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The influence of spatial patterns in foraging habitat on the abundance and home range size of a vulnerable arboreal marsupial in southeast Australia

Benjamin Wagner | **Patrick J. Baker** | **Craig R. Nitschke**

School of Ecosystem and Forest Sciences, The University of Melbourne, Richmond, Victoria, Australia

Correspondence
Benjamin Wagner, School of Ecosystem and Forest Sciences, The University of Melbourne, Richmond, VIC 3121, Australia.
Email: benjamin.wagner@unimelb.edu.au

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Abstract

Wildlife can persist in a range of landscape configurations, but population densities can vary due to resource availability. Resources and environmental conditions shaping habitat suitability may be spatially dispersed or clumped, which can drive habitat availability. We explored how spatial configuration and aggregation of favorable feeding resources and climatic conditions affect populations of the greater glider (*Petauroides volans*), an arboreal marsupial in southeast Australia, vulnerable to climate change and disturbances. We hypothesized home-range functionality from literature and field observations and used a generalized spatial framework based on neutral landscape models to test how spatial aggregation influences home-range sizes and population structure. At the landscape scale, any decrease in climatic suitability also decreased potential population density, independent of the initial spatial configuration of the feeding landscape. At the stand scale however, the spatial configuration of feeding habitat drove population density. Dispersed resources required increased home-range sizes for individual greater gliders to obtain feeding resources and resulted in smaller populations. Clumped resources supported larger populations, even when only small fractions of the stand contained feeding habitat. Disturbances to these resources could either retain populations or lead to extinction, depending on spatial aggregation and disturbance intensity. Increasingly severe dispersed disturbances caused potential home ranges to disappear more rapidly and remaining home ranges to become larger and contain less feeding habitat. The ability of greater gliders to establish populations and persist under disturbance was therefore highly dependent on the spatial aggregation of habitat resources and the type and severity of disturbance. Changes in climate act at a different scale and may override favorable habitat conditions at the stand level. Our results have implications for the conservation and retention of critical feeding habitat for greater gliders and provide insights into important factors to ensure population persistence under climate change and forest management.

KEYWORDS
disturbance, foraging, greater glider, habitat resources, habitat suitability, home ranges, neutral landscape models, population persistence, spatial patterns

1 | INTRODUCTION

A species' habitat niche is comprised of favorable conditions and required resources, which allow the establishment of populations and their persistence in a landscape (Warren, Glor, & Turelli, 2008). Different combinations and availability of these elements lead to some habitat being higher or lower in quality, which is measured as habitat suitability (Hirzel & Le Lay, 2008). Although it is possible to determine and monitor habitat requirements at the patch scale (e.g., through forest surveys), it remains difficult to extrapolate from field observations to scales relevant to entire populations (With & King, 2001). Factors determining habitat suitability may occur at different scales and vary in spatial arrangement (Huston, 1999). For example, a species' tolerance of certain climatic conditions will be influenced by landscape-scale climate and weather patterns and variability (Briscoe, Krockenberger, Handasyde, & Kearney, 2015; Wagner et al., 2020), whereas foraging or nesting resources are the result of stand-scale forest dynamics (McLean, Bradstock, Price, & Kavanagh, 2015; Moore, Lawler, Wallis, Beale, & Foley, 2010). Although species may be able to persist in a range of landscape configurations and variations in habitat suitability, population density will vary as it is driven by resource availability (Wallis et al., 2012). Resources and conditions shaping habitat suitability may be spatially dispersed or aggregated and drive abundance and density of habitat (Nitschke et al., 2020) and therefore density of individuals in a given area (Fahrig, 2001). Furthermore, disturbances to these resources may change the amount, distribution, and configuration of suitable habitat within forest stands and across landscapes (Devictor, Julliard, & Jiguet, 2008). A loss of habitat may reduce the ability of individuals or populations to persist (Fahrig, 2001). The extent and intensity of a disturbance can lead to a spatially aggregated or dispersed habitat structure. For example, catastrophic, stand-replacing fires can cause an aggregated spatial effect (Walker et al., 2019), whereas certain forest management methods such as selective timber harvesting may lead to resources and habitat becoming more dispersed (Kavanagh & Webb, 1998; McLean, Kavanagh, Penman, & Bradstock, 2018). To facilitate informed decisions in species management and conservation, it is important to quantify how both abundance and patterns of resource availability may drive the persistence or loss of wildlife populations (Lande, 1987). Such knowledge is critical for understanding how populations respond to disturbances of different spatial extents, patterns, and severity.

Species with distinct habitat requirements are well suited for testing the effects of habitat configuration and abundance on their occurrence (Mazerolle & Villard, 1999). Examples exist from wetland bird and turtle species in Canada, where habitat amount was more important than spatial configuration (Quesnelle, Fahrig, & Lindsay, 2013), and the northern spotted owl (*Strix occidentalis caurina*) in the Pacific Northwest, for which a mosaic of old-growth forests and other vegetation types improved population fitness and persistence (Franklin, Anderson, Gutiérrez, & Burnham, 2000; Jones, Keane, Gutiérrez, & Peery, 2018). In southeastern Australia, the southern greater glider (*Petauroides volans*) is well known for its distinct habitat requirements, which are strongly influenced by climate, nesting space and feeding resources and which operate over multiple spatial scales. At the landscape scale, climate shapes the distribution of the species due to a narrow thermotolerance, which restricts populations to cooler and wetter parts of the landscape (Kearney, Wintle, & Porter, 2010; Rübsamen, Hume, Foley, & Rübsamen, 1984; Wagner et al., 2020). Forests at high elevation are mostly climatically suitable. At low elevations, arid conditions make most of the area unsuitable, restricting the greater glider to landscape features such as riparian gullies that act as microclimatic refugia (Wagner et al., 2020). At the stand scale, a specialized diet consisting entirely of nutrient-rich *Eucalyptus* leaves and the need for multiple tree hollows for denning, shapes the establishment and spatial configuration of individual home ranges (Kavanagh & Lambert, 1990; Lindenmayer, Cunningham, Tanton, Smith, & Nix, 1990; Smith, Mathieson, & Hogan, 2007). Suitable tree species with leaves rich in foliar nitrogen are typically dispersed at low elevation but highly aggregated at mid- and high-elevation sites (Wagner, 2021). In tall, mature forests, hollow-bearing trees used for nesting can be abundant and typically do not limit habitat suitability where forest areas have not been disturbed by fires or timber harvesting (Wagner, 2021). However, areas subjected to timber harvesting or forest fires may experience drastic reductions in nesting resources and therefore habitat suitability (Lindenmayer & Sato, 2018; McLean et al., 2015; McLean et al., 2018). Across the greater glider's range in Victoria, feeding, and nesting resources occur in different abundances and spatial arrangements

(Bennett, Lumsden, & Nicholls, 1994; Fox, Hamilton, & Occhipinti, 2009; Wagner, 2021). This shapes habitat suitability and acts as a filter on occurrence and abundance of greater gliders. Individual greater gliders have been reported to increase their home range sizes where resource availability is limited (Kavanagh & Wheeler, 2004; Smith et al., 2007). This suggests that occurrence and population density may be closely related to the spatial arrangement of favorable climatic conditions and habitat resources (Wallis et al., 2012), as well as the amount of available habitat in an area (Youngentob, Wood, & Lindenmayer, 2013).

Populations of greater gliders are in decline (Lindenmayer et al., 2011; Lindenmayer & Sato, 2018; Smith & Smith, 2020). Their conservation is of great concern; however, their capacity to persist in different parts of the landscape is still unclear (DELWP, 2019). At the landscape scale, a changing climate has led to a contraction of greater glider distribution to higher elevations (Smith & Smith, 2020; Wagner et al., 2020). Stand-altering or -replacing disturbances, as a result of forest fires and timber harvesting, have been found to influence persistence at finer scales (Kavanagh, 2000; Lindenmayer et al., 2013; McLean et al., 2018; Pope, Lindenmayer, & Cunningham, 2004; Possingham, Lindenmayer, Norton, & Davies, 1994; Youngentob et al., 2013). With continued climatic change, it is important to understand the effects of decreasing climate suitability on populations but also the interacting impacts of disturbances, which are increasing in severity (Ward et al., 2020). The severity and extent of disturbance influences the amount and arrangement of habitat, which can influence population persistence and abundance in disturbed areas (Kavanagh, 2000; McLean et al., 2018). Understanding how changes in the amount and spatial arrangement of habitat influences populations of greater gliders at coarse- and fine scales is critical for successful conservation planning.

Given the broad-scale influence of climate on greater gliders (Wagner et al., 2020), we previously hypothesized that a reduction in climatic suitability will reduce animal abundance and density, independent of the finer-scale spatial configuration and amount of feeding habitat. Climate should limit greater glider occurrence to areas with both suitable climate and available feeding and nesting resources. This has been observed in the mature forests of East Gippsland, Victoria, where areas that contain high-quality feeding habitat today, but are no longer climatically suitable, have seen a decline in greater gliders since the 1980s (Wagner, 2021; Wagner et al., 2020). Here, we extend this approach to incorporate the spatial pattern of foraging resources. We hypothesize that both the spatial configuration of feeding habitat and disturbances will affect resource availability and therefore population density. Earlier studies have shown that greater gliders can persist in forests that retained ≥40% of their initial basal area after disturbance (Kavanagh, 2000) and are better suited than other arboreal mammals to survive in aggregated strips of managed forest landscapes due to their diet (Lindenmayer, Cunningham, & Donnelly, 1993). However, evidence shows that in other parts of the distribution, a higher retention is required. For example, for the central greater glider (proposed as *Petauroides armillatus*, McGregor et al., 2020), at least 85% of original tree basal area was needed to maintain greater glider populations (Eyre, 2006). While greater gliders can persist in areas of selective timber harvesting, population density decreases with logging intensity (McLean et al., 2018). However, the exact role of spatial aggregation of either the feeding habitat itself or the disturbance affecting it, on greater glider abundance and density, is still poorly understood. Studies from different forest types within the geographic range of the greater glider reveal that their home range can vary between one to 18 hectares, which may be a response to resource availability (Comport, Ward, & Foley, 1996; Henry, 1984; Kavanagh & Wheeler, 2004; Kehl & Borsboom, 1984; Pope et al., 2004; Smith et al., 2007). We expect that dispersed habitat or disturbances that create more dispersed feeding resources will lead to more drastic increases in home range sizes and reduce available or accessible feeding habitat in individual home ranges more rapidly, therefore reducing population density more drastically.

Our aim was to assess the relationship between spatial aggregation of habitat resources, different types of disturbances and greater glider population density and persistence. We further aimed to identify greater glider population responses and thresholds of habitat suitability to aid in estimating the likelihood of population persistence under climate change and after disturbances from forest fires (Berry, Driscoll, Banks, & Lindenmayer, 2015; Chia et al., 2016; Lindenmayer et al., 2013) or timber harvesting (Kavanagh, 2000; McLean et al., 2018).

2 | METHODS

We developed a generalized modeling framework to test relationships between spatial patterns and species abundance, density, and persistence using neutral landscape models (With & King, 2001). Neutral landscapes simulate landscape patterns based on theoretical spatial distributions or properties of real landscapes (Gardner, Milne, Turner, & O'Neill, 1987; Gardner & Urban, 2006; With, 1997). To test our hypotheses, we used field observations as well as observations from published literature, to make assumptions about what makes greater glider home ranges functional and under which conditions functionality would be lost and reductions in animal abundance or density may be expected to occur. The key criteria we identified were:

1. A maximum home range size of six hectares. This is based on observations of maximum home range sizes for female greater gliders, which share home ranges less frequently and express only limited rates of home range extension with resource scarcity (Comport et al., 1996; Henry, 1984; Kavanagh & Wheeler, 2004; Kehl & Borsboom, 1984; Pope et al., 2004; Smith et al., 2007).
2. Home ranges need to include at least 2.6 ha of foraging habitat. This is based on the average observed home range size in mature undisturbed forests dominated by preferred, nitrogen-rich *Eucalyptus* species (Comport et al., 1996; Henry, 1984; Kavanagh & Wheeler, 2004; Kehl & Borsboom, 1984; Pope et al., 2004; Smith et al., 2007).
3. At least 25% of the total home range area needs to be favorable feeding habitat (where Eucalyptus foliage has ≥1% nitrogen per gram dry mass, Cork, 1992). In a previous study, greater gliders were not detected in sites that were predicted to have <25% favorable feeding habitat (Wagner, 2021).
4. As our models are based on observations made from undisturbed mature mixed-species forests with abundant nesting resources, we assumed tree hollows were not limiting site occupancy (Wagner, 2021).

All spatial and statistical analyses for this study were carried out in R 4.0.3 (R Core Development Team, 2021). Neutral landscapes were generated from random clustering according to Saura and Martínez-Millán (2000) using the package *NLMR* (Sciaini, Fritsch, Scherer, Simpkins, & Golding, 2018).

2.1 | Simulating landscape-scale effects of climate change on feeding landscapes

To test the effect of a gradual decrease in climatic suitability on a landscape containing high-quality feeding habitat, we generated neutral landscapes, based on the relative proportions and spatial aggregation of predicted favorable feeding habitat (canopy nitrogen is ≥1% N DM), unfavorable feeding habitat (<1% N DM), and non-habitat (neither feeding or nesting trees or features such as canopy gaps) from 4-ha survey plots located in high-elevation, mixed-species *Eucalyptus* forests in East Gippsland, Victoria ($n = 10$; Table S1) (Wagner, 2021). Per-class fraction was derived by dividing the area of the three classes by the total area and spatial aggregation was determined using the package *landscapemetrics* (Hesselbarth, Sciaini, With, Wiegand, & Nowosad, 2019). As climatic suitability occurs at coarser resolution than favorable feeding habitat and over large (landscape) scales (Wagner et al., 2020), we extrapolated predicted properties and aggregated the spatial resolution to simulate 1,000 ha landscapes at a 1 ha cell size from fine-scale (4 ha at ~2.5 cm^2 resolution) spatial predictions of favorable feeding habitat (Figure 1a,b).

Next, we generated nine neutral landscape climate masks, simulating climatic suitability extent between 10 and 90% of the total area over 1,000 ha (Figure 1c). As climatic suitability occurs clumped over large areas (Wagner et al., 2020), we generated these masks at maximum class aggregation, using an 8-neighborhood rule ($p = 0.58$; Saura & Martínez-Millán, 2000). Each climate mask was applied to the simulated feeding habitat landscapes using the package *raster* (Hijmans, 2019). Masking any of the three existing classes with the climate layers added a new class to the feeding landscapes, describing areas that have become climatically unsuitable and therefore non-habitat (Figure 1d). Along with the 10 initial neutral landscapes (i.e., 100% climatic suitability), these maps ($n = 100$, 10 initial neutral landscapes as control $+$ [9 masks $\times$ 10 initial landscapes]) were analyzed for changes in suitable and unsuitable habitat area caused by a simulated decrease in climatic suitability. We calculated area and aggregation metrics such as number of patches or edge density for (remaining) favorable feeding habitat. Using the selected assumed minimum home-range size for greater gliders in mature forests as minimum area of favorable feeding habitat required (2.6 ha; Smith et al., 2007), we calculated the potential number of animals per hectare based on remaining accessible favorable feeding habitat (i.e., favorable feeding habitat in climatically suitable areas) for each resultant neutral landscape.

2.2 | Simulating stand-scale clumped and dispersed feeding habitat

To test what influence spatial aggregation of feeding habitat may have on home-range structure and density at a finer (stand) scale, we generated binary neutral landscapes that contained either favorable feeding habitat or no feeding habitat (Figure S1). Home range structure refers to the individual home range sizes and ratio of favorable feeding habitat area to the total area within a home range (i.e., feed-area-ratio). Home range density (number of home ranges) was used as a proxy for animal abundance (i.e., number of animals per 100 ha). Depending on elevation, topography, and resulting forest structure and composition, feeding habitat can be either clumped or dispersed (Wagner, 2021).

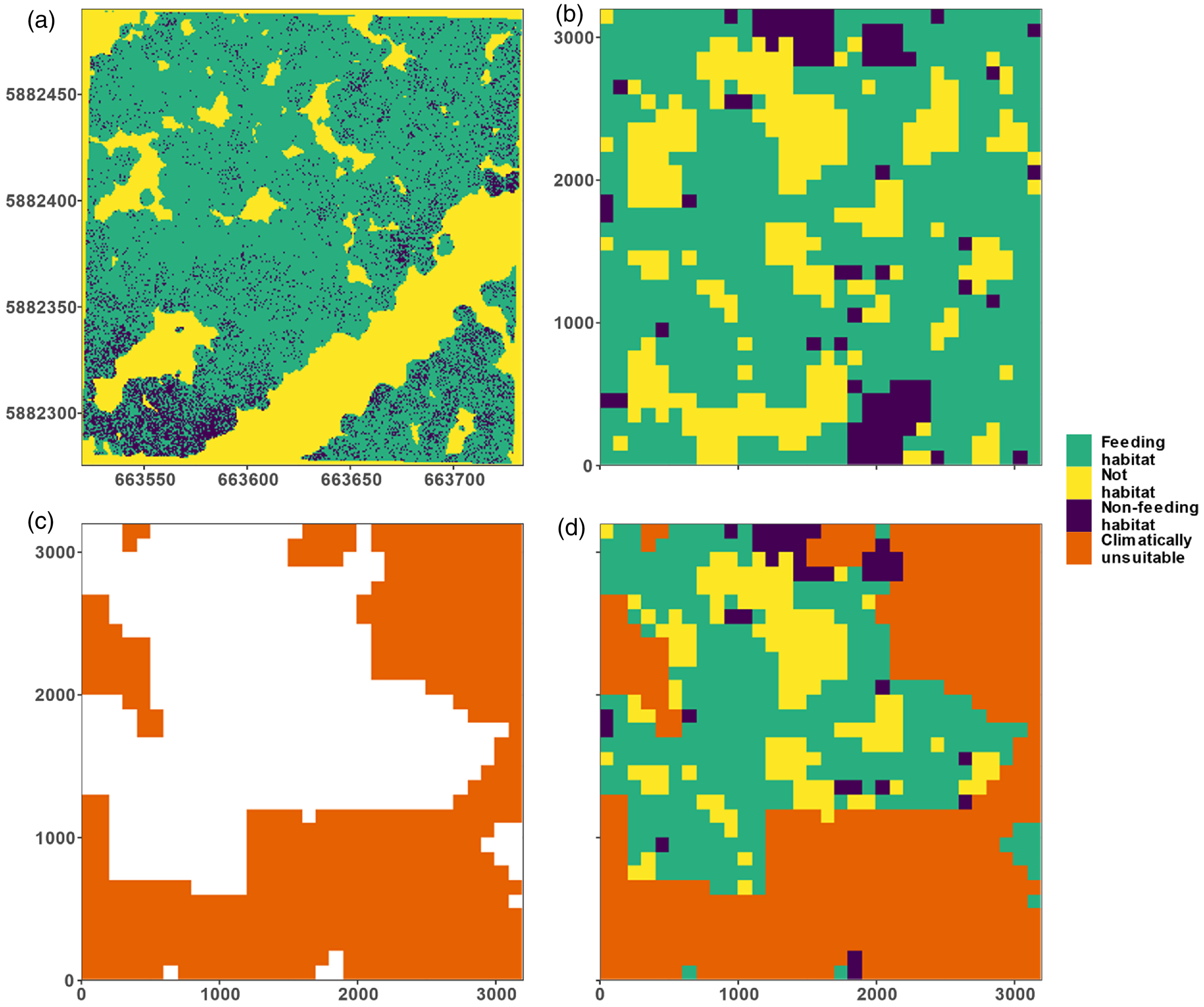


FIGURE 1 Analysis steps to simulate landscape-scale effects of climate change on feeding landscapes. (a) A 4-ha spatial prediction of favorable feeding (green), non-feeding (unfavorable feeding resources, blue) and no habitat (yellow) to an actual high-elevation mixed-species stand (Wagner, 2021) and its 1,000 ha neutral landscape equivalent (b). A climate mask (c) simulating ranges of climatic suitability (in this case 50% of the total area becomes climatically unsuitable – orange) is applied to these neutral landscapes (b), resulting in a landscape with an additional class of climatically unsuitable habitat (d), rendering the other classes inaccessible

To account for this variation, we generated nine (10–90% area of the total area is favorable feeding habitat) 100-ha random cluster landscapes at a 10 m^2 resolution both at maximum ($p = 0.58$), and minimum ($p = 0.1$; Saura & Martínez-Millán, 2000) aggregation ($n = 18$). For each landscape, we calculated the potential maximum number of home ranges (or animals) based on the total area of available favorable feeding habitat, divided by the hypothesized minimum area of favorable feeding habitat required to form a functional home range (2.6 ha). To determine the optimal spatial arrangement and size of home ranges that met this requirement within all generated neutral landscapes, we used *k*-means clustering (Hartigan & Wong, 1979) on cells of favorable feeding habitat only (Figure S2a). *K* equaled the potential maximum number of home ranges in any generated feeding landscape (Equation (1)). Cells were assigned their cluster number and a convex hull was calculated for each cluster, outlining the home range boundaries (Figure S2b),

$$k = \frac{\text{Amount of total feeding habitat in ha}}{\text{Assumed minimum home} - \text{range size (2.6 ha)}}. \tag{1}$$

For each feeding landscape we tallied the total number of home ranges and calculated the size and feed-area-ratio of all potential home ranges. Next, we removed any home ranges from further analysis that were unlikely to be functional based on size (>6 ha; see Smith et al., 2007) and/or feed-area-ratio (<25% of total home range area, Wagner, 2021). The resulting dataset was then used to compare differences in habitat potential between types of aggregation based on the data distribution and to determine critical thresholds for the formation of suitable conditions across simulated sites.

2.3 | Simulating stand-scale effects of disturbance

To test the influence of spatial aggregation and intensity of disturbances on home range, and population potential based on the feeding properties of real landscapes, we generated 100 ha neutral landscapes (10 m^2 cell size) based on aggregation and class fraction of all available study sites in East Gippsland, Victoria ($n = 30$, classes = favorable feeding, unfavorable feeding (or non-feeding) habitat, and not habitat), according to methods outlined above (Figure 2a). Next, we generated aggregated and dispersed (maximum and minimum aggregation) disturbance masks for 10–90% area affected ($n = 18$) in a similar process to generating our climate suitability masks (Figure 2b,d). These were used to change any covered area in the generated neutral landscapes to non-habitat ($n = 570$, i.e., 30 initial undisturbed landscapes as control and 540 landscapes [30 landscapes × 18 disturbance masks] resulting from disturbances at different aggregations and intensities; Figure 2c,e). As above, we used *k*-means clustering and created convex hulls of potential home ranges for each of these feeding landscapes. We filtered for functional home ranges and analyzed differences between, and effects of, clumped and dispersed disturbances at different intensities (fraction of area disturbed) on home range potential and population structure.

3 | RESULTS

3.1 | Effects of decreasing climatic suitability on feeding habitat

Simulated 1000-ha feeding landscapes ranged in total favorable feeding habitat area from 427 to 715 ha, which equated to an average potential population density of 0.2 (±0.04) animals per hectare. By gradually reducing the climatic suitability within these landscapes from 100 to 10%, we observed a near-linear decrease in potential population density and a decrease in deviation from the mean density (Figure 3). As climatic suitability decreased, landscapes converged in area and arrangement of remaining suitable habitat. When only 10% of the total area was climatically suitable, accessible favorable feeding habitat ranged from 33 to 81 ha (out of 1,000 ha), equivalent to an average density of 0.02 (±0.005) animals per ha. On average, a 10% reduction in climatically suitable area led to a 10% reduction in potential population density, independent of the initial spatial arrangement of feeding habitat across these landscapes. The reduction in accessible favorable feeding habitat was also associated

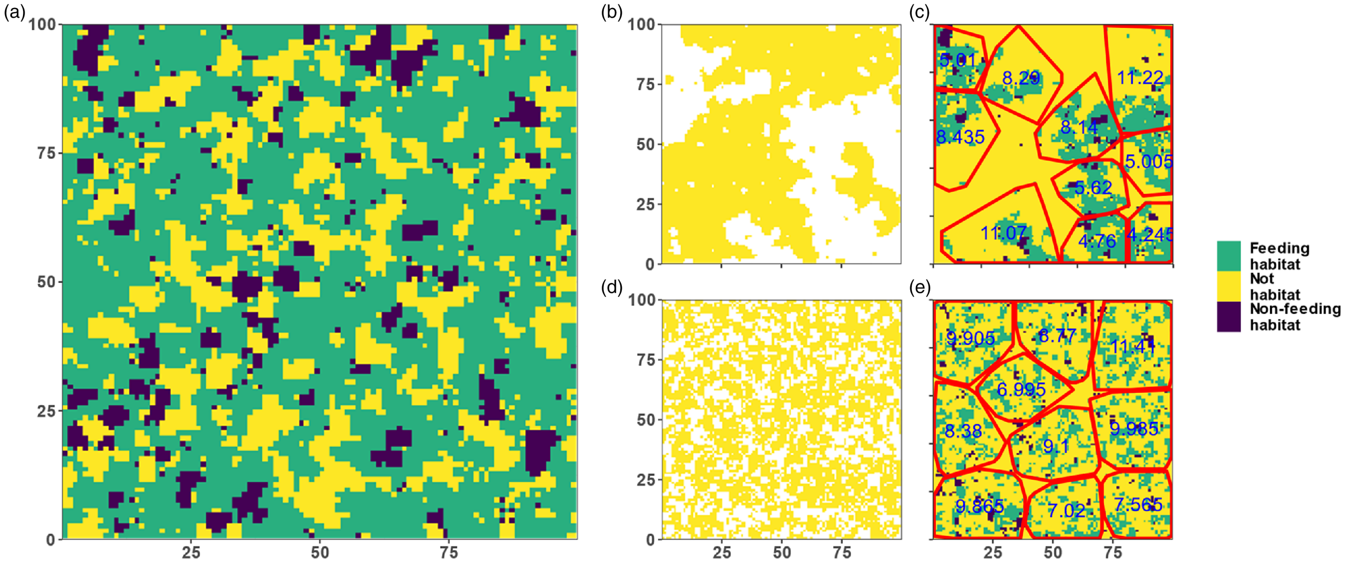
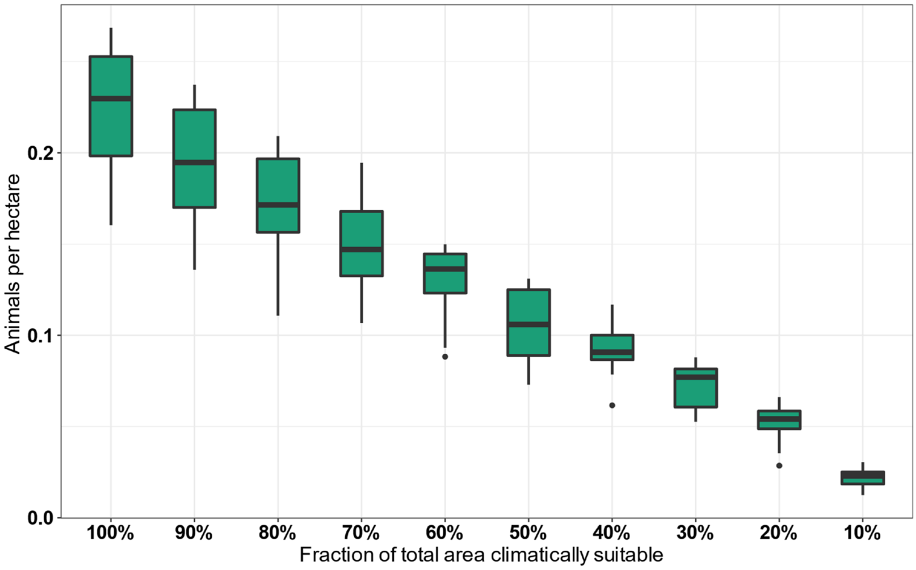


FIGURE 2 (a) 100 ha neutral landscape based on properties from spatial predictions of favorable feeding habitat (Figure 1a, Wagner, 2021) were subjected to randomly generated clumped (b) and dispersed (d) disturbances affecting 10–90% of the total area (yellow). Disturbed areas were masked to become nonhabitat (c, e, yellow) and remaining home ranges were analyzed for size, amount of favorable feeding habitat and feed-area-ratio. Any home ranges that did not match assumptions of functionality were removed from further analysis. In this case, a disturbance removing 60% of the initial basal area, led to either persistence of five functional home ranges (c) or a local extinction, where all remaining potential home ranges were too large to be functional (e)

FIGURE 3 Observed declines in animal density with reductions of climatically suitable area across all 1,000-ha neutral feeding landscapes



with a decrease in edge density and increasing patch aggregation, indicating not only that accessible favorable feeding habitat had decreased but that it also became spatially more clumped (Figure S3).

3.2 | Effects of spatial aggregation of feeding habitat on stand scale population potential

A linear decrease in population density was observed when simulating different rates of feeding habitat at the 100-ha (stand) scale. For both clumped and dispersed favorable feeding habitat, a 10% decrease led to a ~10% reduction in the number of potential home ranges across the 18 simulated landscapes. We observed ~35 home ranges at 90% and ~4 at 10% favorable feeding habitat for both aggregation types (Figure S4a). Differences between clumped and dispersed feeding habitat were found in home range (cluster) area and feed-area-ratio within the modeled home ranges ($n = 343$). Average home range area was significantly larger (CI = [0.26, 1.58], $p < .01$) and feed-area-ratio per home range significantly lower (CI = [−18.82, −7.67], $p < .001$) for dispersed than clumped feeding habitat (Figure S4b,c). With decreasing favorable feeding habitat, the coefficient of variation increased from 10 to 60% for home range area and from 12 to >95% for feed-area ratio, while remaining stable below 10% in dispersed habitat for both variables (Figure S5).

When filtering for functional home ranges (home range area ≤ 6 ha, feed-area-ratio ≥ 25%, $n = 292$), spatial distribution became more important. Landscapes with dispersed favorable feeding habitat had lower home range potential than landscapes with clumped feeding habitat, when total favorable feeding habitat was below 50%. The potential for the landscape to contain functional home ranges (i.e., where the number of home ranges dropped to zero) was lost at 30% dispersed favorable feeding habitat. Landscapes with clumped feeding resources lost all home range potential when favorable feeding habitat comprised 10% of the landscape; however, only one home range remained at 20% favorable feeding habitat (Figure 4a). A similar coefficient of variation (Figure S6) in both home range area and feed-area-ratio was observed for landscapes with clumped favorable feeding habitat after functional home range formation occurred at 30% total favorable feeding habitat (Figure 4b,c).

Here, even at a low total favorable feeding habitat area, relatively small home ranges (minimum of 3.5 ha) with large amounts of feeding resources (maximum of 98% feed-area-ratio) could exist at realistic numbers of individuals per 100 ha ($n = 7$ home ranges across 100 ha; Figure S7). In landscapes with dispersed favorable feeding habitat, functional home range formation first occurred at 40% total favorable feeding habitat. When feeding habitat was dispersed, similar home range areas and feed-area-ratios attained at 30% clumped favorable feeding habitat were not reached unless ≥70% of area (70 out of 100 ha) was favorable feeding habitat (Figure 5).

3.3 | Effects of intensity and spatial aggregation of disturbance on feeding habitat and population persistence

For a hypothesized minimum required favorable feeding habitat area of 2.6 ha per home range, our analyses resulted in a total of 5,885 modeled home ranges across

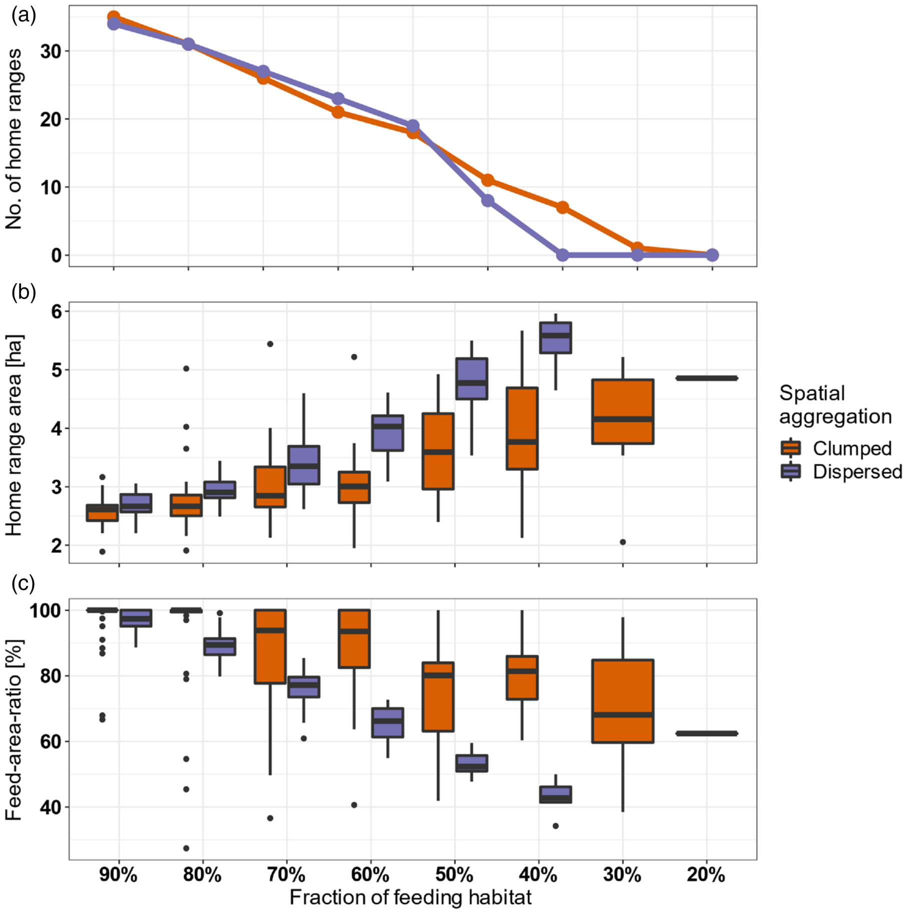


FIGURE 4 Reduction in number of home ranges (a), increases in home range area (b) and changes in feed-area ratio (c) for functional home ranges with decreases in favorable feeding habitat area in 100 ha neutral landscape simulations of clumped (orange) or dispersed (purple) feeding resources

simulated sites and disturbance types (clumped or dispersed disturbances at different intensities). We observed a similar linear trend of decreasing number of home ranges with remaining undisturbed area and only slight differences between clumped or dispersed disturbance (Figure S8a). Differences were observed in home range area and feed-area-ratio resulting from different disturbance types, where dispersed disturbances lead to larger home ranges containing less favorable feeding habitat at lower intensity. For feed-area-ratio, the coefficient of variation, and therefore range of potential favorable feeding habitat within a home range, was larger when the disturbance was aggregated. However, with increasing extent of disturbance, many modeled home ranges became either too large or too scarce in favorable feeding habitat (or both) to be functional according to the assumptions on functionality that we specified. Modeled home ranges approached hypothesized loss of functionality earlier at landscapes based on properties of low elevation sites and when landscapes were affected by dispersed disturbances (Figure S8b,c).

When considering only functional home ranges ($n = 3{,}414$), the potential of a 100-ha feeding landscape to support a population size of >1 home range was lost sooner for landscapes affected by dispersed disturbances (<40% in landscapes based on mid- and <50% area undisturbed in landscapes based on high elevation properties). Landscapes generated using low-elevation site properties lost their potential to support home ranges at <80% remaining undisturbed area (Figure 6). A large variation in both home range area and feed-area-ratio for landscapes affected by clumped disturbance allowed for home ranges to form at higher disturbance intensity (80% disturbed at mid-elevation and 70% at high elevation). Even when affected by severe clumped disturbance, some landscapes retained the potential for small home ranges, largely covered by favorable feeding habitat. For example, at 30% remaining undisturbed area, the smallest home range was 2.6 ha and the largest feed-area-ratio was 94% (Figure S9).

Size, feed-area-ratio, and number of home ranges were dependent on the initial spatial aggregation of the feeding landscape and the intensity and aggregation of the disturbance mask. Landscapes affected by dispersed disturbances exhibited less variation in home range size and feed-area ratio. Increasingly severe dispersed disturbances caused home range numbers to drop more rapidly, and individual remaining home ranges to become larger and contain less favorable feeding habitat. Therefore, an exhaustion of habitat potential was reached at

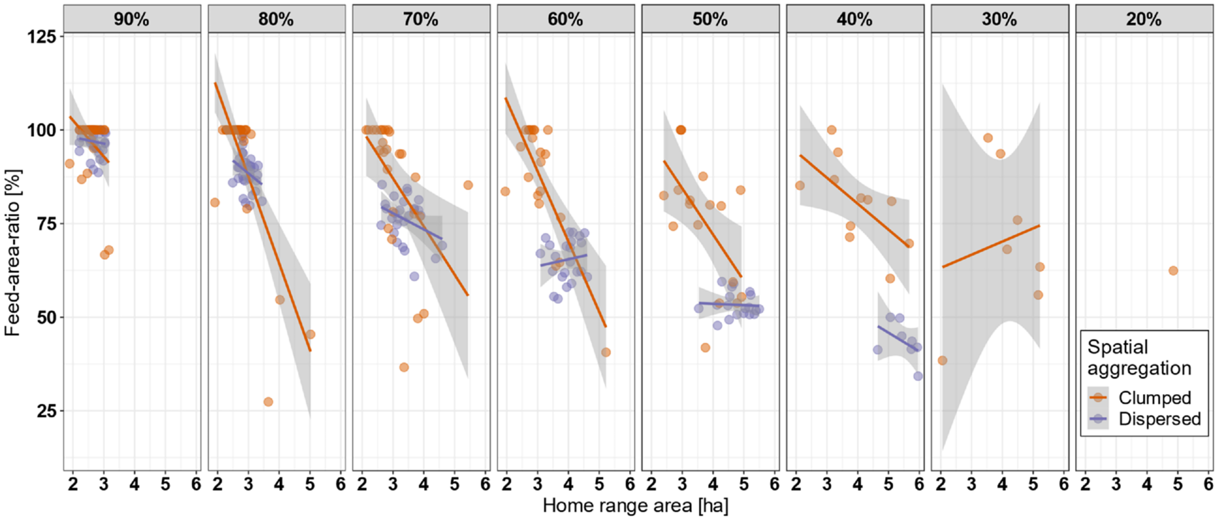


FIGURE 5 The relationship between home range area and feed area ratio of simulated home ranges for clumped (orange) or dispersed (purple) feeding resources at different rates of total favorable feeding habitat (90–20%)

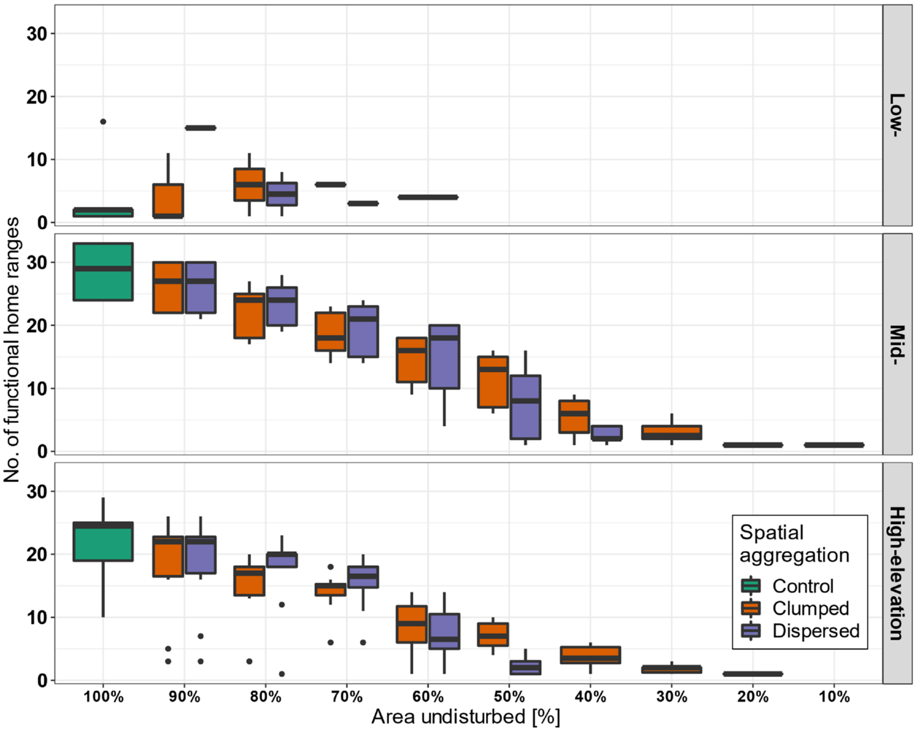


FIGURE 6 Observed declines in number of functional home ranges in neutral landscapes based on the spatial configuration and properties of survey sites in East Gippsland, Victoria (faceted by elevation band; see Wagner, 2021) with increasing disturbance intensity (remaining undisturbed area, *x*-axis)

lower fractions of disturbed area. We observed a linear relationship between feed-area-ratio and home range area as an effect of dispersed disturbance. The relationship was nonlinear for high intensity clumped disturbances. Across all simulated landscapes, ranges of feed-area-ratio and home range size were comparable only up to 80% undisturbed area, after which effects on home ranges from both types of disturbance started diverging (Figure 7). With increasing intensity of disturbance, the range and standard deviation (*SD*) for both home range area and feed-area-ratio remained stable in landscapes affected by clumped disturbance and decreased with dispersed disturbance (Table 1).

4 | DISCUSSION

While regional and global drivers of habitat loss, such as climate- and land-use change are altering ecosystems and threatening species at an increasing rate (Butchart

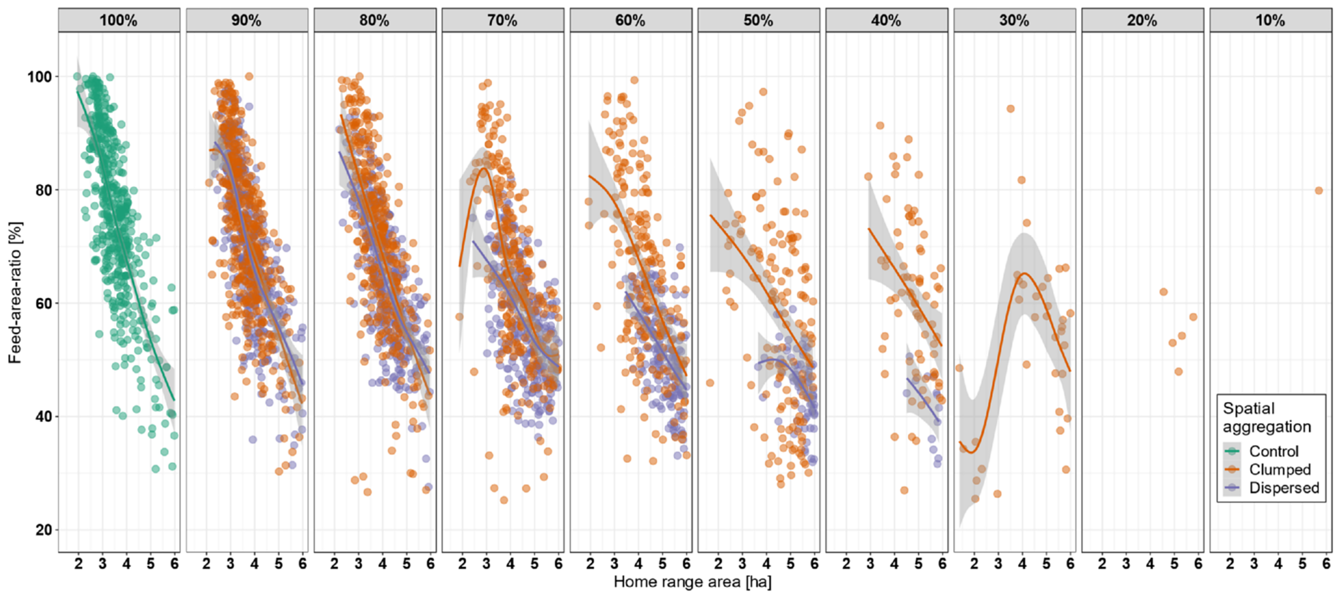


FIGURE 7 The relationship between home range area and feed area ratio of simulated home ranges for undisturbed areas (green) and under clumped (orange) or dispersed (purple) disturbances. Facets illustrate the conditions under different disturbance intensities (100–10% area undisturbed)

et al., 2010; Lindenmayer, Cunningham, & Young, 2012; Rosenzweig et al., 2008), the importance of drivers at finer spatial scales is often overlooked (Villard & Metzger, 2014). While large scale drivers may cause complete losses of habitat suitability (Adams-Hosking, Grantham, Rhodes, McAlpine, & Moss, 2011; Kearney et al., 2010; Wagner et al., 2020), the spatial configuration of habitat may mitigate some of the effects of habitat loss from disturbances that occur at finer scales (Villard & Metzger, 2014). Using a generalized simulation framework to develop neutral landscapes, we observed both coarse- and fine-scale effects on the suitability of southern greater glider habitat.

4.1 | Climate

In our simulations unfavorable climatic conditions overwhelmed the impacts of feeding resource availability. These findings further reinforce recent conclusions that coarse determinants of habitat suitability have a strong effect on greater glider population persistence at a landscape scale (Kearney et al., 2010; Wagner et al., 2020). The average linear decrease in potential greater glider population density from decreasing climatic suitability was unrelated to the initial amount and spatial arrangement of the high-quality feeding landscapes we used to test these effects. The observed population decline related to climate and independent of habitat availability has been observed on worldwide biodiversity (Mantyka-Pringle, Martin, & Rhodes, 2012) and was for example reported for greater gliders (Smith & Smith, 2020; Wagner et al., 2020), butterflies (Parmesan et al., 1999), mountain pygmy possums (*Burramys parvus*; Hoffmann et al., 2019), koalas (*Phascolarctos cinereus*; Adams-Hosking et al., 2011), or moose (*Alces alces*; McCann, Moen, & Harris, 2013). Continuous unsuitable climatic conditions in the form of high ambient temperatures and low water availability will negatively affect the greater glider's ability to forage, reproduce, and persist in the landscape (Foley, Kehl, Nagy, Kaplan, & Borsboom, 1990; Kavanagh & Lambert, 1990; Rübsamen et al., 1984; Youngentob, Lindenmayer, Marsh, Krockenberger, & Foley, 2021).

Our finding also aligns with recent observations of local extirpations of greater glider populations from otherwise suitable landscapes at mid-elevation forests in East Gippsland, Victoria (Wagner et al., 2020) and in areas in New South Wales such as Booderee National Park (Lindenmayer et al., 2011) and low-elevation forests of the Blue Mountains (Smith & Smith, 2020). These results highlight that greater gliders are vulnerable to climate-driven habitat loss, even in areas with ample feeding and nesting resources. As such, climate change should be considered a key threatening process when assessing, managing, and conserving the species. Any area that is conserved or retained for greater glider populations but is unsuitable due to unfavorable climatic conditions will likely not contribute to population persistence. As the climatic conditions in the real landscapes that our simulations were based on (high elevation mixed species forests

TABLE 1 Observed changes in home range area and feed-area-ratio of simulated home ranges under different rates and spatial aggregations of disturbance

Spatial aggregation	Home range area range (ha)	*SD* home range area	Feed-area-ratio range (%)	*SD* feed-area-ratio
100%				
Control	4.04	0.75	69.26	14.75
90%				
Clumped	3.86	0.74	69.69	14.24
Dispersed	3.66	0.75	66.31	13.22
80%				
Clumped	3.69	0.78	73.33	15.25
Dispersed	3.76	0.74	65.57	11.58
70%				
Clumped	4.12	0.84	73.62	14.98
Dispersed	3.58	0.76	45.49	9.67
60%				
Clumped	4.08	0.88	67.21	15.39
Dispersed	2.54	0.62	36.72	7.84
50%				
Clumped	4.28	0.97	69.24	16.89
Dispersed	2.35	0.54	26.99	5.95
40%				
Clumped	3.06	0.71	64.35	13.91
Dispersed	1.34	0.47	18.96	6.16
30%				
Clumped	4.62	1.40	68.81	15.86
20%				
Clumped	1.24	0.46	14.06	5.24
10%				
Clumped	0		0	

of East Gippsland, Victoria, Australia) are climatically suitable (and may be for the foreseeable future), their protection remains crucial for southern greater glider conservation (Wagner et al., 2020).

4.2 | Spatial aggregation of feeding habitat

While climate change is the dominant driver of habitat suitability within these landscapes, in areas where the climatic conditions are suitable, other factors may limit habitat suitability. The aggregation and amount of foliar feeding resources can vary throughout mature forest landscapes (Table S1) (Moore et al., 2010). Based on our simulations, these conditions may lead to different abundances and densities in greater glider populations at the stand scale. The spatial aggregation of favorable feeding habitat drove the configuration of potential functional home ranges in our simulations (i.e., amount of home ranges and size and feeding resources per home range). Simulated stands with dispersed favorable feeding resources exhibited more stable and predictable patterns of home range density. But these conditions also led to an earlier loss of home range potential. When forage resources were scarcer, home range areas needed to increase to cover the required 2.6 ha of favorable feeding habitat, while feed-area-ratios within simulated home ranges decreased. This resulted in a loss of functionality and reduction in number of home ranges at higher rates of total feeding area per stand. In actual forest stands populated by greater gliders that had trees selectively removed, population densities decreased dependent on the amount of harvesting (McLean et al., 2018). Based on our findings, this decrease in population density may therefore be explained by the reduction and increased dispersal of feeding resources that lead to larger individual home ranges. Greater gliders are known to extend home-range sizes when habitat resources are scarce or fragmented (Smith et al., 2007; Youngentob et al., 2013). Clumped favorable feeding habitat allowed for more stable populations at lower rates of total feeding area, but this was dependent on spatial arrangement of favorable feeding habitat (Figure 5). Even at low rates of total available favorable feeding habitat, a population of greater gliders could theoretically reach higher densities when feeding resources were clumped. Similar effects on home range sizes and population density have been observed in capybaras (*Hydrochoerus hydrochaeris*; Corriale, Muschetto, & Herrera, 2013), river otters (*Lutra canadensis*; Blundell, Bowyer, Ben-David, Dean, & Jewett, 2000), and Tengmalm's owls (*Aegolius funereus*; Santangeli, Hakkarainen, Laaksonen, & Korpimäki, 2012).

If the initial amount and aggregation of favorable feeding habitat drives greater glider population structure at the stand scale in mature forests, conservation and management should take these factors into account when carrying out wildlife surveys, establishing reserves, or altering forest structure. Based on our simulations, only when a forest habitat is composed of ≥70% favorable feeding habitat, are potential population and home range structures comparable between forests with clumped and dispersed resources (Figure 5). These conditions however, are rare in real landscapes (see Table S1). Below this amount, anticipated conservation targets may only be met by increasing reserve areas or higher rates of habitat retention during timber harvesting. Similarly, the response of these different habitat configurations to disturbance will vary.

4.3 | Disturbance

The primary disturbances impacting forest-dependent wildlife in southeast Australia at a scale relevant to populations are forest fires and timber harvesting operations (Lindenmayer et al., 2013; Nitschke et al., 2020). Both have been identified as major threats to arboreal species such as southern greater gliders, as they alter the structure of the forest by removing foraging and nesting resources (Franklin et al., 2000; Lindenmayer & Sato, 2018; McLean et al., 2018). Greater glider populations have the ability to persist in forests that have experienced basal area losses of up to 60% (Kavanagh, 2000), an effect that we observed in our simulations of different disturbance intensities as well (Figure 6). The ability of populations to persist, however, was strongly dependent on the initial spatial configuration of the stand and the spatial aggregation of the disturbance itself. When disturbances were spatially clumped, greater glider habitat features persisted at higher densities, even when only small areas remained undisturbed (Figure 7). The level of spatial aggregation was the difference between a local population persisting or going locally extinct when subjected to disturbances of identical intensity (e.g., removing 60% of initial basal area, Figure 2). Some habitat configurations were therefore able to mitigate negative effects of habitat loss (see Villard & Metzger, 2014). Disturbances leading to dispersal of resources, for example resulting from certain silvicultural techniques such as single-tree retention (Ashton & Kelty, 2018), may lead to more severe stand-scale losses of feeding resources and reduce the ability of greater gliders to form or retain functional home ranges. In fact, different forms of tree retention following timber harvesting may lead to distinctly different configurations of habitat and could have the potential to influence population persistence (DELWP, 2019; Lindenmayer, 1994). Persistence of greater glider populations though, may also depend on forest productivity (e.g., retention needed to be 85% in lower productivity forests of southern Queensland; see Eyre, 2006), so our findings need to be investigated for different parts of the geographic range of all proposed *Petauroides* species.

The ability to determine where critical favorable feeding resources are, and what their spatial configuration is, may allow retaining them fully under certain retention strategies. High-resolution data from multispectral remote sensing that allows assessing and mapping favorable feeding resources at operational scales may therefore be an important tool in arboreal folivore conservation (Wagner, 2021; Wu, Levin, Seabrook, Moore, & McAlpine, 2019; Youngentob et al., 2012; Youngentob, Yoon, Stein, Lindenmayer, & Held, 2015). Our findings suggest that current (voluntary) prescriptions that retain a minimum of 40% basal area (DELWP and ARI staff, personal communication, April and May 2021; DELWP, 2019) or single-tree retention (Ashton & Kelty, 2018; DEPI, 2014) may not suffice for permanent greater glider persistence at a stand scale, if forage trees are poorly spatially distributed (Figures 6 and 7). Similarly, determining habitat resources remotely after high intensity disturbances such as wildfires (Catling, Coops, & Burt, 2001; Haslem et al., 2011; Ward et al., 2020) may allow mapping functional fire refugia (Berry et al., 2015), which may still act as greater glider habitat, or estimate remaining suitable habitat. With this knowledge, managers can protect and support surviving populations by guiding silviculture or designing reserves at finer scales.

4.4 | Limitations and future research

In this study we used neutral landscape simulations as models of landscape structure to test theoretical effects of changing foraging resources on populations of southern greater gliders. We were able to quantify potential population responses to changes in climate or the quantity and configuration of forage habitat and identify critical thresholds for persistence. These are two of the major contributions neutral landscape models may provide in ecological research (With & King, 1997). Our simulated landscapes were based on, and extrapolated from, real and modeled landscape features. In the absence of data, hypothesized effects were tested using generalized assumptions on greater glider population structure such as maximum home range sizes (Pope et al., 2004; Smith et al., 2007) and minimum amount of favorable feeding habitat per home range (Wagner, 2021). However, in the studies used to determine an average home-range size for the purpose of our analysis, sample sizes and duration of tracking, as well as the statistics and models used to estimate home ranges of greater gliders vary notably. For example, methods and models used to determine home-range size were Minimum Convex Polygons (see Comport et al., 1996; Kavanagh & Wheeler, 2004; Kehl & Borsboom, 1984; Smith et al., 2007), Kernel estimates (adaptive, fixed or isopleth values; see Comport et al., 1996; Kavanagh & Wheeler, 2004; Pope et al., 2004; Smith et al., 2007), and harmonic estimates (see Comport et al., 1996). These factors influence the derivation of home range estimates, which makes comparisons between methods problematic (Börger et al., 2006; Lawson & Rodgers, 1997). Our results regarding species persistence and animal density matched field observations (Kavanagh, 2000; McLean et al., 2015), which suggests our assumptions were robust and logical. It is important though to test this theoretical knowledge with field experiments that control for the assumptions made when using simulated neutral landscapes (With, 1997; With & King, 1997). This will provide a means to validate the critical persistence thresholds that our neutral models suggest. Radio- or GPS-tracking studies could help identify differences in minimum and maximum home range sizes (Girard, Ouellet, Courtois, Dussault, & Breton, 2002; Harris et al., 1990) in different parts of the landscape with different configurations of habitat after recent disturbance events such as the 2019/20 Black Summer wildfires (Ward et al., 2020). Coupling this data with spatial predictions of feeding (Wagner, 2021; Wu et al., 2019; Youngentob et al., 2012) and nesting resources (Owers, Kavanagh, & Bruce, 2015) will provide a better understanding of the greater glider's perception of its habitat (Moore et al., 2010) and its ability to persist in different parts of the landscape before and after disturbances.

5 | CONCLUSION

Using a generalized spatial simulation framework based on neutral landscape models, we demonstrated that the spatial configuration of favorable feeding resources and disturbances affect population density and persistence of southern greater gliders in mature *Eucalyptus* forests. Unfavorable climatic conditions acting at larger spatial scales, unrelated to the spatial arrangement of feeding habitat, may create constraints to accessing favorable feeding and nesting resources. At the stand scale greater glider density depended on the spatial arrangement of feeding resources, with clumped favorable feeding habitat allowing earlier population formation and larger populations. Similar population structures in dispersed or clumped habitat were observed only when 70% or more of an observed area was favorable feeding habitat. Disturbances to feeding resources could either retain a population or lead to extinction, depending on spatial aggregation and intensity. Compared to clumped disturbance events, increasingly severe dispersed disturbances caused potential home ranges to disappear more rapidly, and remaining home ranges to become larger and contain less favorable feeding habitat. Our results have important implications for the conservation and retention of critical feeding habitat of southern greater gliders and provide insights into important factors to ensure that greater gliders persist in these landscapes.

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CONFLICT OF INTEREST

The authors declare no potential conflict of interest.

AUTHOR CONTRIBUTIONS

All authors conceived of the study. Benjamin Wagner designed the study and spatial methodology with contributions from Craig R. Nitschke. Benjamin Wagner carried out simulations, processed and analyzed data and drafted the manuscript with contributions from Craig R. Nitschke and Patrick J. Baker.

DATA AVAILABILITY STATEMENT

Presence and absence data for Petauroides volans used in this study and all other animal observations recorded during surveys in the landscapes our neutral models were based on are available on the Victorian Biodiversity Atlas (https://vba.dse.vic.gov.au/vba/). Supporting code, functions, datasets, and spatial data are available at https://github.com/BennyWag/gliderNL

ORCID

Benjamin Wagner https://orcid.org/0000-0002-6955-9203
Patrick J. Baker https://orcid.org/0000-0002-6560-7124
Craig R. Nitschke https://orcid.org/0000-0003-2514-9744

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