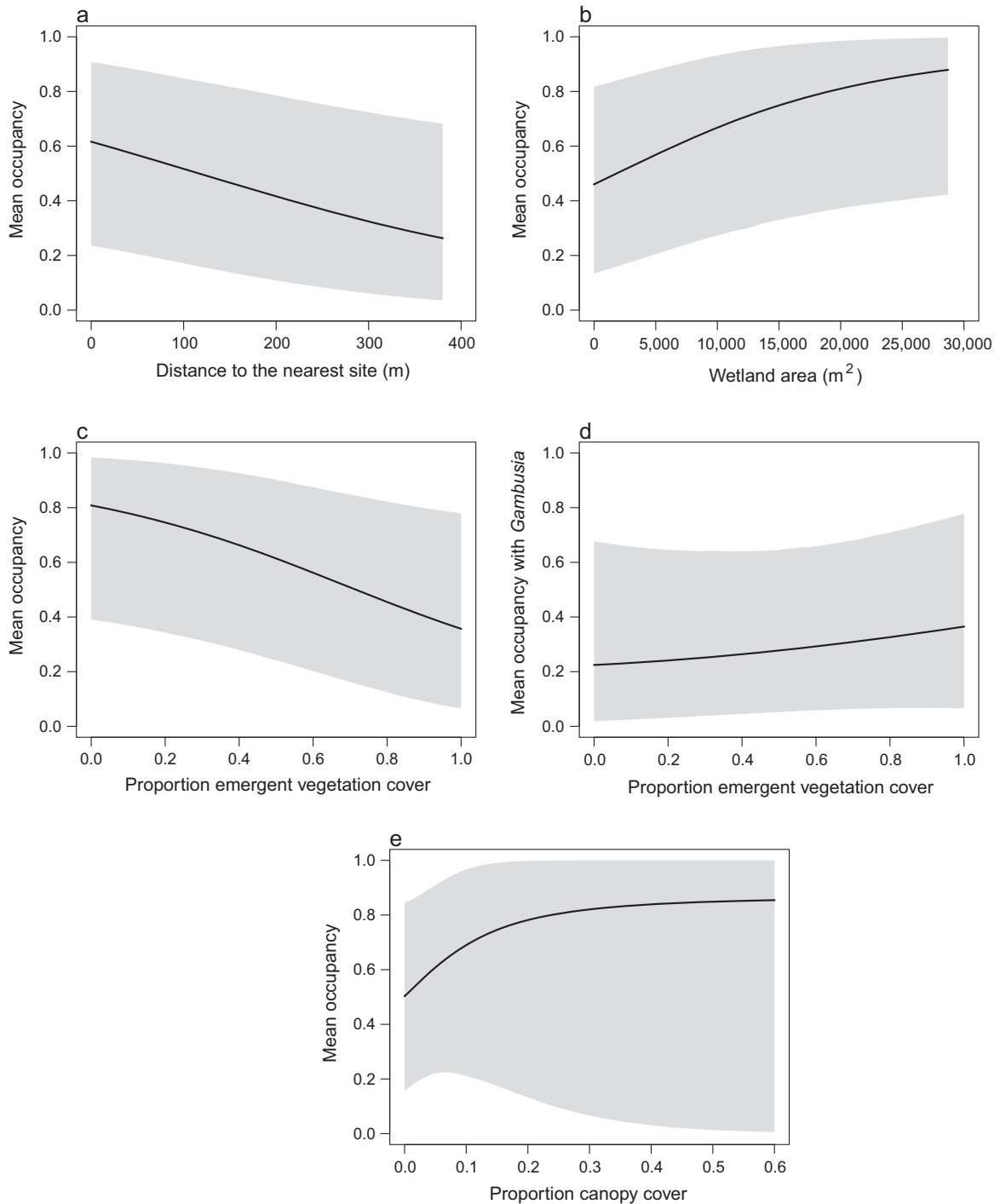


FIG. 1. (a, b, c, e) Mean estimates of the probability of occupancy (shaded areas are 95% Bayesian credible intervals) across the frog metacommunity vs. four habitat covariates recorded on Kooragang Island, Australia. (d) The mean estimated occupancy probability in the presence of an interaction between *Gambusia* and emergent vegetation cover is also shown.

This interaction was stronger and more certain than the relationship between mean occupancy and emergent vegetation cover ($\mu_{\alpha 4} = -0.871$, 95% BCI: $-1.816-0.030$; Table 2). When *Gambusia* is present at

a site, mean occupancy is predicted to increase from 0.225 at sites with no emergent vegetation cover, to 0.366 at sites with 100% emergent vegetation cover (Fig. 1d).

There was a positive but ambiguous relationship between mean occupancy and proportion canopy cover, with the 95% BCI widely overlapping zero ($\mu_{\alpha 6}$; Table 2; Fig. 1e).

There was a clear negative relationship between the mean estimated probability of detection across all frog species and the number of days since the survey season began ($\mu_{\beta 1}$), although a positive quadratic effect of the number of days ($\mu_{\beta 2}$) also indicated that detection across all species peaked during the season (Table 2). The probability of detection also increased with air temperature ($\mu_{\beta 3}$) and if a site contained water during a survey ($\mu_{\beta 4}$; Table 2). There was no clear relationship between mean detection and survey year ($\mu_{\beta 5}$; Table 2).

Species-specific summary

There was a negative relationship between the estimated probability of occupancy for all 11 species and distance to the nearest site (Figs. 2a, 3a), although only *Lit. fallax* had a clear negative relationship with the 95% BCI not overlapping zero (Appendix S5: Table S1). The mean probability of occupancy for all species was positively related to wetland area, with the clearest relationships for *Lim. peronii*, *Lit. aurea*, and *Lit. peronii* (Appendix S5: Table S1). There were small to negligible increases in predicted occupancy with wetland area for ground frogs (Fig. 2b), while most tree frog species showed larger increases (Fig. 3b).

There was a negative relationship between the estimated probability of species occupancy and the presence of *Gambusia* (Fig. 4), with *Lit. latopalmata* and *Platyplectrum ornatum* having clear negative relationships (Appendix S5: Table S1). There was a negative relationship between the estimated probability of occupancy for species and emergent vegetation cover at a site (Figs. 2c, 3c; Appendix S5: Table S1). The predicted decrease in occupancy was greatest for *Lit. aurea*, *Lit. latopalmata*, and *P. ornatum*. For example, occupancy by *Lit. latopalmata* was predicted to decrease from 0.610 at sites with no emergent vegetation, to 0.029 at sites with 100% emergent vegetation cover (Fig. 3c).

There was a positive interaction between the presence of *Gambusia* at a site and emergent vegetation cover, with clear relationships for *Lim. tasmaniensis*, *Lit. aurea*, and *Lit. dentata* (Figs. 2d and 3d; Appendix S5: Table S1). For example, when *Gambusia* are present, occupancy by *Lim. tasmaniensis* was predicted to increase from 0.167 at sites with no emergent vegetation cover, to 0.938 at sites with 100% emergent vegetation cover (Fig. 2d).

There were mixed relationships with canopy cover; there was a strong clear negative relationship with the predicted occupancy for *Lim. peronii* while the other ground frogs showed negligible increase with canopy cover (Fig. 2e), whereas there were strong clear increases in predicted occupancy for the tree frogs *Lit. caerulea* and *Lit. dentata* with an increase in canopy cover at a site (Fig. 3e; Appendix S5: Table S1).

Species richness summary

There was no strong correlation between the estimated number of species at a site and distance to the nearest site ($r = -0.112$) or emergent vegetation cover ($r = 0.063$; Appendix S6: Figs. S1 and S4). There were positive correlations between estimated species richness and wetland area ($r = 0.374$) and canopy cover ($r = 0.286$); Appendix S6: Figs. S2 and S5). Mean estimated number of species at sites where *Gambusia* was absent and present was 5.3 (95% BCI: 3.4–8.0) and 4.5 (1.6–7.1), respectively (Appendix S6: Fig. S3).

DISCUSSION

Our application of multi-species occupancy modeling (MSOM) clearly showed habitat relationships for both very common and rare frog species that would not have been possible using either single-species occupancy models or statistical methods under the EMS framework. Even despite the relatively high survey effort, there was a low probability of occupancy and detection for several rare species, which would have likely produced biased and imprecise parameter estimates from single-species occupancy models (see Guillera-Arroita et al. 2010). Our application of a MSOM should be considered as an example of improvement to the EMS framework under the detection error-corrected EMS (DECEMS) framework because it enabled insight into both species-specific and metacommunity-wide patterns in occupancy. In many instances, habitat relationships for individual species were also consistent with the mean community response, thereby providing evidence of how species-specific responses can generate broader patterns in metacommunity structure. However, there were divergent responses in occupancy amongst some species to local habitat covariates. Our results also demonstrated a link between abiotic and biotic factors at the local scale and landscape processes (connectivity) arising from dispersal within an amphibian metacommunity. We discuss these results according to metacommunity theory and provide recommendations for wetland restoration projects seeking to accommodate the ecological requirements of amphibians and other wetland-dependent taxa.

Our results at both the species-specific and community levels are aligned with metacommunity theory: the mean estimated probability of occupancy increased with wetland area and connectivity (i.e., less distance to the nearest site). Consistent relationships at multiple response levels to wetland area and connectivity emphasize that habitat patch size and dispersal are important in maintaining species composition within amphibian metacommunities (Wright et al. 2020). Metapopulation theory posits that larger patches can support larger population sizes and that connectivity will increase population persistence (Hanski 1998). Hence, there is likely to be frequent dispersal of the individuals of many species among the wetland sites in the study area. For instance,

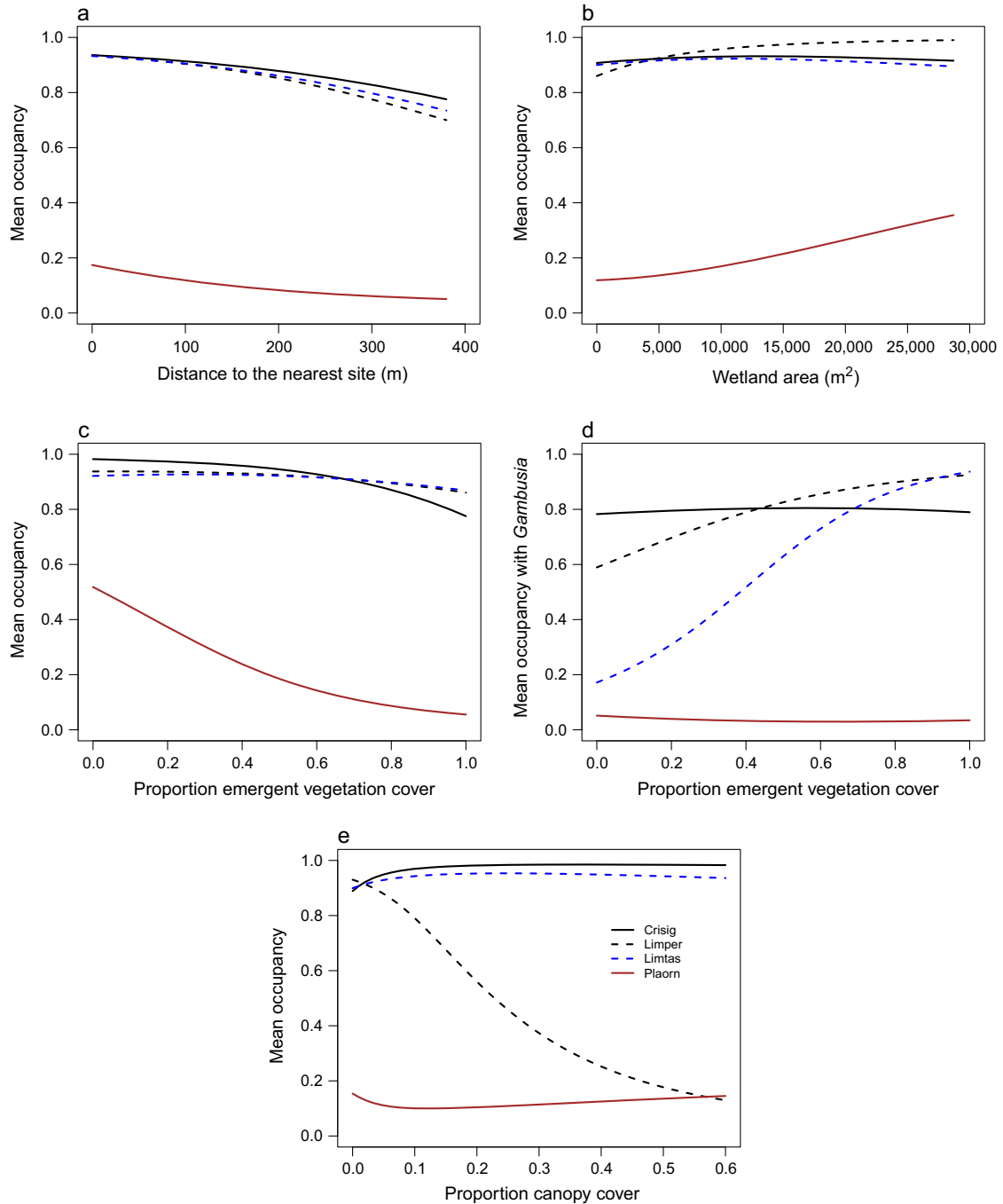


FIG. 2. (a, b, c, e) Mean species-specific estimates of the probability of occupancy for four frog species from two families: Limnodynastidae and Myobatrachidae (ground frogs) detected on Kooragang Island vs. four habitat covariates, (d) including an interaction between *Gambusia* presence and emergent vegetation cover. Credible intervals are omitted for clarity. Species codes: Crisig, *Crinia signifera*; Limper, *Limnodynastes peronii*; Limtas, *Lim. tasmaniensis*; Plaorn, *Platyplectrum ornatum*.

a mark-recapture study of *Litoria aurea* in the study area detected frogs moving to the nearest wetland site (Hamer et al. 2008). This result therefore illustrates that the mass-effect perspective of metacommunity theory,

which emphasizes the role that immigration and emigration affects local population densities (Leibold et al. 2004), is partly driving metacommunity structure in our study area. Larger habitat patches are also hypothesized

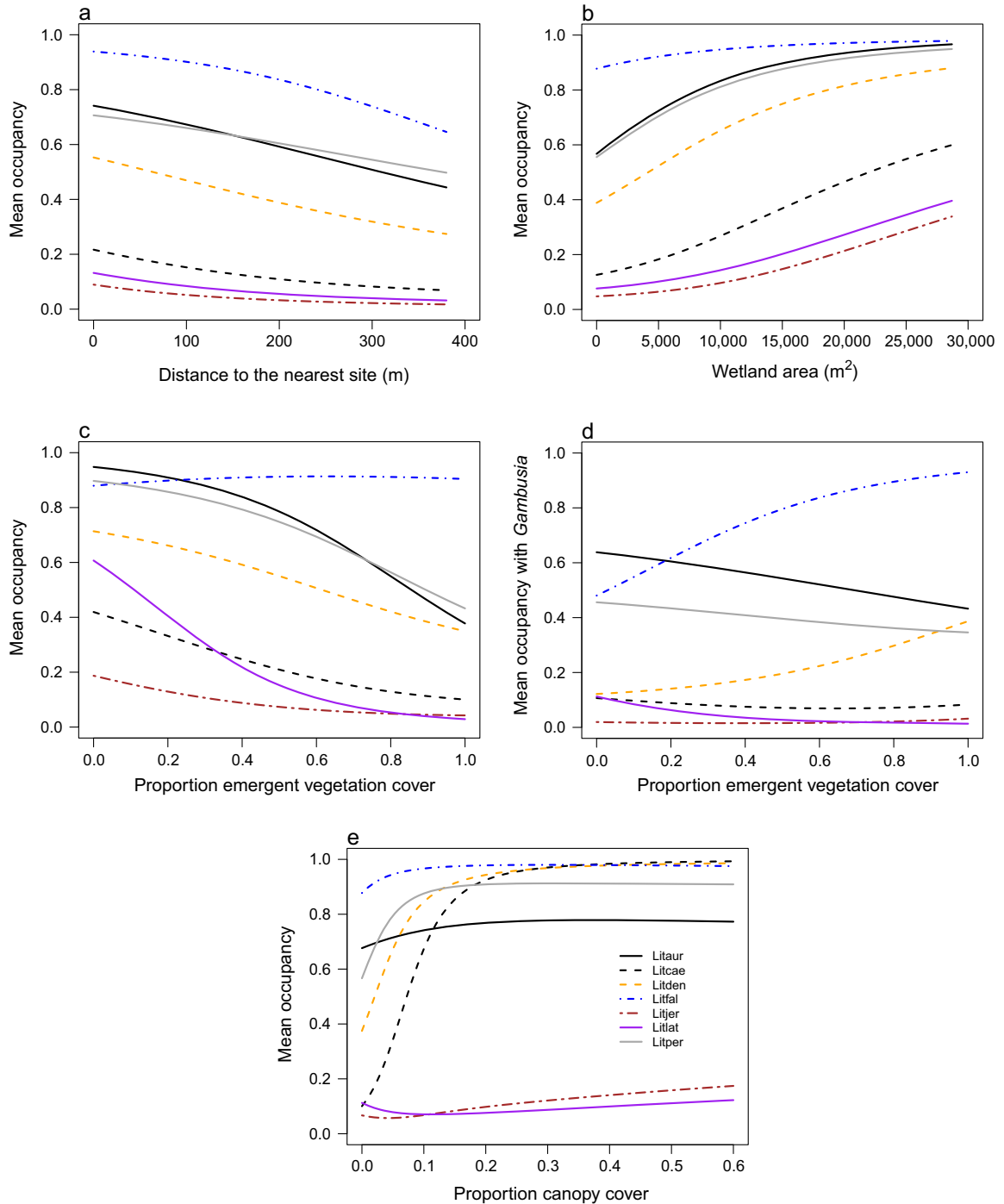


FIG. 3. (a, b, c, e) Mean species-specific estimates of the probability of occupancy for seven frog species from the family Pelodyridae (tree frogs) detected on Kooragang Island vs. four habitat covariates, (d) including an interaction between *Gambusia* presence and emergent vegetation cover. Credible intervals are omitted for clarity. Species codes: Litaur, *Litoria aurea*; Litcae, *Lit. caerulea*; Litden, *Lit. dentata*; Litfal, *Lit. fallax*; Litjer, *Lit. jervisiensis*; Litlat, *Lit. latopalmata*; Litper, *Lit. peronii*.

to support a greater number of species (species–area relationship; Hanski 1994) and we found a positive relationship between wetland area and species richness

(Appendix S6: Fig. S2). Our results suggest that wetland restoration programs should create large, well-connected wetlands to increase the chance of amphibian

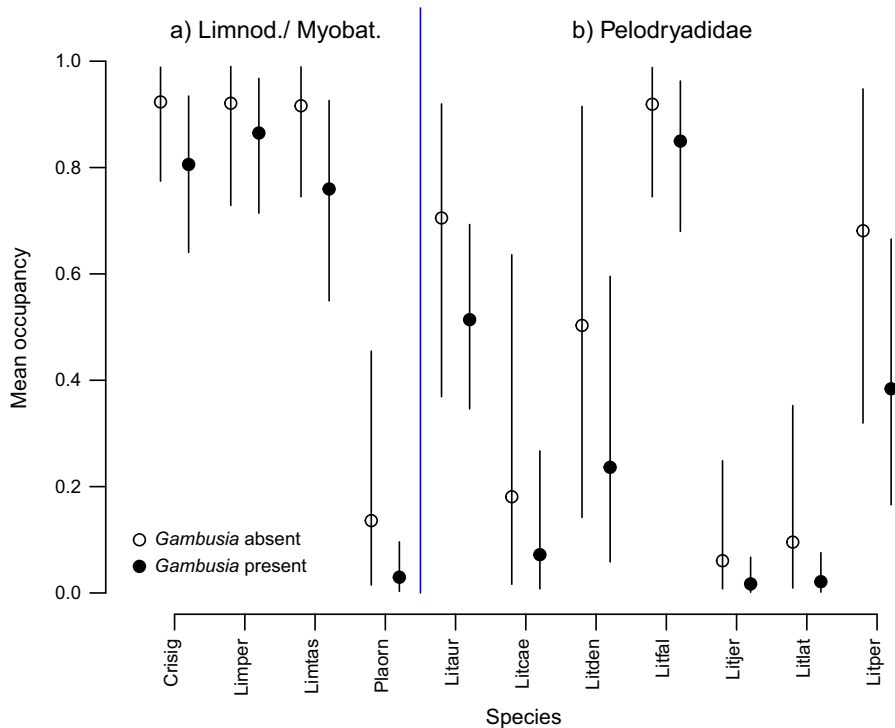


FIG. 4. Mean species-specific estimates (and 95% Bayesian credible intervals) of the probability of occupancy for 11 frog species from three families (a) Limnodynastidae and Myobatrachidae (ground frogs) and (b) Pelodyridae (tree frogs) detected on Kooragang Island vs. the presence or absence of the eastern mosquitofish (*Gambusia holbrooki*) at wetland sites. See Figs. 2 and 3 for species codes.

colonization and persistence. This approach would also likely benefit a range of wetland species including aquatic macroinvertebrates (Hill et al. 2015), freshwater turtles (Roe and Georges 2007), and waterbirds (Murray et al. 2013) that require landscape-scale management to conserve populations.

There was a strong negative relationship between mean occupancy and the presence of *Gambusia* at the community and species-specific levels. This result highlights the importance of fish as aquatic predators in structuring amphibian metacommunities. The presence of *Gambusia* has been previously shown to shape amphibian communities by reducing the occupancy, abundance or survival of some species (Baber and Babbitt 2004, Hamer and Parris 2013, Shulze et al. 2013). Strong negative associations have been reported between *Gambusia* and detections of tadpoles of several frog species (e.g., *Lit. aurea*) in wetlands on Kooragang Island, but that adults do not avoid sites with *Gambusia* (Klop-Toker et al. 2018). Aside from amphibians, *Gambusia* also have detrimental impacts on populations of aquatic invertebrates and other fish species in freshwater wetlands (Pyke 2008), and so an ecosystem-based approach may be required to control the negative effects of this fish on freshwater communities.

Within the frog metacommunity, the strongest negative relationships were between *Gambusia* and species

that breed in ephemeral ponds such as *Lit. latopalmata* and *Platyplectrum ornatum*. For instance, *P. ornatum* has a short larval development period suited to temporary ponds (Anstis 2013), and ephemeral-pond-breeding frog species typically do not possess behavioral defenses against fish predators (Kats et al. 1988). Moreover, these relationships were independent of the effects of hydroperiod, as there was no strong correlation between ephemerality and *Gambusia* presence in the study area, and *Gambusia* have been observed colonizing ephemeral wetlands during localized flooding after heavy rainfall (Hamer 1998). As such, it appears that the distribution of these and other frog species in the study area was restricted by the presence of *Gambusia*. Experimental evidence suggests that *Gambusia* has the potential to significantly affect larval populations of *P. ornatum* in natural waterbodies where these species co-occur (Komak and Crossland 2000), but there are also several other frog species detected in the study area that have tadpoles observed to be attacked and eaten by *Gambusia* in experiments, including *Limnodynastes peronii*, *Lit. aurea*, *Lit. dentata*, and *Lit. peronii* (Morgan and Buttemer 1996, Webb and Joss 1997, Pyke and White 2000).

There was a negative relationship between mean community and species-specific occupancy and emergent vegetation cover. However, there was also no clear relationship with species richness. While most amphibian

studies reported an increase in occupancy with increased emergent vegetation cover at a site (Appendix S2: Table S1), there are some exceptions. For example, Knutson et al. (2004) found that amphibian reproductive success was highest in ponds with less emergent vegetation and lacking fish. In a field manipulation experiment on Kooragang Island, increased emergent vegetation cover did not increase occupancy rates by *Lit. aurea* in wetlands (Fardell et al. 2018). Our measure of aquatic vegetation complexity only considered emergent vegetation and there may also be relationships between occupancy and other vegetation strata, such as submerged and floating vegetation, which provide shelter for both frogs and tadpoles, and egg-laying sites (Semlitsch 2000). Nonetheless, sections of waterbodies with open water provide calling sites for breeding aggregations. Within the frog metacommunity we examined, *Lit. aurea*, *Lit. latopalmata*, and *Platyplectrum ornatum* had the strongest negative relationship with emergent vegetation cover, implying that these species require areas of open water as calling sites. For instance, Fardell et al. (2018) reported that occupancy by adult female *Lit. aurea* on Kooragang Island was higher at sites with a medium density of emergent vegetation, but that occupancy by males was also equal in sparsely vegetated wetlands. Wetland managers therefore need to ensure that emergent vegetation does not smother wetlands, and that some wetland sections may require careful thinning of emergent vegetation to provide open pools of water. Elsewhere, created wetlands with little aquatic vegetation are preferred breeding sites by some amphibian species (Porej and Hetherington 2005, Swartz et al. 2020).

There was no support for a model that included ephemerality rather than emergent vegetation cover, indicating that wetland hydroperiod had no discernible influence on occupancy. However, we used a simple categorical variable for hydroperiod that may not have represented the full complexity of wetland hydrology experienced at sites during the study. While a previous synthesis highlighted the strong role that hydroperiod plays in structuring freshwater communities (Wellborn et al. 1996), primarily because of the relationship with fish predation (Snodgrass et al. 2000b), this study found that emergent vegetation was more important in determining community composition. Accordingly, our findings do not fully concur with the freshwater habitat gradient model proposed by Wellborn et al. (1996), although there may be other unmeasured covariates that were affecting this relationship in our study area. For instance, this model was found to be not applicable to frog communities in urban ecosystems due to a greater prevalence of permanent waterbodies in urban areas (Hamer and Parris 2013). Hydroperiod was not an important factor in determining community structure in other studies that detected similar frog species in Australian wetlands (Hamer and Parris 2011, Hamer 2016). Further investigations into the effect of hydroperiod on Australian frog species in wetland restoration and

monitoring programs are warranted, including the need to develop a standard measure of hydroperiod that accurately encapsulates the ecological requirements of individual species within the broader community as well as the complexities of wetland hydrology. Nonetheless, current evidence suggests that wetland restoration programs should aim to create waterbodies with varying hydroperiods to address the life-history requirements of individual amphibian species (Semlitsch 2000) and other taxa (e.g., macroinvertebrates [Hill et al. 2017], freshwater turtles [Roe and Georges 2007]).

The relationship between emergent vegetation cover and the presence of *Gambusia* was accentuated through the strong interaction between the two covariates; mean community occupancy increased with vegetation cover at sites where *Gambusia* was present, thereby providing evidence that aquatic habitat complexity may reduce predation rates. Moreover, there was a strong clear positive interaction for *Lim. tasmaniensis*, *Lit. aurea*, and *Lit. dentata*. There is evidence that *Gambusia* attacks and consumes *Lim. tasmaniensis* tadpoles (Turner 2017), although experimental evidence suggests that *Lim. tasmaniensis* can detect and subsequently avoid *Gambusia* (Lane and Mahony 2002), presumably by taking refuge amongst aquatic vegetation in wetlands. Moreover, *Lim. tasmaniensis* and *Lit. aurea* do not possess life-history traits that may otherwise permit coexistence with predatory fish (i.e., both species have relatively long larval development periods; Lane and Mahony 2002, Hamer et al. 2002b), and so tadpoles may depend on habitat structure or reduced activity to evade fish (Jansen and Healey 2003, Sanders et al. 2015). High aquatic habitat complexity reduces *Gambusia* predation on amphibian larvae (Baber and Babbitt 2004), and the planting of aquatic vegetation cover has been advocated in wetland restoration to increase amphibian occupancy and reproductive success (Pearl et al. 2005, Shulse et al. 2012, Holgerson et al. 2019, Rowe et al. 2019). Predation by *Gambusia* on eggs and tadpoles is recognized as a key threat to *Lit. aurea* (Pyke and White 2001), although the presence of aquatic vegetation is thought to ameliorate the impact of *Gambusia* in many populations (White and Pyke 2008). Similarly, our results suggest that establishing emergent vegetation cover may offset the negative effect of *Gambusia* at wetland sites. However, as discussed previously, emergent vegetation should not be allowed to completely cover wetlands, and the best management regime may be to create a mosaic of both sparsely and densely vegetated habitats (Fardell et al. 2018). This outcome could also be achieved by pond draining to both eradicate *Gambusia* and thin macrophytes (Pollard et al. 2017). One experimental study suggested that aquatic vegetation may provide insufficient refuge for aquatic invertebrates and amphibian larvae from *Gambusia* predation, and that direct removal of this fish is the best method to improve the conservation potential of restored wetlands (Shulse et al. 2013).

There was an increase in mean community occupancy with increasing canopy cover, although the wide credible

interval around the estimate reflected the uncertainty arising from low canopy cover recorded at most sites. Nonetheless, there was a strong positive response by *Lit. caerulea* and *Lit. dentata* to increasing canopy cover. Although occupancy by *Lit. caerulea* was predicted to increase sharply with canopy cover, the species was observed at one site perched on a dead tree (stag) on the waterbody bank, which was the only tree at this site. This species uses tree hollows as shelter sites (Reynolds 2005), is more abundant in wooded habitats (Ocock et al. 2016), and there have been significant declines in populations of *Lit. caerulea* in the wider region due to urbanization (Lemckert and Mahony 2018, Rowley and Callaghan 2020). Accordingly, the importance of fine-scale habitat features cannot be overlooked when assessing metacommunity composition, as they may provide crucial microhabitats as shelter (e.g., cracks and hollows in tree branches). This result also highlights the role of terrestrial habitat structure for amphibian occupancy of wetlands. Our results suggest that, for wetland restoration, providing canopy cover around a wetland is likely to increase habitat quality for *Lit. caerulea* and other tree frogs, but should be balanced by the need to retain open, sunny sections of the waterbody for other species that may require higher water temperature or basking sites (e.g., *Lit. aurea*; Pyke and White 2001). Heterogeneity around wetland perimeters also provides greater habitat availability and diversity for waterbirds (Murray et al. 2013) and freshwater turtles (Marchand and Litvaitis 2004), and should be incorporated into the design of new wetlands.

Our results provided insight into two perspectives of metacommunity theory. Clear relationships between mean community and individual species occupancy and distance to the nearest wetland site highlights the potential role of immigration and emigration in shaping the frog communities at sites. Spatial dynamics characterize the mass-effect perspective of metacommunity theory, and patch area can influence mass effects by creating differences in population size or density in different patches (Leibold et al. 2004). There was a clear positive relationship between mean community and species occupancy and wetland area, and spatial dynamics may be affecting local population densities in wetland patches of different sizes owing to the relationship between population size and patch area (Hanski 1998). For instance, in the study area the probability of wetland occupancy by *Lit. aurea* increased with increasing wetland area and population size, and decreasing distance to the nearest site where the species was detected, all of which decreased the probability of turnover (Hamer and Mahony 2010). Our results also highlighted the strong role that the species-sorting perspective of metacommunity theory played in shaping the frog communities in the study area, because there were clear and sometimes contrasting relationships between mean community and individual species occupancy and local habitat quality (presence of *Gambusia*, emergent vegetation, and canopy cover). The species-

sorting perspective emphasizes that niche separation along environmental gradients generates strong differences in population persistence whereby patch quality (biotic and abiotic factors) and dispersal determine local community composition (Leibold et al. 2004). Hence, we demonstrated that the mass-effect and species-sorting perspectives of metacommunity theory are structuring frog communities in the wetland system we examined. These two perspectives were also likely to be responsible for influencing composition within amphibian metacommunities in different landscape types (Urban 2004, Parris 2006, Richter-Boix et al. 2007, Johnson et al. 2013).

We assumed that the frog metacommunity was closed over the two breeding seasons. This is a reasonable assumption given that the study area was located on an estuarine island where immigration/ emigration to surrounding wetlands on the mainland is unlikely across the north and south arms of the Hunter River. However, two species detected in the study area during surveys conducted for a previous investigation in 1999–2000 were not detected during our surveys in the following two seasons (*Litoria verreauxii* and *Uperoleia laevis*; Lane et al. 2007). Both species were detected at relatively few sites in 1999–2000 and so it is likely that their rarity contributed to failed detections in 2000–2001 and 2001–2002, although the possibility of local extinctions should not be discounted. It appears that the inherent rarity of some frog species in the study area is likely to produce temporal differences in detection trends, perhaps due to climatic fluctuations. Nonetheless, there were no differences in mean rainfall between the two seasons we examined (87.8 mm and 91.1 mm, respectively), and there was no clear relationship between the probability of detection and survey year for all frog species except *Lit. aurea*, which was higher in 2000–2001 (Appendix S5: Table S1).

The hierarchical framework of Zipkin et al. (2009) is a powerful tool for conservation managers who need to effectively monitor rare and threatened species at multiple spatial scales. The main advantage of MSOM for monitoring programs is their ability to derive unbiased estimates of occupancy and species richness that can be compared over time to gauge potential trends in animal communities (Zipkin et al. 2010). For instance, we intend to compare occupancy estimates generated from our model to those produced from models based on more recent data sets (post-2010), in order to determine if any species have declined in the proportion of sites occupied. This approach may be especially important for monitoring the occupancy status of rare species and those with declining populations. However, analysis of monitoring data using MSOM to gauge occupancy trends for declining amphibian species needs to be done concurrently with the development of management plans that identify when early interventions may be warranted to prevent substantial decreases in occupancy (Grant et al. 2013). Importantly, monitoring programs for restoration projects should be closely connected to

testing ecological concepts and theory, so that the underlying ecological mechanisms giving rise to observed patterns can be identified (Lindenmayer 2020). Here, we present empirical evidence that metacommunity theory provides an appropriate framework for developing monitoring programs for wetland-dependent taxa such as amphibians. Besides monitoring for rare species, we also advocate monitoring common species as declines in their populations may go unnoticed (Gaston and Fuller 2008). We urge ecological managers to use MSOM in monitoring programs so that community-wide trends in animal populations can be derived while accounting for uncertainty arising from the sampling process.

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SUPPORTING INFORMATION

Additional supporting information may be found online at: <http://onlinelibrary.wiley.com/doi/10.1002/eap.2293/full>

DATA AVAILABILITY STATEMENT

Data are available from the Dryad Digital Repository (Hamer et al., 2020): <https://doi.org/10.5061/dryad.b8gtht7b5>