Future extinction risk of wetland plants is higher from individual patch loss than total area reduction

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ABSTRACT

Quantifying the risk of extinction due to habitat loss is an increasingly urgent task for the design and implementation of effective conservation interventions. Methods based on species- and endemics-area relationships are well developed, but applications to date have concentrated primarily on the fragmentation of formerly continuous habitats such as forests and woodlands. Applying these area-based methods to predict extinction risk in habitat types occurring naturally as spatially discrete patches has been largely ignored. We address this knowledge gap using a network of seasonally connected wetlands. We modelled the risk of extinction associated with native wetland plant communities under two alternative scenarios: the loss of (*i*) entire wetlands (*patch loss*) versus (*ii*) an equivalent area distributed across the wetlands (*area loss*). Patch-loss scenarios resulted in more than twice the number of species going extinct than the equivalent loss of area. Extinction due to patch loss was highest when wetlands were removed in increasing size order (smallest to largest) – a plausible scenario arising from forecast climatic drying in the region. Small wetlands contained >16% of endemic species in only <5% of wetland area, largely explaining this result. Extinction risk associated with naturally occurring habitat patches depends on the distribution of regionally endemic species; where this is not solely a function of habitat area, the loss of small patches can represent higher risk than an equivalent reduction in total habitat area across the network.

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1. Introduction

Habitat reduction and fragmentation have long been identified as factors increasing species' extinction risk (e.g., Ehrlich and Ehrlich, 1981), so quantifying the relationship between area and species loss has been an important tool for conservation planning. The simplest and most common approach for predicting change in species number from habitat loss or fragmentation is the species-area relationship, where the expected number of species decays non-linearly with declining total habitat area (e.g., Brooks et al., 1997; Pimm and Askins, 1995). An alternative approach, first introduced by Harte and Kinzig (1997), uses the endemics-area relationship. It is generally accepted that the choice of method should be determined based on the geometry of the cleared area, although in reality habitat loss is almost always irregular and so both methods provide only approximations (Kinzig and Harte, 2000; Harte and Kitzes, 2012).

Endemic species are those occurring over limited geographical areas (Harte and Kinzig, 1997; Kinzig and Harte, 2000), and this restricted spatial distribution generally places them at higher extinction risk than those with broader distributions (Sodhi et al., 2009). As a result, protecting the most species-rich sites does not necessarily achieve the lowest extinction rate because sites with the highest species richness do not always have high endemicity (Prendergast et al., 1993; Zurlini et al., 2002). Therefore, considering the spatial distribution of endemics is important for conservation planning (Rodrigues and Gaston, 2001), and predicting extinction risk (He and Hubbell, 2011). Although the term 'endemic' commonly refers to global distributions, it can also be applied to distinguish "… species found only in a sub-patch of a larger distinct biome" (Harte and Kinzig, 1997).

A common theme in extinction studies using species- or endemics-area methods is a focus on patches that remain after the fragmentation of a formerly continuous habitat area. Examples include temperate woodlands (Pimm and Askins, 1995) or tropical forests (Brook et al., 2003), with studies typically evaluating risk at continental or larger scales (e.g., Malcolm et al., 2006; Ulrich, 2005). Species-area-based methods used to predict extinction patterns on true islands also have some validation (e.g., Brooks et al., 1997; Gibson et al., 2013), but

there has been no attempt to apply these methods to their habitat-island analogues: ecosystems that occur naturally as discrete patches in a contrasting and largely hostile matrix. Many such systems (e.g., wetlands or coral reefs) support high biodiversity and many are losing both area and entire patches (Davidson, 2014; Mellin et al., 2016), but the use of species- or endemics-area-based methods in this context has not yet been investigated. We address this gap, applying the endemics-area relationship to determine the extinction risk arising from habitat loss for a network of discrete wetland patches.

Understanding the consequences of reduced wetland area for biodiversity is necessary; global wetland area has already been reduced to between 29 and 36% of what it was just over a century ago, declining on average at a rate of >1% year^{-1}, with mean annual losses of up to 2% in Asia and the Neotropics (Davidson, 2014). These rates of loss currently show no signs of slowing (Davidson, 2014) and are similar to the estimated 1.4% annual loss of humid tropical forest occurring between 2000 and 2005 (Hansen et al., 2008). The high diversity and endemicity of freshwater biota (Balian et al., 2008; Dudgeon et al., 2006) suggests that many wetland species are likely to have been extirpated already. While there have been studies quantifying the risk of habitat loss for freshwater fish (Giam et al., 2012; Xenopoulos and Lodge, 2006) and riparian vegetation (Ström et al., 2012), the effect of area loss on wetland plant communities at regional or broader scales has not been quantified.

We modelled the risk of extinction for wetland plants in a typical (temperate) agricultural landscape, comparing the loss of entire patches with the equivalent area spread evenly across wetlands, using both species- and endemics-area-based methods. Our a priori hypothesis is that wetland patch loss will elicit a higher extinction risk because of high β-diversity and the many rare terrestrial species found in the study region (Deane et al., 2016). We show that the loss of entire wetland patches not only leads to a higher extinction risk compared to an equivalent reduction in area, but that the loss of smaller wetlands creates the highest risk of species extinctions for any given amount of area lost.

2. Methods

Our study region was the Fleurieu Peninsula in South Australia, covering an area of 1200 km^2 centred approximately on latitude 35.5°S. The climate of the region is Mediterranean with warm, dry summers and cool, wet winters. Rainfall varies from 500 to 900 mm/yr and falls predominantly during winter and spring months. We used a regional vegetation dataset (Deane, 2016) created by combining multiple vegetation surveys with a state agency database, selecting only wetlands with near-complete censuses data (as described in Deane et al., 2016). We removed exotic plants from the analysis, but retained terrestrial species. The final dataset included 76 wetlands ranging in size from 0.41 to 34.7 ha (total 343 ha), with native plant species richness ranging from 10 to 60 wetland^{-1} (Fig. 1; Fig. A1, online Appendix A). Total native plant species richness was 215 species and the median area of occupancy was 24.0 ha (see Fig. A2, online Appendix A for the range-size distribution). To provide a more general result, we converted both richness and area to proportions of total values.

2.1. Patch loss: loss of entire wetlands

In the patch-loss scenarios, we assumed that conversion to agriculture is likely to occur (e.g., wetland conversion for row crop expansion in the U.S.; Johnston, 2013), resulting in the loss of native species. We considered situations where the loss of wetlands happens at random and where the loss followed a specific wetland size-based order of removal.

2.1.1. Random loss of wetlands

We used a random wetland patch-loss model to establish a baseline expectation of likely species loss as wetlands were removed. We used this to provide a point of comparison for other patch- and area-loss scenarios. We calculated random patch loss as follows:
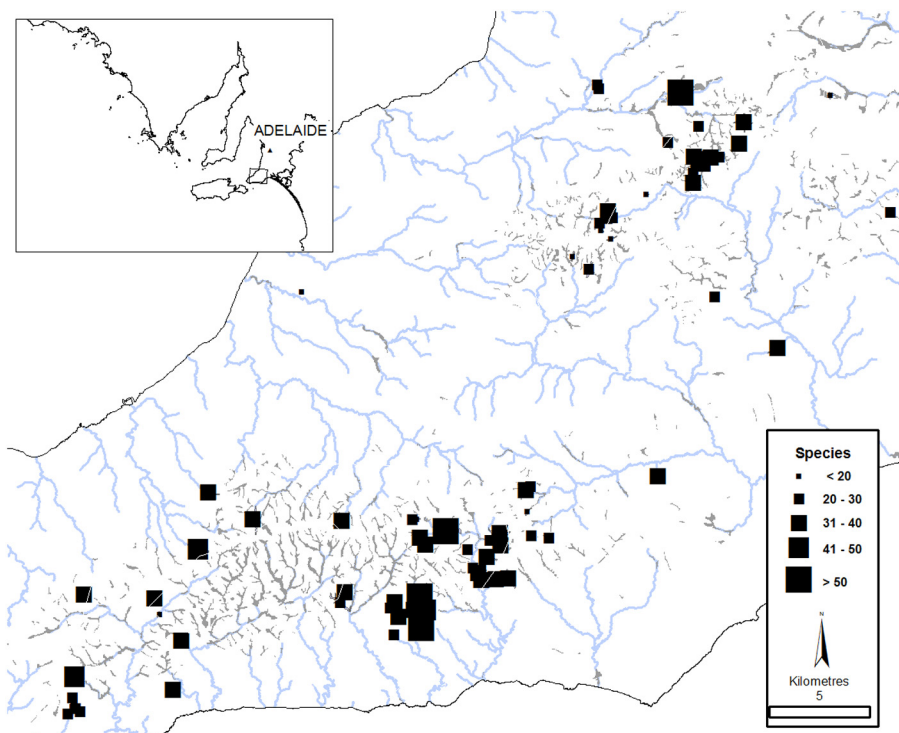

Fig. 1. Location and species richness of study wetlands. Symbols are located at wetland centroids and the relative size denotes the range of native plant species richness.

1. We first randomly sampled one wetland from the entire pool of wetlands and counted the number of endemic species (defined as occurring in only the selected wetland). We then set this sampled wetland as 'destroyed', eliminating the endemic species it contained. We repeated this sampling 76 times from the wetland database, providing 76 one-wetland samples. We used the average of these 76 one-wetland samples to estimate random patch loss for the loss of one wetland and to estimate the 0.025 and 0.975 quantiles to quantify the uncertainty of species loss.

2. We then randomly sampled two wetlands from the pool of wetlands. This time the two sampled wetlands were the wetlands destroyed and the endemic species within them removed. In this case we did not sample all possible combinations of two wetlands. Rather, we randomly sampled two wetlands with replacement, eliminating the endemic species these contained. We repeated this step 200 times to obtain 200 two-wetland samples, averaging to obtain the random patch-loss estimate for two wetlands.

3. We continued this procedure by sampling three wetlands, and so on, until all wetlands were destroyed.

2.1.2. Size-ordered patch-loss

The above random loss of wetlands is one possible scenario, but it is perhaps more likely that some systematic process would be involved, where the risk of wetland loss was related to its size. For example, the loss of the smallest wetlands could occur because they are more susceptible to drying from projected reductions in annual rainfall in the region (Charles and Fu, 2014). In contrast, larger wetlands could be lost first due to the reclamation of wetlands for productive uses via direct drainage, where larger wetlands were targeted because of the increased area returned per unit investment. We therefore simulated the effects of the size-ordered loss of wetlands from smallest to largest and vice versa. To do this we basically repeated the random-patch loss method, but rather than selecting wetlands at random, we removed them in order according to their size. In this way we constructed two patch-loss curves. One described the species lost when wetlands were removed from smallest to largest patches, while the other described the opposite (the destruction of largest to smallest wetland patches).

Compared to the random loss of wetlands, size-ordered removal has only one possible value of species loss as each wetland is removed according to its specific size. To quantify the uncertainty in the loss of species in the two size-ordered removal scenarios, we therefore bootstrapped as follows:

1. We first resampled with replacement a new set of wetlands from our original 76 wetland set. The new resampled set is the same size (76), but with some of the wetlands replicated.

2. We then repeated the size-determined order of removal (either smallest-largest or vice versa); this gave one realisation of a bootstrapped estimate of the number of endemic species lost in either case.

3. We repeated the resampling and size-ordered endemic-species calculations 1000 times and estimated 95% confidence limits in endemic-species losses as the 0.025 and 0.975 quantiles of this distribution.

2.2. Area loss: decreases in wetland area, but not number

In addition to the above patch-loss scenarios, we were also interested in estimating area-based habitat loss where each wetland lost a proportion of its total area, but where no patches were entirely removed. We were interested in predicting the loss of species due to loss of contiguous areas. To achieve this, we needed to construct species- and endemics-area curves for the wetland system. However, because we did not have data on the spatial distribution of each species within each wetland, we were unable to calculate directly the loss of species by destroying part of a wetland patch. To solve this problem, we collected data from four vegetation associations of contrasting structure within a large wetland (34.7 ha) typical of the region, allowing us to construct contiguous species- and endemics-area relationships. Two vegetation associations were located in wetland fringes and two near the wetland core. In each vegetation association, we sampled a square 32×32 m plot divided into 100 equal-sized cells of dimension 3.2×3.2 m (~ 10 m^2) and we recorded the presence and absence of each species in every cell.

We built an endemics-area relationship for each of the four plots by sampling increasing proportions of the total area. We first calculated the average number of species found only in a single grid cell, which represented the endemic species at 10-m^2 scale. We then did the same for a 2×2 cell area (40 m^2) by repeating the calculation over every combination of 2×2 cell windows (note that the endemics-area relationship did not change when we instead sampled using a rectangular sampling window – see Fig. A4 in online Appendix B). We increased the sampled area in this fashion (e.g., 3×3 cells, 4×4 cells, etc.) up to plot scale for each plot, resulting in four endemics-area relationships. We used the same sampling approach to estimate the species-area relationship, but counted the average number of new species encountered with each increase in sampling area. To provide a more general result, we converted all estimated species lost to the proportion of the total number for that plot.

To estimate the proportion of species lost for different area-loss scenarios, we used the following equation derived from the power-law species-area model (He and Hubbell, 2011):

$$S_{loss}/S_A = 1-(1-a/A)^z \tag{1}$$

where S_{loss}/S_A is the fraction of species lost, a/A is the fraction of area destroyed, and z is a fitted slope parameter. We estimated z using three different datasets to provide a range in area-loss predictions to compare with the patch-loss estimates.

First we used Eq. (1) directly to fit the within-wetland endemics-area relationship from our grid data. We refer to this z as z_{EAR}. By doing this, we assume that endemic-species distributions in other wetlands are comparable to the spatially sampled wetland. Second, we fitted a power-law species-area curve ($S = cA^z$, where $A =$ the sampling area, $S =$ recorded species, and c and z are constants) to our within-wetland species-area relationship from our gridded data, denoting the slope as z_{SAR}. Finally, we fitted a power-law species-area curve among-wetlands using the total dataset, where the area was the wetland area and the species numbers were the observed species richness. In the classification system proposed by Scheiner (2003), the within- and among-wetland SAR represent Type IIA and IV species-area relationships, respectively, with the latter also known as the 'island' species-area relationship (Triantis et al., 2012). We refer to this as z_{iSAR}. Thus, we had three z values with which to estimate the number of extinctions for a reduction in area using Eq. (1). In area-loss scenarios, we used 95% confidence limits on the estimated z to quantify uncertainty in the number of species lost.

We fitted Eq. (1) and the power-law species-area curves using non-linear least squares in R (R Core Team, 2014). We calculated confidence intervals from likelihood profiles using the R library MASS (Venables and Ripley, 2002) and prepared all figures using library ggplot2 (Wickham, 2009).

2.3. Comparing patch- and area-loss scenarios

We compared the results of the three area-based methods with the random patch-loss model (Section 2.1.1) at five arbitrary area-loss increments of 20, 40, 50, 60 and 80% of wetland area. The actual increments were constrained to take values that were multiples of the average wetland area (4.52 ha), so they did not correspond to even fractions of the total. The five proportional losses of total wetland area that we used to calculate extinctions in both patch- and area-loss scenarios were: 19.7, 39.4, 50.0, 60.5 and 80.3%, which we report as 20, 40, 50, 60 and 80%, respectively.

3. Results

The number of endemic species found in a wetland (defined as occurring in a single wetland) was positively correlated with both total wetland species richness (Kendall's $\tau = 0.38$, $n = 76$, $p < 0.001$) and wetland area (Kendall's $\tau = 0.20$, $n = 76$, $p = 0.01$). The 18 smallest wetlands (<1.5 ha) contained 16.2% of all endemic species in <5% of total wetland area, which was consistent with a null expectation for the observed occupancy pattern (mean of 1000 simulated communities [±95% confidence intervals] = 14.8 [7.4, 23.5]%; online Appendix B). In comparison, the 18 largest wetlands contained 23.5% of endemic species within 62.3% of total wetland area.

For a given loss of wetland area, species extinctions predicted from patch loss were always higher when smaller wetlands were removed first and were similar to a worst-case rate of loss (Fig. 2; Fig. A3, online Appendix A). Removing wetlands in order of decreasing size resulted in fewer extinctions for a given area than did random patch loss (Fig. 2; Fig. A3, online Appendix A). For a 50% loss of regional wetland area, the random patch-loss scenario predicted the extinction of up to one quarter of the regional species pool (mean [95% confidence limits] = 20.4 [16.0, 24.8]%).

Both Eq. (1) (endemics-area) and the power-law (species-area) explained most of the variation in the gridded data ($R^2 = 0.85$ and 0.97, respectively; Fig. 3). The fit of the island species-area relationship was not as good, explaining less than half of the variation in richness ($R^2 = 0.39$; Fig. 4). The slope (z_{EAR}) for the endemics-area relationship $z_{EAR} = 0.13$ [0.11, 0.15] (mean and 95% confidence limits) was smaller than that of both the gridded data ($z_{SAR} = 0.19$ [0.18, 0.21]) and island ($z_{iSAR} = 0.21$ [0.15, 0.27]) species-area relationships.

Area loss resulted in fewer species extinctions than random patch loss, irrespective of the model used in predictions (Fig. 5). Mean expected species extinctions from area loss using the endemics-area estimate are less than half of those predicted based on the random patch-loss scenario (mean difference = 43%). Based on the species-area relationship, the predicted number of extinctions due to area-loss never exceeded 70% of those calculated using random patch loss (Fig. 5).
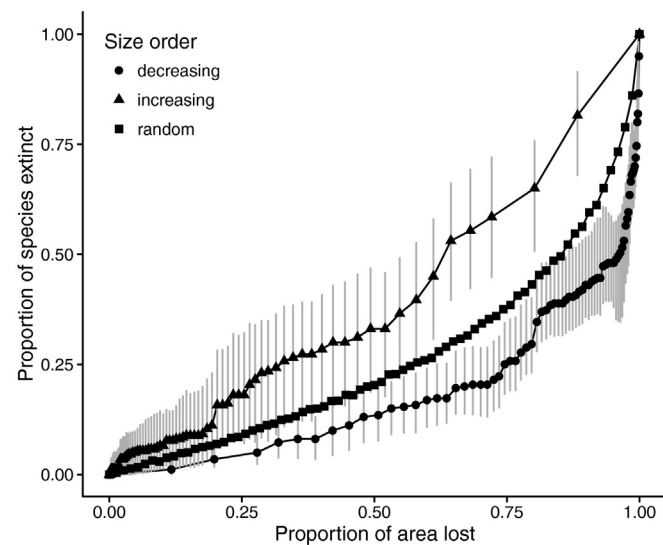

Fig. 3. Predicted change in proportion of species for a given change in proportion of wetland area for gridded data. *Lower curve: y*-axis values show the proportion of species lost for the endemics-area relationship. *Upper curve:* the proportion of species accumulated under the species-area relationship for the proportional change in area indicated on the *x*-axis. The endemics- ($z_{EAR} = 0.13$) and species-area ($z_{SAR} = 0.19$) relationships were modelled using Eq. (1). Grey triangles show observed data. Dashed lines show curves fit using the 95% confidence limits for parameters z_{EAR} and z_{SAR}.

4. Discussion

Removing entire wetlands resulted in a higher risk of plant extinctions than the loss of an equivalent area of habitat spread evenly across the network of wetlands. The choice of area-based model made no difference to this conclusion. Losing smaller wetland patches led to more regional species extinctions for a given proportion of wetland area lost. This is a plausible risk to wetlands in the region under forecast climatic change. Given our prior knowledge of the distribution of rare species in these wetlands (Deane et al., 2016), this result was predictable. However, whether area- or patch-loss would result in the greater regional species loss depends on the distribution of endemic species, particularly with respect to the nestedness of their distribution (Fig. A5). If only the largest, most species-rich wetlands contained rare species, then the opposite pattern could arise.

Fig. 2. Predicted proportion of regional species extinctions as entire wetlands are removed. The *x*-axis shows the proportion of total wetland area that is accounted for as individual wetlands are removed based on three different orderings: decreasing (circles) and increasing (triangles) size order, and random selection (squares). Grey lines are bootstrapped 95% confidence intervals, shown only for the decreasing and increasing response for clarity.
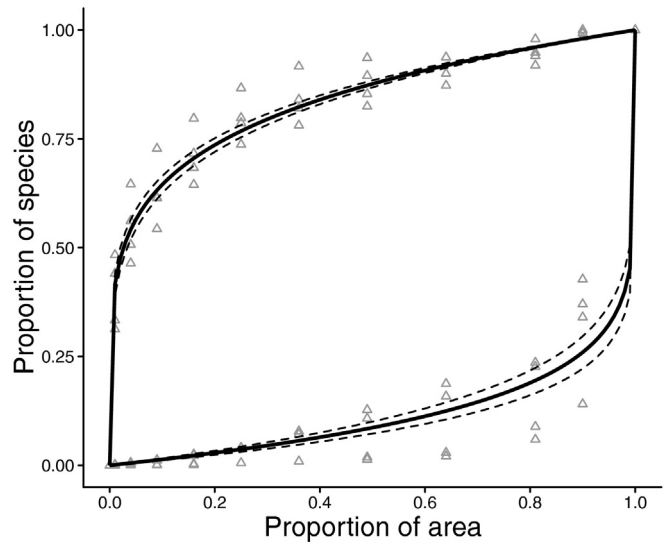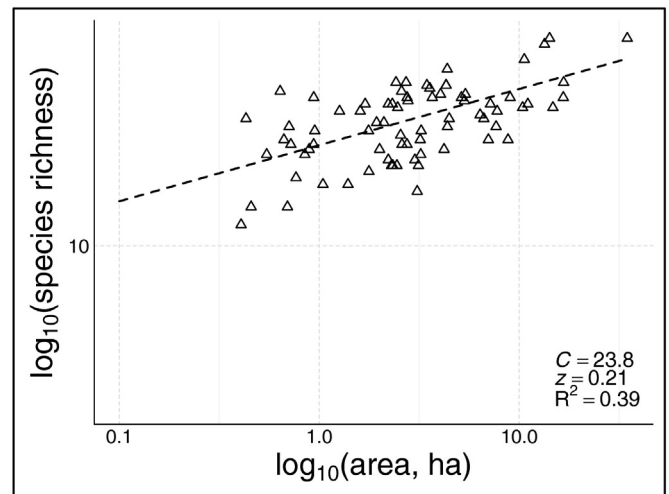

Fig. 4. 'Island' (Type IV) species-area relationship fitted to all wetlands. Each datum represents the total wetland area and wetland species richness. The dashed line represents the best-fit power-law species area model, with model coefficients and R^2 indicated in the lower right. Note data presented in log-log space to improve clarity, but the species-area model was fitted in arithmetic space.

We found that the total number of species accumulated more rapidly from small to large habitat (wetland) patches, which has also been shown for calcareous fens (Peintinger et al., 2003) and terrestrial forest fragments (Honnay et al., 1999). Our result is also consistent with an observation that found smaller prairie and forest remnants in the American Mid-West had more species (including more rare species) than expected under an area-based random colonisation model (Simberloff and Gotelli, 1984), which would result in a similar accumulation curve as ours. The contribution to total species richness made by both small and large wetlands and terrestrial fragments supports prior calls to conserve habitat patches of all sizes to maintain regional biodiversity (Davies et al., 2008; Della Bella et al., 2008; Maltchik et al., 2010; Scheffer et al., 2006). Protecting the largest or most species-rich patches in heavily cleared landscapes does not guarantee the lowest extinction risk.

Seasonal wetlands of temperate climatic zones such as our study region are among the most threatened (Holland et al., 1995), but can have species-rich ecotones that include native terrestrial species (Brock and Casanova, 1997; Brose, 2001; Flinn et al., 2008; Haukos and Smith, 1994; Kaeser and Kirkman, 2009). Changing hydrology is the most likely area-loss mechanism for our study wetlands, with down-scaled climate forecasts for the region suggesting declining annual rainfall and increasing temperatures (Charles and Fu, 2014). Future changes in catchment water balance will mean that smaller wetlands, which have a reduced storage volume to buffer drought periods, will be at higher risk of drying completely. In this case, conversion to agricultural land use is a likely outcome resulting in loss of the entire wetland patch. Our study shows that such losses could result in many regional species extinctions, at least from within wetland habitats.

Prior to our study, few studies have predicted wetland plant species loss under regional change scenarios. Rare exceptions include Rosset et al. (2010) who used generalised additive models to predict the species richness of different taxonomic groups in Swiss ponds based on projected temperature and related water-quality changes, reporting only pond-scale changes in richness. Ström et al. (2012) used forecasted changes in inundation patterns to predict corresponding changes in the species richness of riparian vegetation associations. Their study was based on changes in the width of parallel riparian vegetation zones, not area, and made only a qualitative estimate of overall species change. Other studies have predicted wetland area loss, but have made no attempt to quantify the resulting species loss (e.g., Alahuhta et al., 2011; Essl et al., 2012; Poiani and Johnson, 1993). Our approach provides regional estimates of species loss under alternative loss mechanisms and is easy to implement. Our use of a generalised endemics-area relationship collated across multiple grids is a novel approach, but the limited extent of sampling on which it was based means some caution is warranted when interpreting the predictions arising. There are few published parameter estimates for the power-law endemics-area equation that can be used to validate our estimated values. He and Hubbell (2011) reported a range of empirical values for forest sites across a climatic gradient at $z_{EAR} = 0.065$ to 0.126 (95% confidence limits; mean $= 0.097$; $n = 8$). Our mean z_{EAR} of 0.131 is double that of their forest systems, suggesting that the distributions of wetland species are much more localised (so that they become endemic). This heightens the importance of protecting a whole system of wetlands, not only part of the wetlands.

We recognise that analytical work shows the sampling design for species-area predictions should match the geometry of destroyed habitats, while endemics-area predictions should match the geometry of remaining habitats (Kinzig and Harte, 2000; Pereira et al., 2012; He and Hubbell, 2013). Higher rates of species loss can occur when habitat is destroyed from the edge toward the centre in contiguous habitat at biogeographical scales, as a result of species range-size distributions (Keil et al., 2015). However, the wetland data as sampled in this study do not allow for assessing the effect of geometry of habitat destruction on species loss. In practice, people rarely sample species diversity data in a way that is compatible with the complementary geometry as defined by the backward species-area model (Pereira et al., 2012; He and Hubbell, 2013). How different spatial configurations of habitat removal affect the loss of species in landscapes is an important question both in theory and application, but is still poorly understood. We suggest that future studies endeavour to sample wetlands from fringing areas inwards to model more accurately the pattern by which wetlands are typically lost.
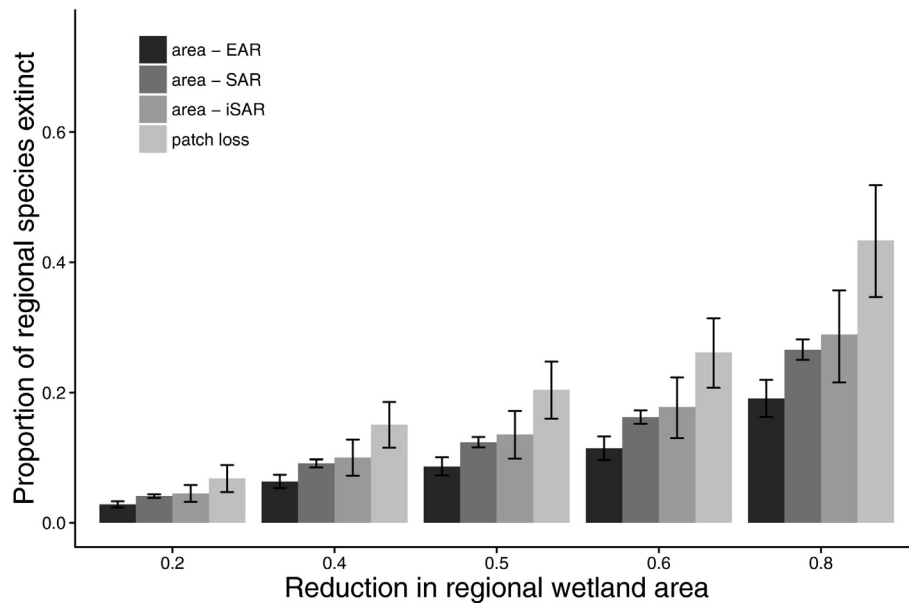

Fig. 5. Comparison of species predicted to become extinct when wetlands are removed (patch loss) or decreased in size (area loss). Each set of comparisons represents the random patch-loss estimate and three area-loss estimates, each of which was based on a different estimate of the z parameter in Eq. (1): z_{EAR} was obtained by fitting Eq. (1) to an endemics-area relationship fitted to gridded data; z_{SAR} is from the power-law species-area relationship fitted to the same gridded data; and, z_{iSAR} is the power-law 'island' species-area relationship fitted to total wetland area and observed species richness. Percentages indicate the proportion of the total wetland estate that is lost. Mean species loss is indicated by the height of the bars, while error bars show 95% confidence intervals obtained using 1000 simulations (calculating using bootstrapping for patch-loss scenarios and resampling under the relevant species sampling probabilities for the area-loss scenarios).

In general, our methods predict only *immediate* extinction, but species losses continue to occur following disturbance due to biotic relaxation (Diamond, 1972; Heywood et al., 1994; Tilman et al., 1994), potentially over many years (Diamond, 1972; Halley et al., 2014; Fordham et al., 2016). Recent theoretical studies have found both species- and endemics-area methods underestimate rates of extinction (Matias et al., 2014; Rybicki and Hanski, 2013), and the inability of area-based methods to consider long-term dynamics remains a limitation (e.g., Halley et al., 2013; Rybicki and Hanski, 2013; Fordham et al., 2016). This also applies to patch loss, which alters species occupancies and reduces connectivity, re-colonisation probabilities following stochastic extinctions (Semlitsch and Bodie, 1998) and source-sink dynamics (Pulliam, 1988). The processes that affect long-term *equilibrium* carrying capacity following changes in landscape geometry are the subject of ongoing theoretical investigation (Halley et al., 2014; Matias et al., 2014; Mouquet et al., 2011; Rybicki and Hanski, 2013). Since much of the Fleurieu Peninsula was only cleared in the 1950s, many species' populations might still be in the process of biotic relaxation (Deane et al., 2016). Ultimately, our work provides an inference of the relative extinction risk associated with patch and area loss, but our methods cannot yet predict final equilibrium species diversity.

We found that the complete removal of small wetlands resulted in the highest risk to regional species diversity for a given decrease in the total area of the regional wetland estate. Although wetland area and species richness were positively correlated with the number of endemic species, small wetlands contained many endemic species in a small total wetland area. This suggests susceptibility of wetland vegetation to regional species loss even when only a few, small wetlands are destroyed. We recommend incorporating both area- and patch-loss scenarios when predicting the extinction prospects of wetland species because of the possible differences in estimates that can arise.

Acknowledgements

Appendix A. Supplementary data

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.biocon.2017.02.005.

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