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ARTICLE

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Spatial prioritization for widespread invasive species control: Trade-offs between current impact and future spread

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Abstract

Spatially explicit prioritization of invasive species control is a complex issue, requiring consideration of trade-offs between immediate and future benefits. This study aimed to prioritize management efforts to account for current and future threats from widespread invasions and examine the strength of the trade-off between these different management goals. As a case study, we identified spatially explicit management priorities for the widespread invasion of introduced willow into riparian and wetland habitats across a 102,145-km^2 region in eastern Australia. In addition to targeting places where willow threatens biodiversity now, a second set of management goals was to limit reinfestation and further spread that could occur via two different mechanisms (downstream and by wind). A model of likely willow distribution across the region was combined with spatial data for biodiversity (native vegetation, threatened species and communities), ecological conditions, management costs, and two potential dispersal layers. We used systematic conservation planning software (Zonation) to prioritize where willow management should be focussed across more than 100,000 catchments for a range of different scenarios that reflected different weights between management goals. For willow invasion, we found that we could prioritize willow management to reduce the future threat of dispersal downstream with little reduction in the protection of biodiversity. However, accounting for future threats from wind dispersal resulted in a stronger trade-off with protection of threatened biodiversity. The strongest trade-off was observed when both dispersal mechanisms were considered together. This study shows that considering current and future goals together offers the potential to substantially improve conservation outcomes for invasive species management. Our approach also informs land managers about the relative trade-offs among different management goals under different control scenarios, helping to make management decisions more transparent. This approach can be used for other widespread invasive species to help improve invasive species management decisions.

KEYWORDS
biodiversity, connectivity, dispersal, optimization, *Salix*, systematic conservation planning, Zonation software

INTRODUCTION

Biological invasions that threaten biodiversity are often so widespread that available funds are insufficient to eradicate or control their full extent (Caplat, Coutts, & Buckley, 2012; Panetta & Cacho, 2012). The management of these widespread species primarily focuses on reducing impacts on biodiversity (e.g., threatened species, native vegetation; Downey, 2010; Panetta et al., 2019; Shackleton et al., 2017) while preventing future impacts, for instance from further dispersal of the invaders (Caplat, Coutts, & Buckley, 2012; Epanchin-Niell & Hastings, 2010).

To provide the greatest benefits to biodiversity, invasive species management needs to target locations with high biodiversity values directly threatened by the target invasive species and where recovery of the ecosystem remains feasible (Povak et al., 2017; Prior et al., 2018; Tulloch et al., 2014). Accounting for the feasibility of ecosystem recovery involves considering the condition of a given site, including the presence of other processes that would continue to threaten native species' persistence after the invasive species is removed (Evans et al., 2011).

Widespread invasive species are also managed with the goal of preventing future impacts, for instance from further dispersal of the invader (Caplat, Coutts, & Buckley, 2012; Epanchin-Niell & Hastings, 2010). Limiting the spread of invasive species requires understanding how specific invaders disperse and prosper (Davies & Sheley, 2007). Many studies focus on modeling population dynamics and spread (Epanchin-Niell & Hastings, 2010; Pepin et al., 2020). Because of the complexity of dynamic, spatially explicit modeling and the need to estimate many parameters, such studies often focus on early-stage invasions for which historical records can be used to estimate key parameters (Baker, 2017; Caplat, Coutts, & Buckley, 2012), provide spatially implicit solutions (Epanchin-Niell et al., 2012), or use simplified analyses or reduced spatial extent (Aurambout & Endress, 2018; Epanchin-Niell & Wilen, 2012; Hall et al., 2018). These approaches often provide general management guidance, such as managing the most upstream infestations first (Chades et al., 2011), managing the dispersal source populations (Baker, 2017), or identifying optimal trap densities (Epanchin-Niell et al., 2012), but are rarely able to identify specific priority locations for management across the landscape (but see Baker, 2017). Indeed, the optimal management strategy often depends on spread patterns, invasion, and landscape size (Epanchin-Niell & Hastings, 2010). Disrupting the spread of an invader becomes even more complex when the target species has multiple dispersal mechanisms and dispersal vectors (Pepin et al., 2022). Finally, the management of widespread invasions typically occurs in the context of limited resources, so there is a strong impetus to identify efficient control strategies that maximize value for money (Epanchin-Niell, 2017) as well as biodiversity benefits (Auerbach et al., 2014; Carwardine et al., 2019). This is often achieved by seeking to minimize the total expected cost of the invasion by balancing control costs against summed damages to biodiversity or the economy if the invasion is left unchecked (Epanchin-Niell et al., 2012; Hall et al., 2018).

Determining how to allocate limited resources between the management goals of protecting currently threatened values and preventing future impacts of widespread invasions is a substantial challenge. Land managers typically seek to identify management sites that will provide a range of biodiversity benefits as well as limit the potential of future spread via a range of mechanisms and often at large scales (Büyüktahtakin et al., 2014; Long et al., 2017; Moore & Runge, 2012). Any effective strategy needs to ensure that the chosen set of priority sites for management efficiently divides resources between achieving multiple biodiversity benefits and meeting current and future goals (Moilanen et al., 2011). A typical rule of thumb is to concentrate effort in places with high biodiversity value, but when there are many such places or numerous biodiversity features of concern, it can be difficult to identify which places to choose when resources are limited.

Systematic conservation planning tools (Margules & Pressey, 2000) are ideal for informing decisions about controlling widespread invasive species at large spatial scales because the approach can incorporate many different conservation features (species, ecosystems, social values), account for costs and conditions, incorporate different types of management goals and spatial processes, identify priorities as available resources change, and provide fine-resolution priorities across large scales (Sarkar et al., 2006). Systematic conservation planning is based on the concept of complementarity (Margules & Pressey, 2000). This means that, in contrast to approaches that rank sites independently, systematic conservation planning accounts for the differences and similarities between the conservation values of each candidate site, such that the chosen set of sites complement each other with respect to the management goals and biodiversity values to which they contribute, ensuring that the benefit of site selection will be spread evenly across all biodiversity values. Systematic conservation planning can also be spatially explicit, incorporating spatial processes such as dispersal by accounting for the connectivity and spatial arrangement of sites, even at large scales (Arponen et al., 2012; Klein et al., 2009; Moilanen et al., 2008). Furthermore, there is computationally efficient software readily and freely available that can address the large problems encountered when managing widespread species (Ball et al., 2009; Lehtomäki & Moilanen, 2013).

Systematic conservation planning was developed to design systems of nature reserves (Kirkpatrick, 1983; Pressey, 1998) and has been widely used for identifying protected area systems and identify large-scale conservation priorities (Balmford et al., 2001; Klein et al., 2009; Margules & Pressey, 2000). It has also been applied to other conservation problems, including identifying where to implement a range of management actions across large regions (Auerbach et al., 2014; Doyle et al., 2019; Thomson et al., 2009; Ward et al., 2022). We are aware of just two studies that use systematic conservation planning tools to identify priority locations for invasive species management that strive to account for spread over time (Adams & Setterfield, 2015; Januchowski-Hartley et al., 2011). Januchowski-Hartley et al. (2011) used conservation planning tools to identify spatial management strategies at priority wetlands and river reaches aimed at minimizing the infestation size of an invasive aquatic macrophyte accounting for connectivity and reinfestation risk between the waterbodies. Adams and Setterfield (2015) used a similar approach to develop a decade-long schedule for exercising control over an invasive grass by integrating systematic conservation planning software with a model of population growth and spread (via wind dispersal).

We build on this previous work by including a broad set of 29 threatened biodiversity features (native vegetation, 27 threatened plants and animals, and one threatened ecological community) and by examining two contrasting dispersal mechanisms within the same framework. Our approach allows for trade-offs and for the potential for co-benefits among a range of management goals to be examined within the same analysis. Specifically, we aimed to (1) prioritize spatial control effort to account for multiple management goals and (2) characterize the trade-offs of managing for current versus future threats.

We use managing willow (*Salix* spp.) invasion in riparian zones and wetlands across a 102,145-km^2 region in eastern Australia as a case study. Our objectives were to protect native riparian vegetation as well as threatened native species and ecological communities that are specifically threatened by willow invasion and to limit the future threat from willow dispersal (vegetative/seed dispersal downstream and wind dispersal by seeds) while minimizing management costs. We expected that, in providing a more complete description of the management problem, which simultaneously accounts for current threats to biodiversity and future dispersal risks, we would be able to identify priority areas for management that would reduce both current and future impacts. However, we also predicted that there would be trade-offs between minimizing current damage and reducing future threats (from dispersal).

MATERIALS AND METHODS

Invasion threat and area

Willow (*Salix* spp.) is a large genus of mostly deciduous trees and shrubs, native to Europe, the Americas, and Asia (Cremer, 2003). Willows can reproduce vegetatively when branches or limbs break off and are carried downstream along waterways (Cremer, 2003). Willows can also reproduce via seed, and the seeds are both wind and water dispersed, with a light pappus allowing for long-distance dispersal of potentially tens of kilometers (Cremer, 2003), which means that they can travel between, as well as within, catchments (Cremer, 2003; Hopley & Young, 2015). Populations of willows have been observed to form quickly after disturbance and to regenerate after fire (Cremer, 2003). Preadaptation to a range of moist environments, long-distance dispersal capacity, and tolerance to disturbance have contributed to many species of the genus being highly invasive in countries to which they have been introduced (including Australia). The genus is listed as a Weed of National Significance in Australia and is a high priority for management (Adair et al., 2006).

This study was conducted in the eastern half of the state of Victoria, Australia (Figure 1), which is predominantly mesic and supports montane, subalpine, and alpine ecosystems. Willows pose a significant threat to

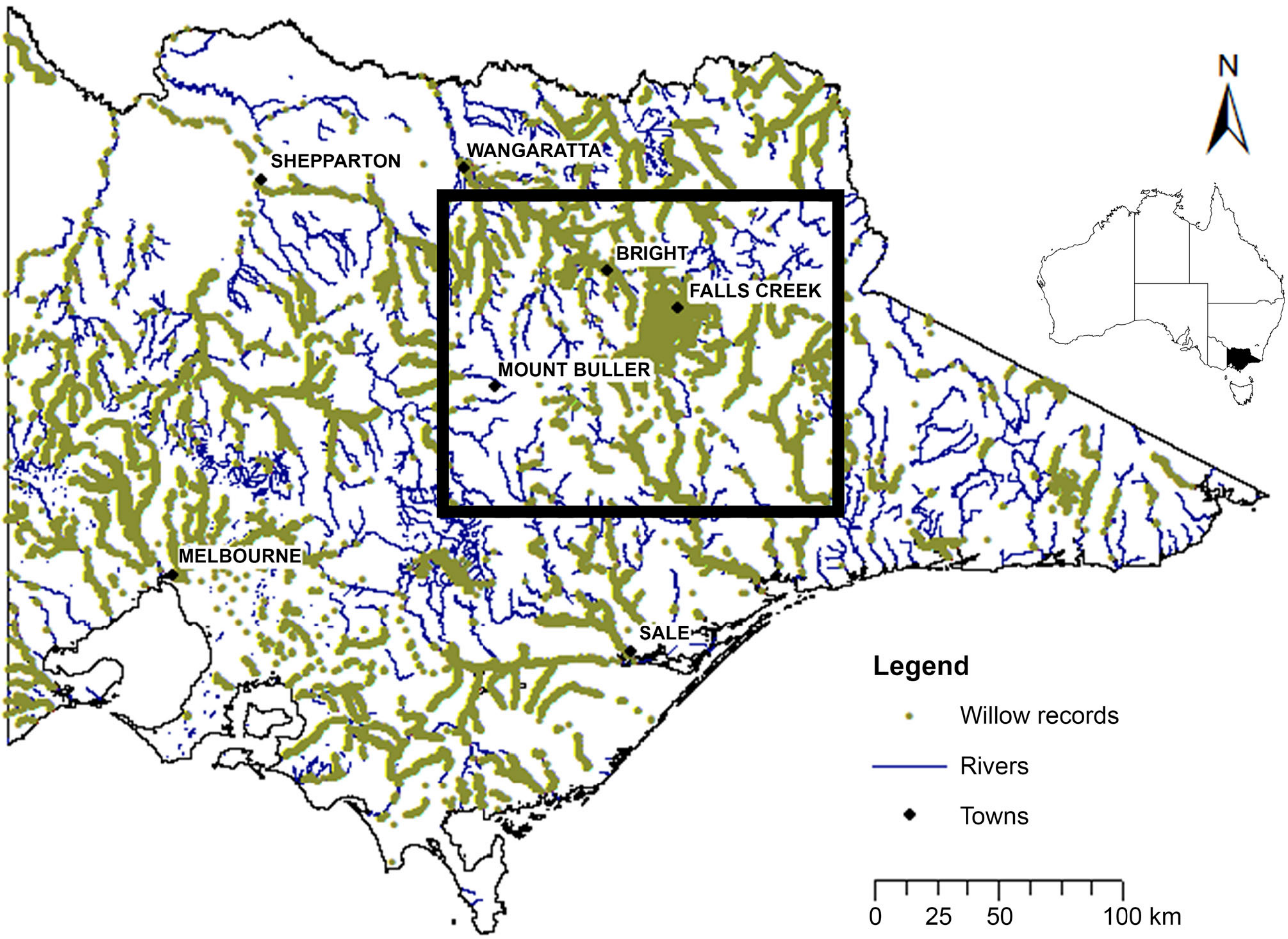

FIGURE 1 Map of study area shows recorded willow localities (green symbols) and rivers (dark blue) within study area. Black rectangle shows location of wind dispersal subregion where long-distance wind dispersal potential was modeled.

biodiversity within the region. Willows increase shade and water turbidity and change the chemical composition of freshwater streams, impacting water quality, freshwater invertebrates, and fish (McInerney et al., 2016). Willows also outcompete native plants, disrupting native vegetation communities and habitat for riparian species such as lizards and frogs (Cremer, 2003).

Identifying management goals

Clear specification of management goals is crucial to developing fit-for-purpose management strategies (Gregory et al., 2012; Moore & Runge, 2012). The fundamental objectives driving decisions regarding where to control willows in eastern Victoria were identified through a semistructured elicitation process and follow-up consultations with ~20 staff from eight public agencies responsible for land management and willow control throughout the region. The process revealed the following management goals:

1. maximise the benefit of willow control to 29 biodiversity features (species, vegetation types and ecosystems) impacted by willow, and
2. preference willow control in locations that have good ecosystem condition (apart from willow invasion),
3. and additionally, to limit the threat of future dispersal; reduce the amount of willow reinfestation via downstream dispersal, and
4. maximise control of willow in locations with high potential for seed to be to wind-dispersed long distances,
5. all within the constraint of minimising the cost of control.

Spatial conservation prioritization

We used the spatial conservation planning software Zonation 4.0 (Lehtomäki & Moilanen, 2013) to find (near) optimal spatially explicit prioritizations of where to control willow that maximized the benefit to biodiversity features and (when relevant) the amount of area managed with high wind dispersal potential. We used two different weighting schemes within Zonation to account for ecosystem condition and downstream dispersal potential. Zonation produces a nested ranking of all sites from highest to lowest priority for conservation action (in this case willow control), which enables decision makers to evaluate what can be achieved with different levels of effort. The ranking is nested in that the top 2% of cells are also included in the top 5% of cells. Broadly speaking, Zonation works by calculating the marginal loss in the distribution of biodiversity features for each planning unit if it was removed and then removing the planning unit with the smallest loss. Marginal loss is then recalculated, excluding the planning unit that was removed, thereby incorporating complementarity. A range of algorithms can be used to do the ranking. We used the core-area algorithm for ranking, which produces a ranking with even representation across biodiversity features (and when relevant wind dispersal threat) compared to other algorithms, ensuring that rare features or features that have unusual distributions would not be overlooked.

To conduct the prioritization, input raster layers describing the planning units, the threat willows pose to biodiversity, ecological conditions at each site, management costs, freshwater connectivity, and wind dispersal potential were prepared (Figure 2). A series of prioritizations was run with different combinations of inputs corresponding to different combinations of management goals. Priority maps and performance curves were used to describe the resulting priorities for the different management goals.

Input layers

All spatial data sets were projected from their native coordinate reference system into the GDA94 zone 55 (EPSG:28355) coordinate reference system and resampled (bilinear interpolation for continuous data and nearest neighbor for categorical data) to a 101.29-m raster grid to match the resolution of the willow habitat suitability model, using ArcMap 10.2. Data sets were then clipped and masked to the eastern Victoria study extent

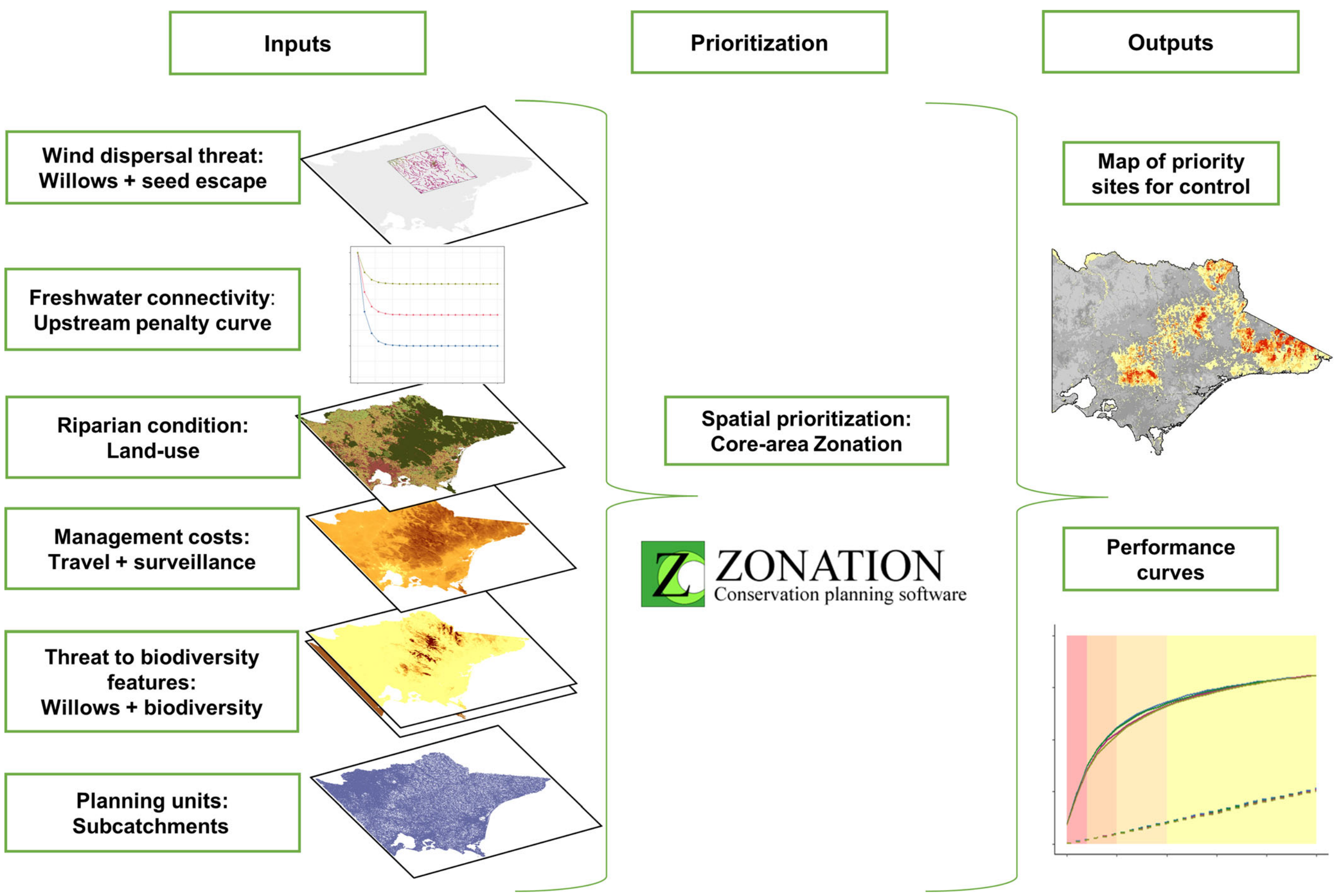

FIGURE 2 Conceptual flow diagram outlining key components of systematic conservation planning approach used to prioritize sites for control of willows in eastern Victoria.

(Figure 1) using the raster package in R version 3.1 (5) (Hijmans & Etten, 2012). A second set of inputs was clipped to the wind dispersal subregion (Figure 1) for use in wind dispersal analyses. The boundaries of this subregion were set based on the availability of predictions from the WALD model (proportion of seeds escaping the canopy).

Planning units

Subcatchments were used as planning units as they represent the natural boundaries of areas of influence in freshwaters (Everard & Powell, 2002) and are the scale at which willow management is often conducted along waterways (Goulburn Broken Catchment Management Authority, 2004, Goulburn Broken Catchment—Willow Management Strategy, public communication). This improves upon the traditional approach in conservation planning of using equal-sized grid cells as planning units, which is not appropriate for freshwater management (Klein et al., 2009; Nel et al., 2007). To map subcatchment-level planning units for eastern Victoria, the Geofabric Surface Hydrology Catchments data set was used (Bureau of Meteorology, 2012). We selected the subcatchments ($n = 101{,}000$, average area 309,858 m^2 or ~0.31 km^2) contained within the study area and rasterized by the value of each subcatchment's HydroID using ArcMap 10.2.

Willow threat: Habitat suitability model

We described the willow threat by fitting a habitat suitability model that predicted the relative suitability of each grid cell and assumed that willow abundance was positively correlated with this suitability (Appendix S1: Figure S1). Presence and background data were used with environmental variables to estimate the habitat suitability for willows using MaxEnt 3.3.3 (Phillips et al., 2006) in the dismo R package (Hijmans et al., 2015). Willow occurrence records ($n = 304{,}351$) were provided by land managers and gathered from online databases. Presence data were thinned to a minimum distance of 3.5 km (Aiello-Lammens et al., 2015) to correct for spatial sampling bias arising from uneven sampling (Hijmans, 2012), with a final data set of 1506 observations used to fit the model (see Appendix S1: Section S1 for further details).

We identified 10 environmental variables likely to be influential in driving willow habitat suitability and available as spatial layers in our regions to use as candidate predictor variables in the willow model (Appendix S1: Table S1). For collinear variables (Pearson's correlation coefficient $>|0.7|$), the variable ranked a priori as having higher ecological relevance was chosen for inclusion in the model.

Model fit and performance were evaluated using five-fold cross-validation (Merow et al., 2013, Appendix S1: Section S1). The predicted habitat suitability for willows was the mean of the model predictions over the five folds. The discrimination accuracy of the models was evaluated as the area under the receiver operating characteristic curve (AUC). Values ranged from 0 to 1, with values above 0.7 indicating sufficient discrimination to be considered potentially useful (Hosmer Jr. et al., 2013). To detect overfitting, the difference between AUC (AUCdiff) calculated using the training and test data sets was examined. As spatial sampling bias also tends to inflate model performance, pairwise distance sampling (PWDS) was also used to calibrate model evaluation metrics (Hijmans, 2012).

The willow habitat suitability model showed good discrimination ($AUCtest = 0.899 \pm 0.014$), with little evidence of overfitting ($AUCdiff = 0.019 \pm 0.016$). The most suitable habitat for willows was predicted to be close to waterways, within riparian vegetation, and at high elevations (Appendix S1: Figure S1). Distance to water, ecological vegetation class, and disturbance drove model predictions (Appendix S1: Figure S1b).

Threat to biodiversity features

The set of threatened biodiversity features were determined from the results of a semistructured elicitation process with land managers (J. Moore, unpublished data). In total, 29 features were identified, including 27 species, one threatened ecological community, and native vegetation more broadly (Appendix S1: Table S2). Maps of native vegetation and threatened ecological community were converted to presence–absence rasters. Preexisting habitat distribution models (Appendix S1: Section S2) were used to create a spatially explicit indicator of willow threat for the 27 threatened species. We assumed that threat was positively correlated with habitat suitability for both willow and biodiversity features. Specifically, we calculated the threat (T) to biodiversity feature j at site i as

$$T_{ij} = x_i f_{ij}, \qquad (1)$$

where x_i is the relative suitability for willows at site i downweighted by previous control effort, and f_{ij} indicates the relative suitability for biodiversity feature j at site i. Separate threat layers were created for each biodiversity feature.

Substantial effort has already been devoted to controlling willow throughout the region. Hence, we downweighted the willow habitat suitability value to account for previous control efforts, using an approach similar to that used in a previous study (Giljohann et al., 2011):

$$x_i = h_i(1-p)^k, \tag{2}$$

where x_i is the downweighted relative suitability for willow occurring at site i, h_i is willow habitat suitability at site i, and $(1-p)^k$ is the proportion of willows surviving previous control effort. Here, p is the proportion of willows successfully treated from previous control efforts and k is the relative likelihood (values between 0 and 1) of control having occurred at a location. The parameter p was estimated as 0.65 based on a control effectiveness study previously undertaken in eastern Victoria (Giljohann et al., 2011). The relative likelihood of control having occurred at each site, k, was estimated using data from management records provided by Catchment Management Austhorities with a spatial smoothing kernel (Appendix S1: Section S3). This spatial layer indicates the relative likelihood of control having occurred between locations that were known to be visited ($k = 1$) and locations never controlled for willows ($k = 0$).

Management costs

To minimize management costs in priority sites, two data sets representing spatial variation in the cost of travel and the cost of site visits for undertaking general on-ground management actions were used (Appendix S1: Figure S4). These cost layers were summed together (raster package in R) and used as the cost layer in Zonation (Appendix S1: Figure S2). The cost values are incorporated into the Zonation ranking algorithm so that cells are ranked by marginal efficiency (benefit/cost). The cost layers were built for the Spatial Conservation Action Planning tool (Thomson et al., 2020). While broadly indicative of spatial variation in management costs, these cost layers were based on cost associated with undertaking on-ground generic management actions rather than willow management, and so they do not capture all of the costs associated with willow control. The aim of the cost data is to capture the relative spatial variation in management costs as this is most critical to identifying an accurate ranking.

Riparian condition

The benefit to biodiversity conferred by invasive willow control is reduced when other threats (e.g., habitat loss, disturbance associated with human land use) continue to negatively impact biodiversity after willows are removed (Panetta & Cacho, 2012). To represent the management goal of preferencing control at locations in good condition, we developed a condition rating based on Victorian land-use data (Morse-McNabb et al., 2015). We used land-use data as they are a good indicator of riparian vegetation and stream condition (Lohse et al., 2008; Zermeño-Hernández et al., 2020) and were readily available (Appendix S1: Section S5). Land-use categories were aggregated into six classes thought to reflect different levels of riparian condition (Appendix S1: Table S3) and allocated scores to represent the relative effect of each land-use category on condition (Appendix S1: Table S4). Riparian condition was included as a condition layer in Zonation (Appendix S1: Figure S3) and applied to downweight the threat layer for each biodiversity feature.

Downstream dispersal threat

The future threat from willow dispersal downstream will be reduced if waterways are managed from the top down to reduce the risk of reintroduction (Chades et al., 2011). To account for downstream dispersal risk, Zonation's directed connectivity feature was used (Moilanen et al., 2008; Appendix S1: Section S6). This method applies a "neighborhood quality penalty," where the benefit of controlling willows in a catchment for each feature is adjusted down based on the proportion of area in upstream catchments that do not receive willow control (irrespective of willow habitat suitability upstream). We were unable to find any studies that quantified how establishment probability changed with upstream population size. Hence, we chose a functional form that corresponded to a high likelihood of reinfestation even when few willows remain upstream (Appendix S1: Figure S4) as many willow species establish easily from vegetative fragments (Cremer, 2003). We chose three values of connectivity penalty or "maximum loss" to compare the relative importance of limiting downstream dispersal relative to other management goals, where a connectivity penalty of 25% means that when no upstream control is undertaken, the maximum benefit is reduced to 75% (i.e., a maximum loss of 25%) of the original benefit of management (Table 1). In this case study, we used one of Zonation's connectivity functions (neighborhood quality penalty) to account for linear dispersal downstream. A similar approach could be applied to nonriparian taxa that disperse along linear networks (e.g., roads, power transmission lines). Furthermore, dispersal need not be constrained to linear networks because Zonation has a range of ways to account for connectivity

TABLE 1 Spatial prioritization scenarios for willow management in eastern Victoria and seed-dispersal study area (Figure 1) used to assess trade-offs between protecting biodiversity and limiting future dispersal for invasive willows.

Problem attribute	Eastern Victoria	Wind dispersal subregion
Management goals	Protect biodiversity in good condition and limit willow freshwater dispersal	Protect biodiversity in good condition, limit willow freshwater dispersal, and limit willow wind dispersal
No. threatened biodiversity features	29	15
Ecological condition	Yes	Yes
Management costs	Yes	Yes
Future threat	Downstream dispersal ($a = 0\%$, 25%, 50%, 75%)[a]	Downstream dispersal ($a = 0\%$, 25%, 50%, 75%),[a] wind dispersal weight ($w = 0$, 1, 5, 10)[b]
No. scenarios	4	16

[a]a is maximum loss, that is, maximum reduction benefit when no upstream willow control is undertaken.
[b]w is weight given to willow wind dispersal potential relative to weight given to each threatened biodiversity feature.

(or dispersal potential) across a landscape within the algorithm (Lehtomäki & Moilanen, 2013).

Wind dispersal threat

Preventing wind dispersal of willow seeds is a high priority for management, as seeds can travel long distances and potentially establish tens of kilometers away (Cremer et al., 1999). Spatially explicit estimates of seed density were not available. Recent advances in understanding of long-distance dispersal have identified that seeds must escape the vegetation canopy to be carried long distances by wind (Kabul et al., 2005; Nathan et al., 2011). We used the fraction of seeds that escape the canopy as our measure of wind dispersal potential estimated using the WALD model (Appendix S1: Section S7). The WALD model is an analytic model that can be used to predict either the proportion of seed that escapes the canopy or a one-dimensional wind dispersal kernel at a specific location (Katul et al., 2005). For each location, inputs required are the mean height from which seeds are released, the canopy height, the leaf area index (LAI, a measure of canopy density), and the friction velocity u^* (averaged over a 1-h time window), a measure of wind speed at the canopy boundary. We estimated friction velocity (u^*) on a 1-km grid (Appendix S1: Table S5, Figures S5 and S6) averaged over hourly intervals using the Advanced Research Weather Research and Forecasting model (ARWRF) version 3.9 (Skamarock et al., 2008), canopy height from the Simard Veg Height data set taken from 2005 (Simard et al., 2011), and LAI from the Auscover LAI data set taken from 2016 (Paget & King, 2008). We used WALD to calculate the mean fraction of seeds escaping the canopy between 2:00 and 3:00 p.m., the time of day when seed release is greatest (J. Moore, unpublished data) across a 19-day window during spring (1–19 October 2017), when willow seeds are typically maturing (Cremer, 2003). We used this prediction of mean escape fraction as our measure of seed dispersal threat (Appendix S1: Figure S7).

We incorporated wind dispersal threat into the analysis in a way that is different from the directed connectivity used to look at downstream dispersal. The benefit of managing locations where willows have a high potential wind dispersal threat is dependent on the probability of willows occurring at the location. Therefore, the threat from potential seed escape is calculated using the same calculation as for biodiversity features (Equation 1) with seed escape entered into the equation as feature j, a_{ij} is the mean proportion of seed that escapes the canopy at site i, and x_i is the relative likelihood of occurrence for willows (Equation 2). In Zonation, each individual feature can be assigned a weight to define its relative importance during the prioritization process (Lehtomäki & Moilanen, 2013). As we included the wind dispersal threat as a feature in addition to the threatened biodiversity feature layers, we used the weighting option to assign the importance of limiting willow wind dispersal, relative to the importance of the biodiversity features. We considered three different weights that corresponded to the case that managing wind dispersal potential was approximately equally (1×), five times (5×) or 10 times (10×) as important as managing willows to protect one biodiversity feature as well as a fourth case when wind dispersal potential was not considered (weight = 0).

Spatial prioritization scenarios

We completed 20 prioritization scenarios with Zonation to assess how different management goals affected willow control priorities and to examine the trade-offs between the different management goals (Table 1). Within the eastern Victoria study region (Figure 1), we used four scenarios to explore the trade-off between biodiversity protection and reducing downstream dispersal, each with different maximum loss percentages for the connectivity penalty curve ($a = 0\%$, 25%, 50%, 75%). For the smaller wind dispersal subregion, we ran 16 scenarios to examine trade-offs between biodiversity protection, future threat from downstream dispersal, and future threat from wind dispersal potential, considering all possible combinations of the four potential seed escape weights ($w = 0$, 1, 5, 10) and the four maximum loss values that describe the importance of managing upstream catchments ($a = 0\%$, 25%, 50%, 75%).

Outputs and postprocessing

Zonation produces a ranking of sites from highest to lowest priority for conservation action. Within the priority ranking map, each subcatchment in the study region is ranked from lowest to highest priority for management (0–1; Lehtomäki & Moilanen, 2013). The maps were examined to determine how priority areas for management differ when future management goals are accounted for and how the weights given to each goal affect the priority areas.

The performance of each scenario was measured as the proportion of biodiversity benefit, wind dispersal potential, and downstream dispersal captured as a proportion of the landscape managed increased. We calculated the condition-weighted biodiversity protection (percentage of threatened range managed, downweighted by ecological condition) and limit to wind dispersal (percentage of potential seed escape threat managed) for each 1% increment of the landscape managed. To evaluate upstream connectivity, we developed a quantitative measure of connectivity (0–1) based on the proportion of catchments upstream of a selected catchment that were also selected as a priority for management. For a given catchment selected for management, the highest connectivity value (1) was allocated if all catchments upstream of it were also selected for management or if it was a headwater. Conversely, the lowest connectivity value (0) was assigned if none of the connected catchments upstream were selected. The connectivity value for all other selected catchments corresponded to the proportion of catchments managed upstream, for instance if half the catchments upstream were managed a value of 0.5 was allocated. The connectivity measure was calculated using the R package igraph (Csardi & Nepusz, 2006). The overall connectivity value was the average across all selected catchments (for each proportion of the landscape managed).

We also calculated the proportional change in performance compared to the biodiversity features-only scenario ($a = 0$, $w = 0$) as the performance of the given management scenario divided by the performance of the baseline biodiversity scenario and then subtracting 1. All postprocessing was undertaken using R (version 4.0.5; R Core Team, 2021) in RStudio (versions 1.2.5033 and 2022.07.0).

RESULTS

When only biodiversity was prioritized across the eastern Victoria study region, priority areas for willow control were concentrated across four main regions (central and southwestern alpine areas and waterways in the east and northeast; Figure 3a). The mean threat to biodiversity that is managed by the strategy was similar across the four spatial prioritization scenarios that differed in the weight applied to minimizing downstream dispersal (Figure 4, Appendix S1: Figure S8). All threatened biodiversity features received some willow management within their range, even when the overall proportion of the landscape managed was very small (e.g., 1% or 2%; Appendix S1: Figure S9).

Including the connectivity penalty reduced fragmentation of priority areas and reduced the number of isolated, lowland catchments selected, shifting priorities toward headwaters. The magnitude of this effect increased as the connectivity penalty increased (Figure 3). As the magnitude of the connectivity penalty increased, there was a large increase in the proportion of upstream sites prioritized for management (Figure 4). This corresponded to a relatively small loss to the average protection to biodiversity features (Figure 4a). The largest gain in upstream connectivity compared to when only biodiversity was prioritized was an increase of 23% of upstream catchments managed and occurred when only 1% of the landscape was managed, corresponding to a 1.5% loss in biodiversity protection on average (Figure 4b,c). The largest loss in average biodiversity protection from including the connectivity penalty was 3.6% and occurred when 5% of the landscape was managed (Figure 4a), corresponding to a 19% increase in upstream connectivity (Figure 4b). All features lost no more than 10% of their protection at any given proportion of the landscape managed, when the largest connectivity penalty was included (Figure 4c).

When only biodiversity was prioritized across the wind dispersal subregion, central alpine waterways, and southerly rivers were prioritized for willow management

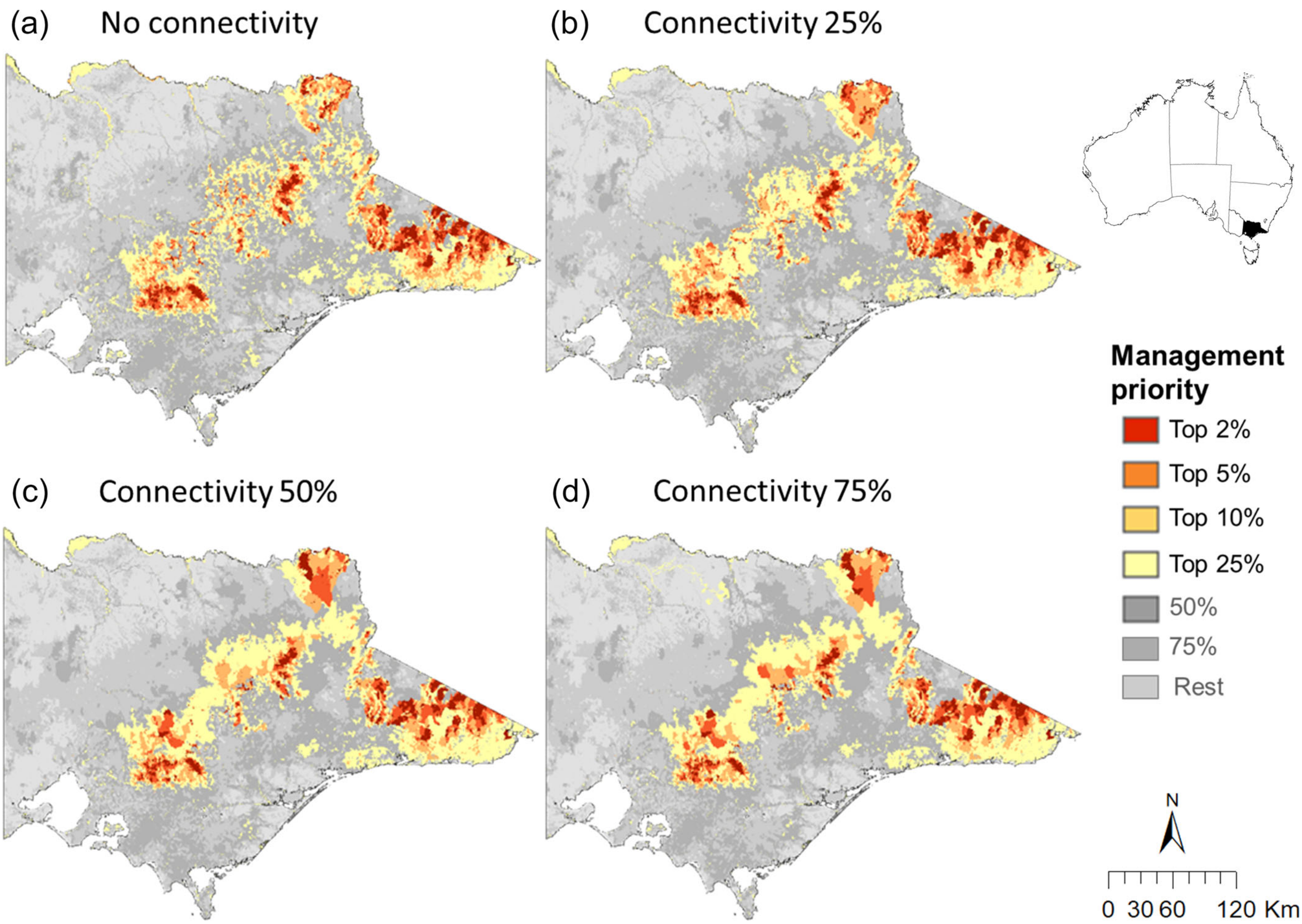

FIGURE 3 Priority ranking maps for willow control in eastern Victoria when the connectivity penalty (maximum loss of benefit when no upstream subcatchments are managed) is (a) not considered, (b) 25%, (c) 50%, and (d) 75%.

(Figure 5, top left corner). Accounting for potential seed escape shifted priority areas toward waterways in the northwestern of the region, away from central alpine areas and from the more southerly (low lying) rivers (Figure 5, top row).

Including seed escape potential at an equal weight to biodiversity features (1×) resulted in a large increase in the proportion of the wind dispersal threat managed, with a relatively small loss in the protection to biodiversity (Figure 6, compare red triangle to red circle, Appendix S1: Figure S10a,d, compare solid green line with solid blue line). When seed escape was weighted higher than biodiversity features (5×, 10×) a smaller increase in the proportion of the wind dispersal threat managed was observed compared to when it was weighted equal to biodiversity protection (Appendix S1: Figure S10d compare solid red and gold lines to solid green line).

When both potential seed escape and a connectivity penalty were included, priority areas became less fragmented and shifted to extensive river sections in the northwest, where the seed escape potential was high, and to alpine waterways and some southeastern waterways, where biodiversity was threatened (Figure 5, bottom right corner). The reduction in biodiversity protection was highest when both wind dispersal potential and upstream connectivity were weighted highly (Figure 6, in which the purple cross has the highest decrease on the *x*-axis), although the gain in reducing the threat from future dispersal was large (Appendix S1: Figure S10b,d). The pattern of reduced protection of biodiversity features with increasing focus on reducing future dispersal was consistent across all biodiversity features (Appendix S1: Figure S11).

DISCUSSION

This study shows how conservation planning tools can be used to identify where to control a widespread invasive species in a way that integrates multiple management goals. The approach evaluates trade-offs between

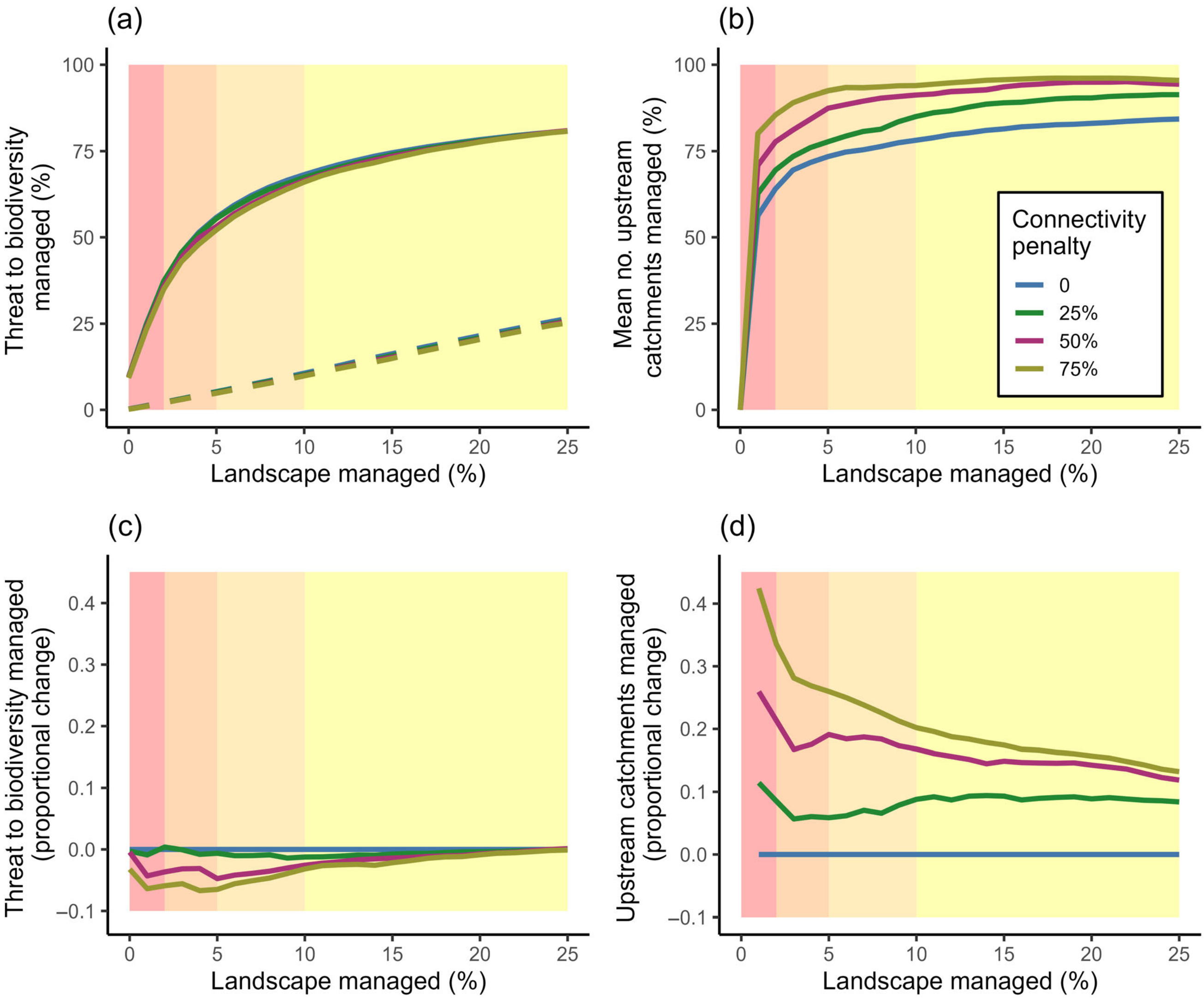

FIGURE 4 Performance curves for willow control in eastern Victoria when limiting downstream dispersal of willows is increasingly important. Curves show (a) average percentage of range of threatened biodiversity features within willow management footprint (solid lines) and minimum percentage of range of threatened biodiversity features within willow management footprint (dashed lines); (b) proportion of connected upstream catchments also prioritized for willow management, averaged across each priority catchment; (c) proportional loss in biodiversity protection; and (d) proportional gain in upstream connectivity compared to when only prioritizing biodiversity. Background colors correspond to top percentage of landscape managed (Figure 3).

managing the invader to reduce biodiversity impacts (across a range of species and ecosystems) and limiting future dispersal via two different mechanisms. Incorporating dispersal into optimal management plans has the potential to increase the overall benefits of control compared to focusing purely on current threats. We were able to identify management win–wins, locations where control reduces both current and future threat, as well as revealing places where separate management goals cannot be met together. By testing a range of management scenarios, with future goals considered at different weights relative to current biodiversity protection, our approach allows the trade-offs between managing current and future threats to be clearly articulated.

Trade-offs between current and future threat

The willow case study revealed that it was possible to undertake willow control at locations that would likely limit downstream dispersal of willows while incurring only a small decrease in expected biodiversity protected. As expected, the optimal allocation of effort was increasingly focused on headwaters and upstream reaches as reducing the downstream dispersal threat was weighted more highly (Figures 3 and 5), consistent with previous work (Hall et al., 2018). We were, however, surprised that the trade-off was minimal given that larger trade-offs are often observed between aggregating priority areas for

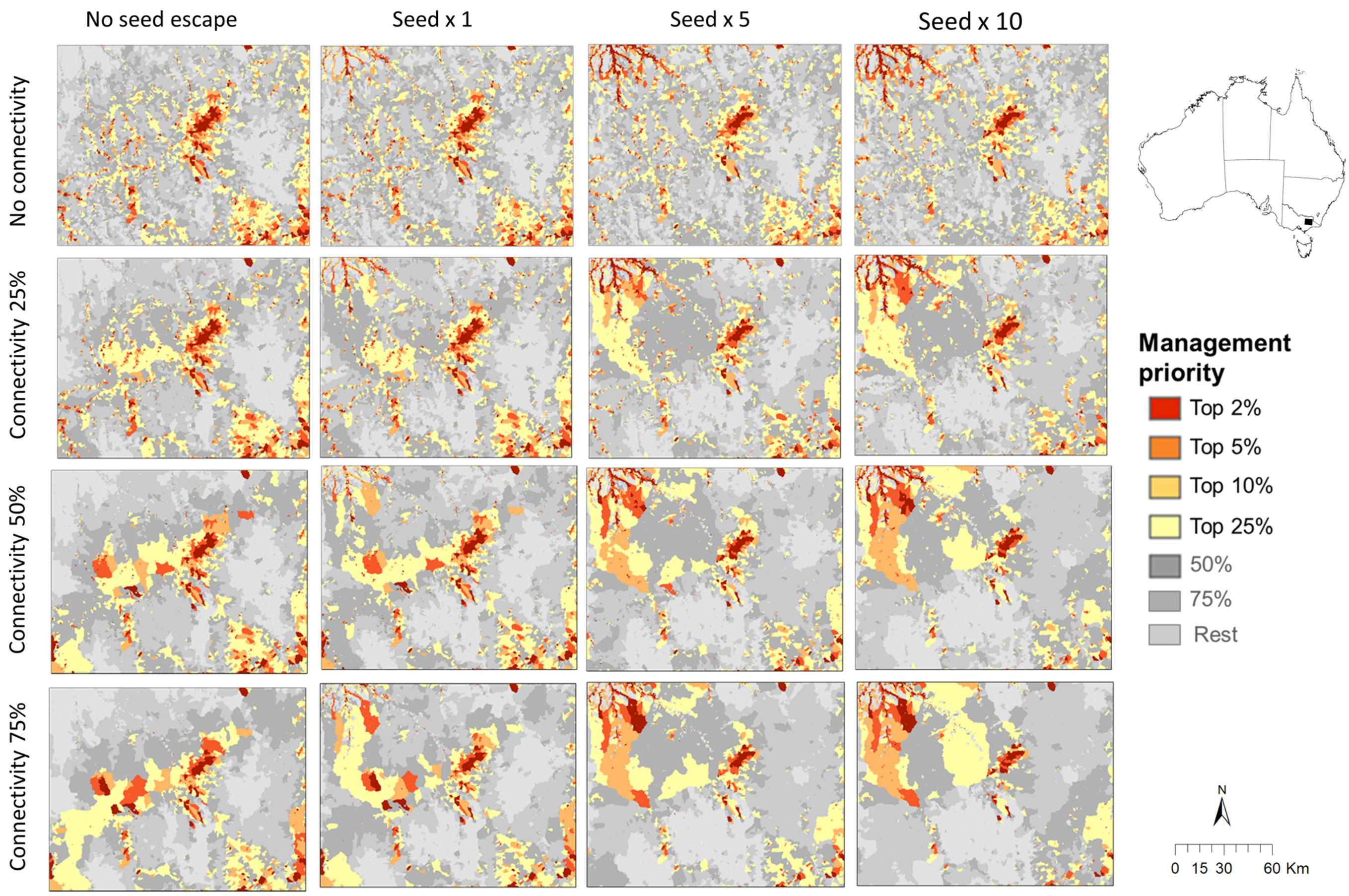

FIGURE 5 Priority areas for willow control in wind dispersal subregion (Figure 1) when limiting wind dispersal (columns) and downstream dispersal of willows (rows) is increasingly important. Each column varies in the importance of limiting willow wind dispersal, relative to the importance of the biodiversity features when limiting seed dispersal via wind is: not considered (wind dispersal 0), weighted approximately equally (wind dispersal 1×), five times (wind dispersal 5×), or 10 times (wind dispersal 10×) as important as a single biodiversity feature. The rows vary in the connectivity penalty (maximum percentage of benefit lost when no upstream subcatchments are managed) ranging from 0% (connectivity not considered) to 75%.

conservation and increasing biodiversity representation in priority sites (Almany et al., 2009; Hodgson et al., 2009). In the case of the willow, the weak trade-off reflected that the headwaters identified to reduce downstream dispersal also supported a substantial proportion of biodiversity and tended to be in good condition (Wilson, 2013).

Larger trade-offs were observed between reducing the threat of long-distance wind dispersal and reducing biodiversity impacts, reflecting that wind dispersal potential was distributed differently from the biodiversity features. Most of the smaller set of biodiversity features considered within the seed-dispersal study region (Table 1, Figure 1) were alpine and subalpine species found at high-elevation sites. Although wind dispersal potential was also high at some of these high-elevation sites, wind dispersal potential was also high in low-lying river valleys in the northwest of the study area (Figure 5). Wind dispersal potential tended to be highest when vegetation canopy was sparse and low, which in our study tended to be in agricultural areas and high-elevation areas of largely treeless vegetation (Appendix S1: Figure S7). Reduced priorities for biodiversity in lower-elevation areas likely reflect the relatively lower benefit of management for biodiversity in areas with substantial agricultural land uses. The trade-off between protecting biodiversity and reducing dispersal potential was greatest when both dispersal mechanisms were included in the prioritization. This was because waterways in low-lying valleys that are priorities for limiting wind dispersal potential are located at substantial distances downstream. Hence, long stretches of river (with lower biodiversity value) need to be prioritized when seeking to reduce both kinds of dispersal.

The magnitude of the trade-offs and the preferred weights will depend on the specifics for each situation. For example, in cases where biodiversity features are more evenly distributed across the study system, we would expect a stronger trade-off between limiting downstream dispersal and biodiversity protection. In this case, managers may wish to set lower values for downstream

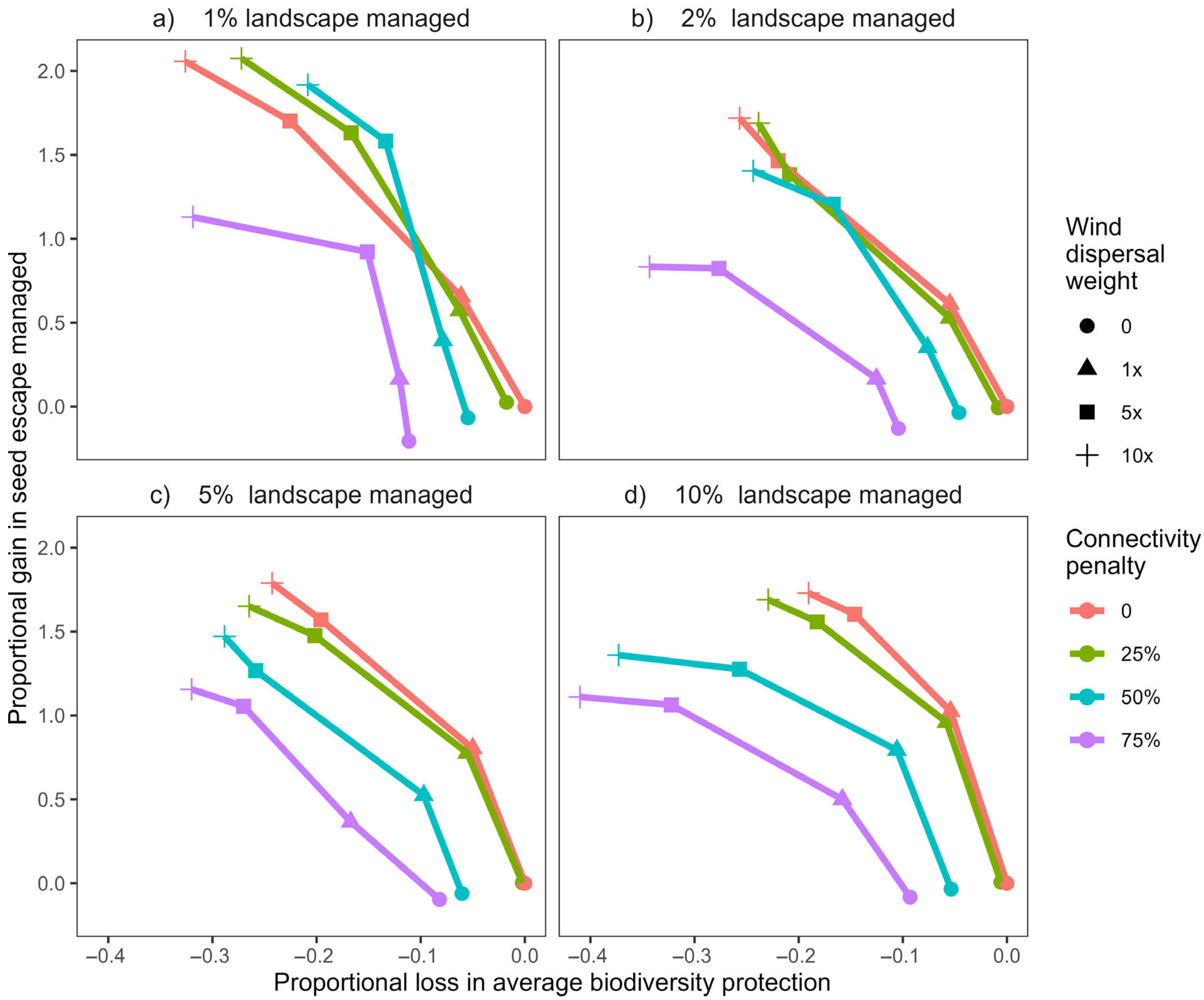

FIGURE 6 Trade-off between controlling willows to protect biodiversity and to limit future dispersal opportunity under different management scenarios when (a) 1%, (b) 2%, (c) 5%, and (d) 10% of landscape is managed. The proportional change is compared to the baseline management scenario where only protecting biodiversity is prioritized (red circle). Management scenarios differ based on the connectivity penalty (point color, lines join same weighting), where the penalty is the maximum proportion of benefit lost when no upstream subcatchments are managed, and limiting willow wind dispersal, relative to the importance of the biodiversity features ranging from 0 (limiting seed dispersal via wind not considered) to 10 times as important as a single biodiversity feature (wind dispersal weight 10×).

dispersal (or wind dispersal) weights so that larger areas for each threatened species are retained later in the prioritization. Conversely, for invasive species in an earlier stage of invasion, managers may wish to use higher values for connectivity and wind dispersal penalties to show a preference for slowing further spread until efficient management methods can be developed to attempt eradication.

Benefits of the approach

One of the benefits of our approach is to simplify the decision problem by considering current and future threats separately. Ideally, one would integrate current and future threats by minimizing cumulative biodiversity impacts accrued over a specified time frame. However, modeling the spatially explicit dynamics of invasion and impact is extremely complicated (Caplat, Coutts, & Buckley, 2012; Pepin et al., 2022), and identifying optimal solutions is often difficult for realistic problems unless it is possible to take advantage of specific problem characteristics to simplify the problem such as slowing spread from source populations (Baker, 2017; Epanchin-Niell et al., 2012), protecting a single location (Baker & Bode, 2013), or utilizing the problem's mathematical structure (Epanchin-Niell & Wilen, 2012). Formulating the problem as a trade-off between current and future threats retains the time dependence but is a simpler problem to solve, reducing the amount of data or modeling needed to identify management priorities.

Another advantage of our approach is that we model dispersal potential (rather than dispersal per se) and can link dispersal potential to landscape characteristics such as hydrological connectivity, vegetation structure, topography, and seasonal weather patterns. This differs from the dynamic models often used to model wind dispersal, which require data on population demographic factors that often are not available at a landscape scale and can be costly to obtain (Pepin et al., 2022). While several studies have incorporated landscape connectivity structures to guide management (Glen et al., 2013; Moilanen et al., 2008; Stewart-Koster et al., 2015), it has been less common to use variation in landscape features (e.g., topology, canopy height, leaf area index) to guide management decisions (Caplat, Coutts, & Buckley, 2012). While some studies have explored these links, they provide general recommendations only as they do not map dispersal potential onto landscape features (Buckley et al., 2005; Caplat, Nathan, & Buckley, 2012; Shea et al., 2010).

Using dispersal potential also makes the prioritization easy to update. The fine-scale modeling of wind patterns meant that we were able to produce a spatially explicit map of wind dispersal potential that reflected variation in weather patterns, topography, and vegetation structure. Similarly, we used existing maps of hydrological connectivity to describe downstream dispersal potential. By linking dispersal potential to the landscape, we were able to decouple dispersal potential from population abundance and so reduce data needs and model complexity. Our calculation of the dispersal potential of a location (given the invader is present) depends only on attributes of the landscape and long-term weather patterns, which means that the risk of dispersal, as calculated here, will stay relevant over time. Consequently, both the distribution of the invader and the management priorities can be easily updated without having to recalculate dispersal risk.

Our approach also takes advantage of the complementarity at the heart of conservation planning to ensure balance in achieving benefits for multiple management goals (in our case, 29 biodiversity features as well as wind dispersal potential). By using complementarity, we were able to ensure that some benefits were provided to each of the biodiversity features threatened by willow invasion and guard against imbalances in protection (Chadés et al., 2015). This contrasts with other optimization approaches that evaluate the contribution of each location to the management goal(s) independently, which can result in unbalanced benefits between biodiversity features and other management goals, even if the overall solution is optimal (Chadés et al., 2015; Firn et al., 2015; Moore et al., 2021).

Limitations of the approach

While increasing the tractability of the problem, modeling static dispersal potential rather than spread comes at the cost of neglecting the dynamic aspect of the problem. Hence, the optimal solution is unlikely to be optimal in the long term as it does not account for population dynamics over time (Hall et al., 2018). We envisage that inputs (willow distribution model, management effort) would be updated regularly and priorities subsequently recalculated to manage this limitation in a similar way to previously developed static optimizations (Giljohann et al., 2011; Hauser et al., 2016; Hauser & McCarthy, 2009).

A second limitation of not modeling dispersal explicitly was that we could not estimate the exact future benefits associated with control, as we could not predict the rate or location of spread and, hence, could not estimate willow density at a specific location. This also means that it is not possible to include density dependence in other inputs such as management costs, which would be expected to vary with willow density. Although we had a substantial amount of occupancy data, abundance data across the entire range are scarce, so we were unable to develop a model of willow density. Furthermore, we had no information regarding the density-impact curve, that is, how invader density translated into impact (Yokomizo et al., 2009). This knowledge gap is common (Januchowski-Hartley et al., 2018), but it makes it difficult for decision makers to identify weights for the dispersal components that capture specific management goals. We addressed this by examining a range of weightings to characterize the trade-off, so that decision makers can choose the weight that reflects their preferences. If the trade-off is weak (as was observed here for downstream dispersal and biodiversity), then it is possible to identify priorities that meet both management goals at once. Because we did not have a density-impact curve, we implicitly aimed for long-term eradication at each site. Estimation of density-impact curves, combined with models of willow density, would also mean we could identify when control is good enough and redeploy our effort to different locations. Developing density-impact curves and willow density models would substantially improve the recommendations and would be a valuable advance.

It can also be difficult to find quantitative estimates of specific dispersal processes, which can increase uncertainty in outputs. For example, we had no quantitative estimates of the distance that willow fragments dispersed downstream on which to base the downstream penalty function, so we chose a function based on general ecological principles that it is most efficient to start management at the source, that is, starting management upstream when dispersal is directionally downstream (Baker, 2017; Chades et al., 2011). A previous value-of-information analysis exploring the eradication of an invasive metapopulation found that accurate estimates of dispersal rates were not as important for decision making when connectivity was directional, because it was most efficient to target source populations regardless of dispersal probability values (Pepin et al., 2020). Hence, despite potential inaccuracies in the shape of our downstream penalty curve, we are confident that accounting for hydrological connectivity will still confer benefits overall.

Broader implications

Our method could be used to develop large-scale control strategies for other widespread invasive species, without necessarily requiring extensive new modeling. By consulting with relevant land managers, we were able to identify biodiversity features threatened by willow invasion and key dispersal mechanisms for inclusion in the prioritization. We calculated spatially explicit management priorities that accounted for the spatial structure of the invasion, using well-established species distribution modeling techniques along with existing observation and control records. Furthermore, we used publicly available data to account for the distribution of habitat for threatened biodiversity, site conditions, and downstream connectivity. The use of publicly available conservation planning software (Zonation) also makes it easier to transfer this approach to other management problems. Using established software means it was computationally efficient, making it feasible to solve large, landscape-scale problems, as is necessary for managing widespread invasions. Furthermore, as the output is a ranking of each site in the landscape by priority for management, this method is particularly useful for identifying priorities when resources are limited.

CONCLUSION

Because we used spatially explicit management prioritization, we were able to account for multiple biodiversity protection goals at once and account for future threats from reinfestation and spread of an invasive species. Priority locations could be identified to account for multiple management goals (biodiversity protection, reduce reinfestation risk), and trade-offs between the goals were characterized. The optimal management strategy depends on the relative importance of the management goals and the spatial distribution of biodiversity. Identifying priorities and characterizing trade-offs help natural resource managers make informed and transparent decisions about where to manage widespread invaders across a large region. Our approach does not require spatially explicit dynamic modeling of invasions but rather links dispersal threat to landscape features that can be mapped independently of invader abundance. It is our belief that this method, in reducing the complexity of the modeling needed to undertake the prioritization, can be applied to a wider range of species and support more effective management of biological invasions.

AUTHOR CONTRIBUTIONS

Joslin L. Moore, John Taylor, Cindy E. Hauser, and Jason Sharples conceived and designed the study. Stephanie Carter, Catherine Mills, Zhenhua Hao, Rowan Mott, and Matthew White undertook the modeling with assistance from John Taylor, Jason Sharples, Cindy E. Hauser, and Joslin L. Moore. Stephanie Carter and Joslin L. Moore wrote the paper (Stephanie Carter wrote the first draft), with all authors providing comments and approving the final draft.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data and code (Moore, 2024) are available in the Open Science Framework (OSF) repository at https://doi.org/10.17605/OSF.IO/GM4A5.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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