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Beyond refuges: Identifying temporally dynamic havens to support ecological resistance and resilience to climatic disturbances

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ABSTRACT

Little can be done by natural resource managers to abate climatic extremes such as drought, so assisting ecological communities to withstand and to recover from extreme events is likely to be an effective strategy for reducing the impacts of changing climate conditions on biodiversity. We present a framework for identifying locations that are likely to increase the capacity of biota to withstand disturbances (‘resistance’) and to recover when adverse conditions abate (‘resilience’). Our study ecosystem was the river red-gum (*Eucalyptus camaldulensis*) floodplain forests of the Murray River, southeastern Australia. We tracked forest-stand condition of river red-gum forests during and after a prolonged drought (the Big Dry) using models based on remotely sensed data and ground-truthed vegetation measurements of forest-stand condition. Native birds and small mammals respond positively to stand condition. We used spatial optimization to rank the region based on forest-stand condition at multiple time-points during a 13 yr drought and 2 yr after the drought ceased. We identified areas that ranked in the top portion of the landscape in either period to identify ‘resistance havens’ and ‘resilience havens’ respectively and assessed the extent to which these overlapped. Although there was overlap in the top ranked areas, there were differences in the areas identified as havens (top 25% ranking) in both periods, with a 55.5% overlap between areas identified as havens in either period. This overlap was lower (40.1%) when considering the most highly ranked (top 10%) areas. Concentrating only on locations that provide protection from adverse conditions (i.e. refugia) is likely to be ineffective for conservation management in increasingly changeable environmental conditions because areas that facilitate resistance will not necessarily be the same as areas that support recovery. Acknowledging and incorporating the concepts of ecological resistance and resilience into landscape management is vital if managers are to lessen the ecological effects of intensified disturbance regimes associated with climate change.

1. Introduction

Climate change is altering the frequency and severity of disturbance regimes around the world, including fire, heat waves and extreme weather events such as cyclones (IPCC, 2013). The frequency of short- and long-term drought is increasing in many parts of the world, and rising temperatures are inducing more severe drying (Sheffield and Wood, 2008; Schwalm et al., 2017). Extreme conditions and declines in ecological resource availability during disturbances can have immediate and sometimes catastrophic effects on native plants and animals, and these effects can be persistent (Parmesan et al., 2000; Jentsch et al., 2007; Jentsch and Beierkuhnlein, 2008). During drought, limitations to water availability from rainfall and run-off deficiencies reduce vegetation productivity (Saatchi et al., 2013) and can lead to widespread plant mortality (Allen et al., 2010). These declines in plant productivity reduce resource availability for animals, including food (seeds, fruit, foliage, prey), shelter (reduced vegetation cover) and nesting resources (Albright et al., 2010).

Little can be done by natural resource managers to combat climatic extremes such as drought, so assisting ecological communities to withstand and to recover from extreme events is likely to be an effective strategy for reducing the impacts of changing climate conditions on biodiversity (West and Salm, 2003; Nimmo et al., 2015). Identifying and protecting locations that increase the capacity of the biota to withstand disturbances (‘resistance’) and to recover if or when adverse conditions abate (‘resilience’) will be critical for effectively prioritizing

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conservation resources in a changing climate. There is increasing interest in the identification of locations that provide refuge from pulse disturbances such as drought, fire and extreme weather events, and ramping pressures such as increasing temperatures (Mackey et al., 2012; Davis et al., 2013; Robinson et al., 2013). Such locations may enhance the resistance of the biota by providing more favourable environmental conditions or higher resource availability during a disturbance than elsewhere, allowing resident populations to persist and, in some cases, to harbour individuals that are fleeing adverse conditions (Selwood et al., 2015b). For example, landscape elements such as gullies and rocky outcrops provide physical protection from fire (Robinson et al., 2013), while mesic locations with high vegetation productivity, such as floodplains and riparian zones, support more stable animal assemblages during drought (Haslem et al., 2015; Selwood et al., 2015b; Nimmo et al., 2016). However, there has been little discussion of the potential for locations to facilitate resilience (recovery).

Increased disturbance severity requires greater magnitudes of recovery, and increased disturbance frequency necessitates faster recoveries (Nimmo et al., 2015). As such, both biotic resistance and resilience are critical for enabling the biota to persist through intensifying disturbance regimes. Locations that facilitate resilience are likely to be those in which resource availability or environmental suitability is high after the release of a disturbance, so that individuals can exploit improved conditions, leading to improved health, reproduction, population growth and, potentially, population expansion. However, locations that facilitate resistance may not be the same as those that facilitate resilience, just as habitat that enhances survival at one extreme of a climate gradient (e.g. cool temperatures) may not be the same habitat that is important for survival of that population in the other extreme of that gradient (e.g., hot temperatures) (Tanner et al., 2017).

1.1. *The Big Dry and Big Wet*

From 1997 to mid-2010, southeastern Australia experienced the 'Big Dry', the most severe hydrological drought in Australian climate records (Leblanc et al., 2012). A sustained positive epoch for the Southern Annual Mode and multiple El Niño events caused below-average rainfall during this period (Murphy and Timbal, 2008; Verdon-Kidd and Kiem, 2009). Unprecedented reductions in run-off significantly reduced inflows into the Murray river system during this time (Chiew et al., 2011; Leblanc et al., 2012). The Big Dry was broken by the 'Big Wet' in mid-2010, which were the two wettest recorded years for Australia as a whole, with extensive flooding in southern Australia (BOM, 2012; Timbal et al., 2015). The total rainfall (excess) anomaly during the Big Wet was about one-third of the total rainfall deficiency during the Big Dry in southeastern Australia (BOM, 2012). The alternation of long, severe droughts and shorter, more intense rainfall periods is expected to become the norm for southeastern Australia over the next 50–70 years (Timbal et al., 2015).

Here, we present a method for identifying locations that are likely to support ecological resistance and resilience during drought, and other pressures. We evaluated spatially explicit changes in the condition of floodplain forests during the Big Dry and the high-rainfall Big Wet using ground-truthed models of remotely sensed vegetation condition, which are linked to the abundance, diversity and breeding activity of native woodland birds (Mac Nally et al., 2014) and the demography of small-mammal (*Antechinus flavipes*) populations (Lada et al., 2014). We identify forest patches that maintained relatively high ecological condition in either period as areas that are likely to facilitate resistance and resilience, which we refer to as 'havens' as a generalization of the refuge concept. We compare the location of these havens in either period to assess whether, and to what extent, there is overlap between locations that are likely to enhance ecological resistance during a disturbance and those that are likely to facilitate resilience after the release of a pressure.

2. Methods

2.1. *Study system*

The study region is the river red-gum floodplain forests of the Murray River, in Victoria and New South Wales, southeastern Australia. This ecosystem consists of open forest and woodlands dominated by the river red-gum, *Eucalyptus camaldulensis* Denh., a species whose survival and reproduction is highly adapted to water availability, especially flooding (Horner et al., 2009; Mac Nally et al., 2011). The understorey consists of shrubs, sedges and grasses, and groundcover includes high levels of fallen timber and litter (Mac Nally et al., 2014). The climate for the region is temperate semi-arid, with a mean annual rainfall (for period 1961–1990) ranging from 290 mm–475 mm (Mildura Airport and Yarrawonga weather stations; accessed 13 March 2017).

Intermittent flooding and shallow groundwater tables allow the river red-gum forests to maintain biomass comparable to forests in higher rainfall areas (Akeroyd et al., 1998; Bren, 1998). High flows historically flooded these forests at a mean interval of approximately five years, but river regulation has increased the interflood return time to c. 11 years, and climate projections suggest return intervals of 21 years by 2030 (CSIRO, 2008). There is substantial variation in forest-stand condition in the ecosystem due to changed flooding regimes, variation in groundwater depth and salinity (Cunningham et al., 2011) and past and present timber harvesting (Horner et al., 2010).

2.2. *Mapping forest-stand condition*

A robust method for mapping condition of river red-gum forest stands was developed by Cunningham et al. (2009, 2018) using satellite-derived variables, validated with on-ground measurements of tree-stand condition (leaf area index, percentage of crown branching structure with live foliage and percentage live basal area), which are linked to physiological stress in *E. camaldulensis* (Cunningham et al., 2007). Spatially explicit models of river red-gum forest-stand condition were built for the study region for the years 2003, 2006, 2008, 2009, 2010 and 2012 (Cunningham et al., 2018). These models provided annual stand-condition estimates for the river red-gum dominated forest along the Murray River (159,507 ha, Fig. 1) at a 25 × 25 m resolution, with stand-condition scores ranging from zero (severely degraded) to ten (good condition). Detailed, extensive methods for producing these models are reported elsewhere (Cunningham et al., 2009, 2018).

Alongside the raw outputs from these stand-condition annual models, we computed maps of variation in relative stand condition on a regional basis each year. There is a pronounced aridity gradient from east to west (Selwood et al., 2018), which prompted us to consider regional differences in potential haven locations. Moreover, some animal species may be mobile enough to traverse the entire study area (i.e., are likely to be influenced by absolute stand condition over the entire Murray River region), but other, less mobile fauna may be capable of only local movements (i.e., more likely to be influenced by regional deviation in stand condition). The entire study area extends > 600 km, so regional variation in ecological condition is likely to be influential. Therefore, we used the Interim Biogeographic Regionalisaton of Australia (DoE, 2012) to partition the study area into regions (Fig. 3) and we computed the mean stand condition for each year using the 'zonal statistics' plugin in QGIS using the raw stand-condition outputs for each region (QGIS Development Team, 2015). We transformed each stand-condition model into regional deviation of stand condition by subtracting the regional stand-condition mean from the absolute stand condition of each cell. Each layer was recalibrated so that the minimum value was zero (i.e., new cell value = cell deviation – minimum regional deviation), enabling it to be used in subsequent analysis in *Zonation* spatial prioritization software (see next section), which cannot handle negative values. Raster transformations were

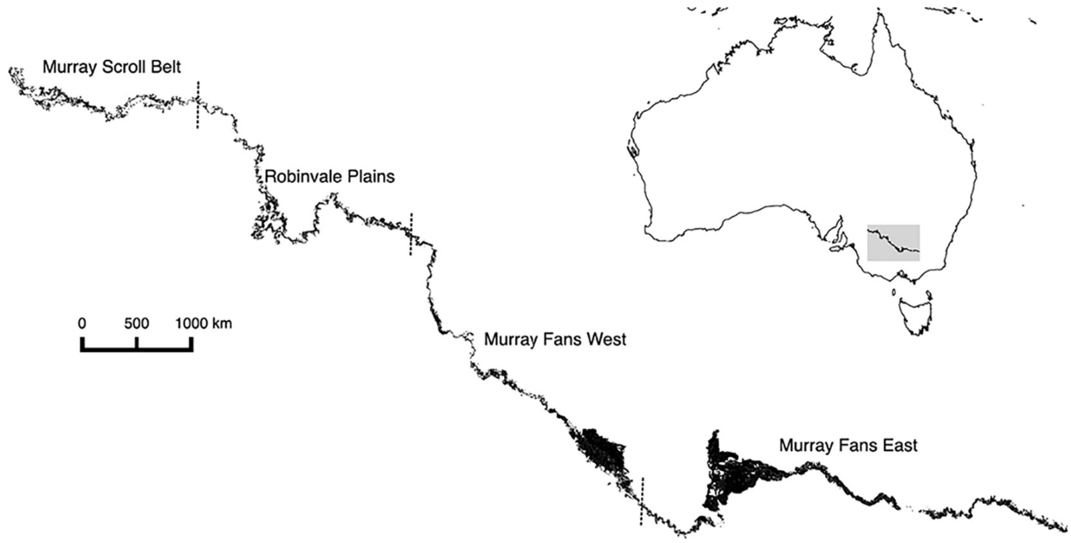

Fig. 1. Map of the study area (river red-gum dominated floodplain forests of the Murray River), divided into four subregions based on the Interim Biogeographical Regionalisation of Australia (DoE, 2012). The Murray Fans IBRA region was divided into 'East' and 'West', just east of Gunbower Island, so that each zone was of similar area to the other regions.

conducted using the 'raster' package in R (Hijmans and van Etten, 2013).

2.3. Spatial prioritization analysis

We used two measures of stand condition to quantify spatially explicit haven quality in each year during the Big Dry (years 2003–2010) and Big Wet (2012) using spatial prioritization. The first measure was absolute stand condition using the raw stand-condition score output, which is consistent and comparable for the entire study area among years. The second measure was the deviation of stand condition from the regional mean (henceforth, 'regional deviation') to quantify the variation in relative stand condition on a regional basis in each year.

We used *Zonation* (Lehtomäki and Moilanen, 2013) to rank the 'haven quality' of each cell (25 × 25 m) in the study region based on (1) absolute and (2) regional deviation of stand condition. *Zonation* develops a priority ranking of the entire landscape based on mapped biodiversity features (e.g. species distributions, ecosystem services), in our case, forest-stand condition. Cells are ranked by comparison with all other cells in the region (i.e. between 0 and 100%), incorporating spatial preferences such as connectivity between cells. A separate *Zonation* analyses was completed for (1) the drought period ('resistance havens', stand-condition layers from years 2003, 2006, 2008, 2009, 2010) and (2) the Big Wet period ('resilience havens', stand condition in 2012). Layers of absolute stand condition and regional deviation of stand condition for the relevant set of years were used as the 'biodiversity components' in *Zonation*, with all layers weighted equally. We used core-area analysis, with a warp factor = 1, which means one cell is removed per iteration, leading to a high-resolution result. A boundary length penalty (BLP) of 0.05 was used to force spatial cohesion of high quality areas. BLP reduces the edge:area ratio of retained areas, and is the most commonly used connectivity method in *Zonation*. This spatial optimization is designed to identify locations that maintain high stand condition throughout each period by ranking most highly those areas that maintain high quality stand condition over several years, on both a whole-system (absolute) and regional bases (regional deviation). We identified the top 25% rankings from *Zonation* in either period as a threshold to define havens to compare the overlap in resistance and resilience havens. We considered a lower threshold (10%) to evaluate the sensitivity of overlap to the amount of high-quality area. A conceptual model of the haven identification process is presented in Fig. 5.

2.4. Spatial analysis of haven locations

We investigated whether rankings of haven quality from the two *Zonation* outputs (resistance and resilience havens) were associated with flood frequency estimated by the 1 km resolution Murray Darling Basin Floodplain Inundation Model (Chen et al., 2012) or from the average frequency of surface water estimated by the 25-m resolution Water Observations from Space (WOFS, Mueller et al., 2016). We calculated correlations between haven quality and each layer using the pairs{graphics} function in R (R Core Team, 2015), and plotted relationships between layers by sampling 10,000 points from each layer.

3. Results

3.1. Overlap between resistance and resilience havens

Of the total area of Murray River floodplain forest identified in the top 25% portion of the study area in either the Big Dry or the Big Wet, 55.5% was in the top portion of the landscape in both periods (i.e. both resistance- and resilience-haven). The remainder differed in importance during the Big Dry and Big Wet. The degree of overlap between resistance- and resilience-havens differed between regions (Fig. 2). The overlap was lower if one considered the top 10% rankings: 40.9% of resistance havens were classified as resilience havens (i.e. top 10% in both periods).

3.2. Location of havens

We report here on the area of each region that was identified in the top 25% of the landscape for each period (results for top 10% are reported in Table S1). The location of resistance and resilience havens derived from *Zonation* cell ranks are shown in Fig. 3. The largest proportional extent (proportion of region identified as haven) and absolute extent of the haven network was in the Murray Fans East region, mostly in the largest floodplain forest of the study area, the Barmah-Millewa forest (Fig. 3). Of the entire haven network, 71.3% of the total haven network, including 74.5% of all resistance havens and 59.6% of all resilience havens, was in the Murray Fans East region despite the region being only 49.6% of the total floodplain forest estate (Fig. 2). This is the most upstream region of the Murray River, with the highest mean annual rainfall. Most of the havens in this region were near to the Murray River channel, in large wetlands and in the main tributaries of the

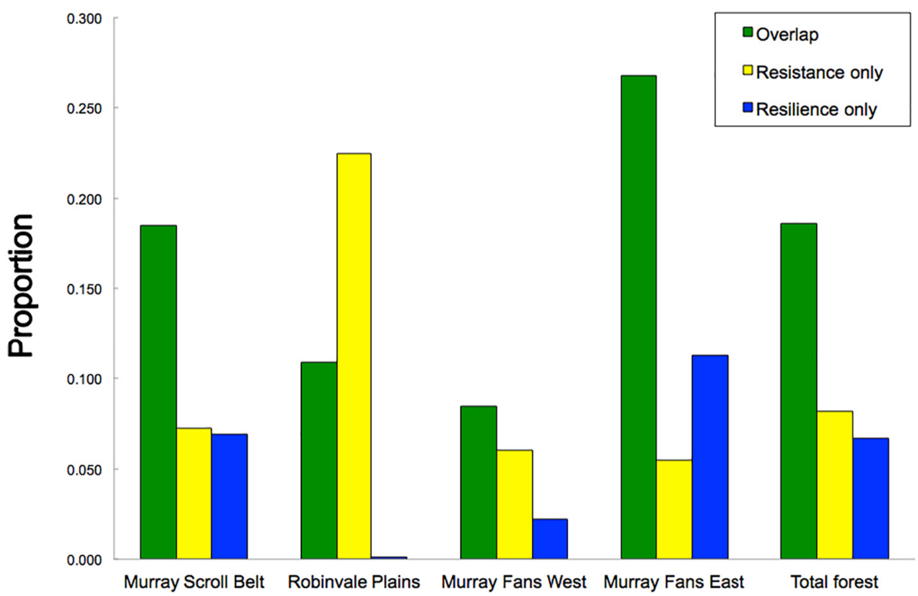

Fig. 2. Proportions of each Murray River bioregion that were identified as resistance havens (yellow), resilience havens (blue) and in common (green), using the top 25% spatial prioritization rankings for the study region. Proportions reported for each region are relative to the total floodplain forest area of that region, and colours correspond to those in Fig. 3. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Barmah-Millewa forest. The resilience havens extended further from the main channels than did the resistance havens (Fig. 3).

A relatively small proportion of the Murray Fans West region, which includes the Gunbower Island and Koondrook-Perricoota floodplain-forest complex, was identified in the haven network: 8.5% of the region was identified as both resistance and resilience haven, 6.0% as resistance havens and 2.2% was resilience havens (Figs. 2, 3). Most of the haven network in this region was on Gunbower Island, largely in the state parks and national parks and along the main river channel (Fig. 3).

To the west, 33.6% of the Robinvale Plains was identified as havens: 10.9% was both resistance and resilience haven, 22.5% was resistance haven only. In the Murray Scroll Belt, 26.8% of the region was identified as both resistance and resilience havens, with smaller areas of resistance havens (5.5%) and resilience havens (11.3%) (Fig. 3).

3.3. Spatial analysis of haven locations

There was relatively little association between flood-return period

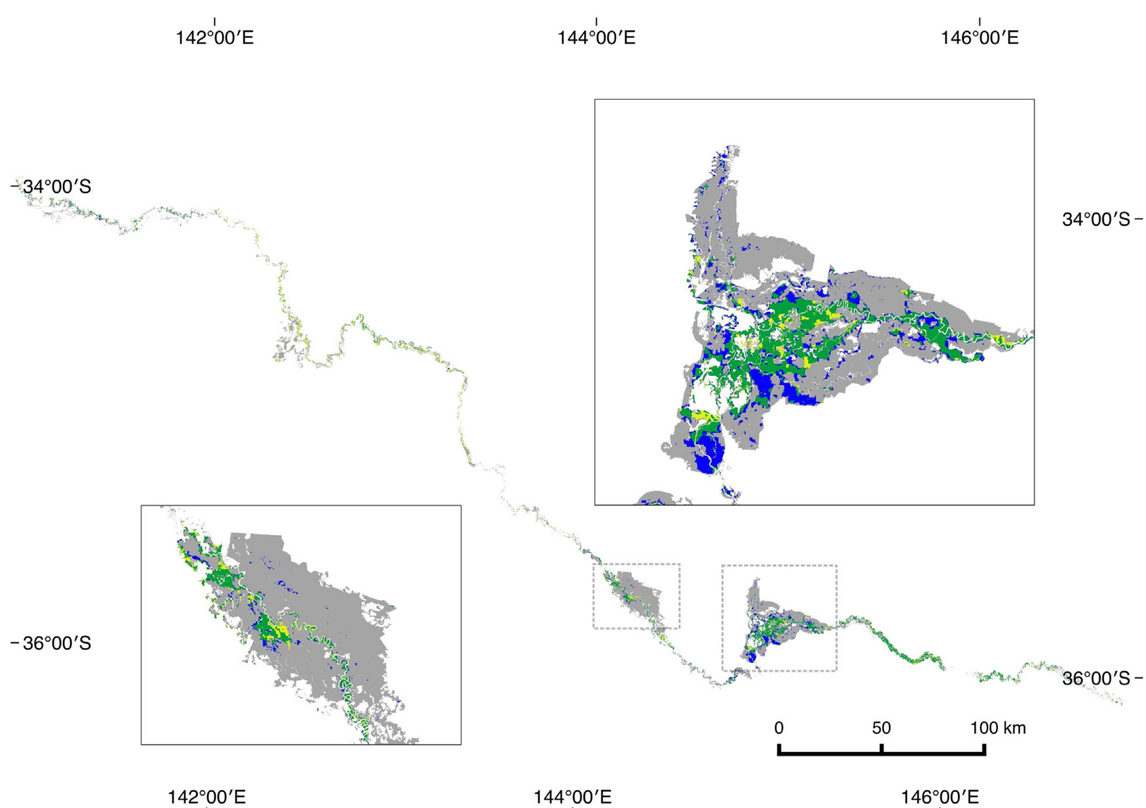

Fig. 3. Map of resistance (yellow) havens and resilience havens (blue), with common areas coloured green (non-priority areas are grey). The inset boxes are the Gunbower-Koondrook-Perricoota floodplain-forest (left) and the Barmah-Millewa floodplain-forest (right), which are the major floodplain forests in this system. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

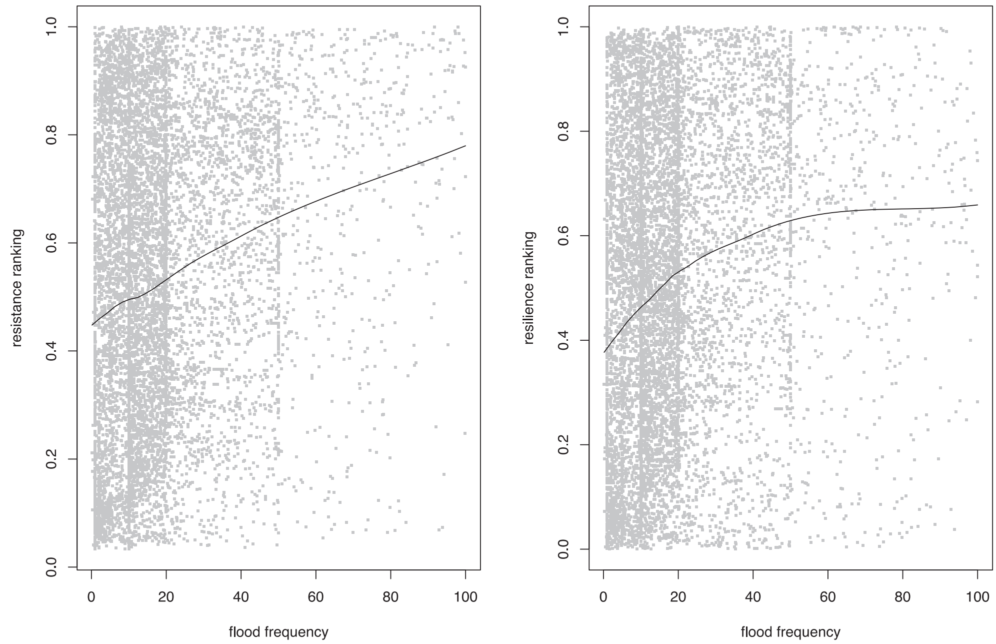

Fig. 4. Scatterplots of resistance ranking (left, r = 0.22) and resilience ranking (right, r = 0.24) against estimated flood frequency (percentage of years flooded, from MDBFIM, Chen et al., 2012) for 100,000 sample points. Smoothed lines are fitted with local polynomial regression using the 'loess.smooth' function.

(MDBFIM) and resistance-haven ranking (r = 0.22) and resilience-haven ranking (r = 0.24) (Fig. S1), although more frequently flooded locations tended to have higher rankings in resistance and resilience (Fig. 4). Although surface water frequency (WOFS) was highly correlated with flood return period (r = 0.78), there was little association with haven-quality rankings (r = 0.05 for both resistance- and resilience-haven rankings; Fig. S1).

4. Discussion

Models of forest-stand condition based on remote sensing are being adopted increasingly as tools to monitor vegetation change and mortality in response to pressures such as drought and fire (Michaelian et al., 2010; e.g. Arnett et al., 2015; Asner et al., 2016). Here, we showed that models of remotely sensed forest-stand condition can be used to identify areas that are likely to facilitate resistance and resilience to drought. We used spatial optimization of maps of forest-stand condition at multiple time-points to identify locations that maintained comparatively high ecosystem condition during the drought ('resistance havens') and during a period of drought recovery ('resilience havens') (Fig. 5). These ground-truthed models of remotely sensed forest-stand condition have been linked positively to the responses of birds (e.g. occurrence, breeding activity and success) and small mammals, and so these havens are likely to facilitate resistance and resilience of these taxa. Ultimately, temporal trends in population viability or abundance of constituent taxa may be used to verify the expectation that havens maintain relatively more stable populations during a disturbance, and have faster population recoveries after the release of a disturbance. Identifying, and then protecting or enhancing havens during disturbance and recovery periods is likely to be an effective strategy for buffering ecosystems from otherwise unmitigated disturbance regimes, many of which are intensifying due to climate change [e.g. drought, fire and extreme weather events (IPCC, 2013)].

Our framework could be applied to other systems by identifying relevant measures of ecosystem condition, which relate to the responses of constituent species or those of management concern, and that can be readily assessed through time and space. Models that are based on remotely sensed data, linked to on-ground measures, are particularly attractive because remotely sensed data offers researchers readily

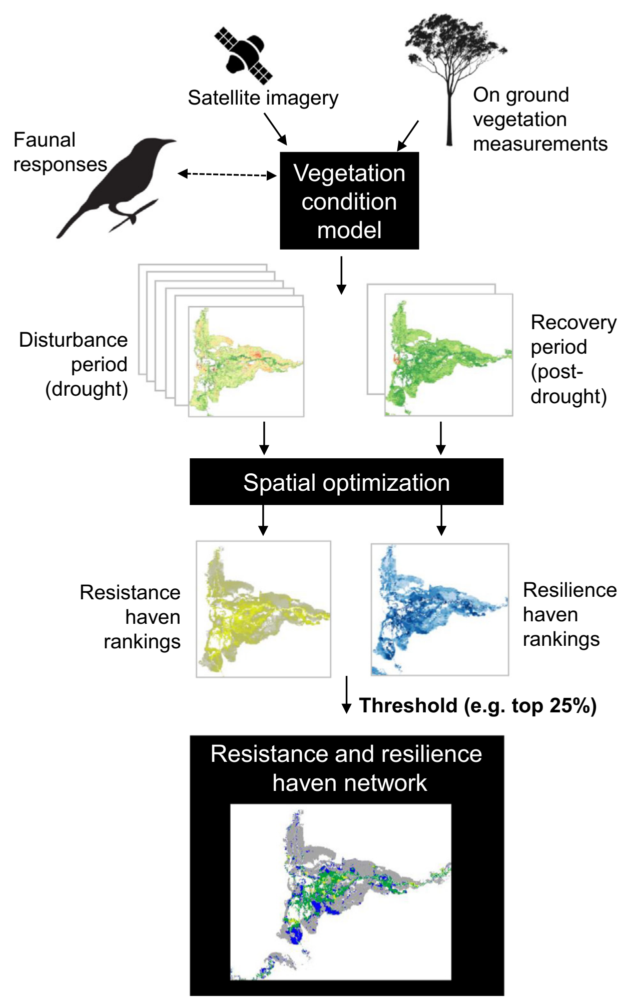

Fig. 5. Conceptual model documenting the framework we present for identifying resistance and resilience havens.

available, spatially continuous data over multiple spatial and temporal scales (Hakkenberg et al., 2018). In particular, our framework would be readily transferable to other forest ecosystems that are affected by changing drought regimes. For example, there is spatial variability in drought severity in the Amazon basin (Aragao et al., 2007), and in drought-induced degradation in Canadian boreal forests (Michaelian et al., 2010) and Patagonian *Nothofagus* forests (Suarez et al., 2004). Mapping ecosystem condition during a disturbance, such as drought, is critical because ecosystem responses to pressures may vary over space due to a range of factors, not only the severity of the abiotic pressure (e.g. rainfall deficit, temperature), but from previous stress and disturbance history, ontogeny, physiology, and fine scale variation in the biotic (e.g. species composition) and abiotic (e.g. topography, geology) environment (Suarez et al., 2004).

We showed that there was a difference in the spatial locations of havens (locations that maintain high forest-stand condition) during phases of a disturbance cycle of drought. Although there was overlap in the locations that maintained vegetation condition during periods of drought and post-drought recovery (c. 55% of the total network of potential resistance and resilience havens), there was still substantial disparity in the locations that are likely to be most valuable for biota during periods of drought and high rainfall. Locations that facilitate resistance of biota during disturbances were not necessarily the same locations that will facilitate recovery after the cessation of a disturbance pressure. West and Salm (2003) found that the characteristics of coral reefs that were resistant to bleaching events differed from those that were resilient. Reefs that were most resistant to bleaching tended to have physical characteristics that reduced water temperatures and reduced damaging incident radiation, while reefs that were most resilient enabled larval establishment after bleaching, such as areas with high connectivity to larval supplies. Spatial patterns of ecosystem resistance and resilience to fire also differ. For example, while factors such as topography may influence the spatial severity of a fire (and thus, vegetation resistance), lithology can have a strong impact on the ability for vegetation to recover such that spatial patterns of vegetation resilience may differ greatly from patterns of fire severity (Torres et al., 2017). Spatial patterns of forest damage from catastrophic wind disturbance can differ from spatial patterns of recovery due to a range of biotic and abiotic factors that influence vegetation damage and recovery, including the presence of pathogens, species' traits and vegetation composition, disturbance history, topography and soil and resource gradients (Everham and Brokaw, 1996). Concentrating only on locations that provide protection from adverse conditions (i.e. refugia) may be ineffective for conservation management in increasingly changeable environmental conditions. While refugia are likely to support more-viable populations during disturbances, if biota cannot bounce back to their pre-disturbance state soon after adverse conditions abate then there almost certainly will be on-going, ecosystem-wide, declines in populations (Mac Nally et al., 2014; Selwood et al., 2015a). Identifying and enhancing or protecting locations that facilitate ecological resilience will be just as critical to ecosystem persistence as focusing on those locations that facilitate resistance.

Resistance and resilience in our floodplain-forest study system were correlated with values from a model of floodplain inundation because the condition and life cycle of the dominant species, *E. camaldulensis* is tightly linked to water availability and flooding (Mac Nally et al., 2011). Why do resistance and resilience havens differ substantially in location? Differences in the fine-scale dynamics of floodplain hydrology (e.g. microtopography, groundwater) may induce dissimilarities in how some tree stands respond to overall water availability during drought and benign periods, which is reflected in measures of tree condition during each period. Some stands may have more access to groundwater during drought, some may receive greater rainfall runoff due to topographical differences, while others may receive more optimally timed inundation regimes (Bren and Gibbs, 1986). Other pressures are also likely to interact with the relationship between water availability and stand condition, such as current and historical grazing, wood harvesting and groundwater salinity (Cunningham et al., 2011; Mac Nally et al., 2011). We did not have comprehensive data on these factors and so we were not able to explore which, and to what extent, these factors may have influenced the location of havens.

Identifying havens for resistance and resilience provides temporally dynamic spatial foci for conservation managers to concentrate limited resources in the face of intensifying disturbance regimes to prioritize areas that maintain high habitat quality during disturbances, and in recovery periods. The location of the havens may be used to prioritize the abatement of manageable threats (e.g. invasive species control, restrictions on human land-use) or the application of conservation actions (e.g., ecological restoration including replantings) to increase population viabilities. Pressures that diminish the capacity for havens to support viable populations should be managed as a priority. The potential for small native mammals (e.g. *Antechinus* sp.) to recover from periods of low rainfall may be reduced by mortality from feral predators or from low resource availability arising from inappropriate fire or timber harvesting regimes (Wilson et al., 2017). Species' resilience might be increased by locating fuel-reduction burns distant from havens, and by concentrating predator management within havens, particularly in periods of high rainfall when breeding is likely to be most successful. Given that conservation funding usually is small, the availability of resources is likely to be the major determinant of the area over which management will occur, rather than the arbitrary thresholds we used (e.g., 10%, 25% total area). However, if havens are designated in a management region to meet conservation goals or commitments (e.g. maintaining minimum viable populations, reducing extinction risk by X %) rather than to prioritize limited resources, then careful consideration needs to be made to define an adequate total area threshold.

In the river red-gum forests of the Murray River, major ecosystem threats include reduced flooding, salinity, grazing and wood removal (standing and fallen) (Mac Nally et al., 2011). A return to more natural flood regimes, including through environmental water provision, is a clear pathway to improving ecosystem condition, and hence, to increasing drought resistance and resilience, in this system (Mac Nally et al., 2011). Restricting wood removal in highly ranked haven locations probably would increase the resistance and resilience of floodplain biota, as would control of domestic stock and invasive herbivores. Floodplain birds and small mammals respond strongly to the availability of fallen timber and the presence of large trees (Mac Nally et al., 2011), so that restoring fallen timber loads in havens and protecting large trees are critical for enhancing the ability for havens to facilitate population resistance and resilience.

5. Conclusions

Here, we expand the refuge concept to develop a framework for identifying ecological havens to support the capacity for biota both to resist and to recover from extreme climatic disturbance, in this case, drought. Acknowledging and incorporating the concepts of ecological resistance and resilience into landscape management will be vital if managers are to mitigate the ecological effects of intensifying disturbance regimes arising from with climate change. Identifying relevant measures of ecosystem condition that relate directly to the responses of constituent species, or those of management priority, is critical for identifying havens for resistance and resilience, as is the ability to measure ecosystem change over time. The rapidly increasing availability, quality and resolution (spatial and temporal) of remotely sensed data means there is much promise for the development of such ecosystem models elsewhere in the world (Hakkenberg et al., 2018). Several teams have used remotely sensed data to identify locations that maintain more stable or 'favourable' environmental conditions (e.g. cooler, wetter) during climatic disturbances (e.g. Mackey et al., 2012; Andrew and Warrener, 2017). The challenge is to ensure that these models link to ecosystem condition and reflect resistance and resilience in the populations of constituent taxa.

Author contributions

RM, SCC and KES conceived the study. KES undertook the analysis with significant contributions from RM and SCC. KES led the writing with significant contributions from RM.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2019.02.034.

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