



Evaluating modelled wildlife corridors for the movement of multiple arboreal species in a fragmented landscape

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Abstract

Context In highly fragmented landscapes, arboreal mammals are limited by their ability to move and disperse between core habitats. Connectivity modelling for multiple species allows scientists to identify the most efficient movement and/or dispersal pathway(s) to prioritise for conservation efforts.

Objectives In this study, we evaluated the most cost-effective corridor pathway for eight species of arboreal mammals, with particular emphasis on an endangered population of greater gliders (*Petauroides volans*).

Methods We use species distribution modelling and circuit theory to calculate connectivity in the landscape for each species. An all-species corridor was then modelled using a least cost path analysis. The final corridor was evaluated for all species through ground-truthing accessible segments.

Results We identified that some segments of the corridor had low suitability for highly specialised species, and those with tree hollow requirements for denning. The all-species corridor also utilised an artificial crossing structure over a highway, and monitoring of this rope bridge found only two species (sugar gliders; *Petaurus breviceps* and ringtail possums; *Pseudocheirus peregrinus*) used the structure on occasion. Thus, the modelled corridor pathway was not suitable for all species, rather it was found to be more suitable for generalist species such as sugar gliders, ringtail possums, brown antechinus; *Antechinus stuartii* and brushtail possums; *Trichosurus vulpecula*.

Conclusions Our study exemplifies the importance of ground-truthing in connectivity conservation studies to ensure conservation outcomes are realised. Furthermore, we provide detailed recommendations for relevant conservation managers, to improve the usage of these existing habitat corridors by arboreal species.

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Introduction

Habitat loss and fragmentation are the most important threatening processes for mammalian species in the Anthropocene (Powers and Jetz 2019). Globally, 27% of mammal species are threatened with extinction

because of habitat loss and decline in habitat quality (Schipper et al. 2008). Habitat fragmentation is the reduction in continuous habitat into smaller, disjunct patches within a dissimilar matrix (Haddad et al. 2015; Wilson et al. 2016). Remnant fragments are often too small and isolated to maintain viable populations of some species, and through environmental, demographic and genetic changes, a vortex of extinction can form (Gilpin and Soule 1986).

The effects of habitat fragmentation are particularly pronounced for arboreal species; particularly obligate canopy dependent species such as greater gliders. Obligate arboreal mammals have limited dispersal potential in a cleared matrix and are therefore most sensitive to habitat fragmentation (Keinath et al. 2017). Some of the consequence of reduced or limited population connectivity for arboreal mammals includes lowered effective population size and potential for genetic drift (Lancaster et al. 2011; Malekian et al. 2015). Morphological changes have been observed, such as reductions in body size due to the limited amount of habitat and resources available (Fietz and Weis-Dootz 2012). Ecologically, the abundance and distribution of an arboreal species can be reduced within a fragmented landscape as it is unable to facilitate movement and connectivity when the matrix contains no trees (Koprowski 2005; Isaac et al. 2014).

Wildlife corridor implementation is considered an important strategy to reconnect habitat patches in a fragmented landscape (Beier and Noss 1998; Mackey et al. 2010; Hilty et al. 2012). For arboreal species, there are examples where corridors are vital for their conservation acting to reconnect once isolated populations (Wilson et al. 2007; Soanes et al. 2017b; Jackson et al. 2020). There are nine published landscape corridors that have either been evaluated for use by arboreal species, or specifically created for arboreal species (Laurance and Laurance 1999; Williams-Guillén et al. 2006; Lees and Peres 2008; Haslem et al. 2012; Anitha et al. 2013; Taylor and Goldingay 2013; Taylor and Rohweder 2013; Teixeira et al. 2013; Soanes et al. 2017b). At smaller scales, artificial corridors have been installed, such as underpasses and overpasses for arboreal species (Taylor and Goldingay 2009; Weston et al. 2011; Goldingay et al. 2013, 2018; Teixeira et al. 2013; Yokochi and Bencini 2015; Chan et al. 2020; Garcia et al. 2022). Given the significance of connectivity for arboreal

species in fragmented systems disturbed by agriculture and urban development, further investigation into identifying and evaluating the usage of different types of corridors is needed.

Maintaining and restoring landscape connectivity is one conservation strategy to mitigate the impacts of agricultural practices and urbanisation (Crooks and Sanjayan 2006). Using wildlife occurrence data, metrics of landscape connectivity can be derived from spatial models, and these modelling approaches provide a quantitative basis to identify potential corridors in fragmented landscapes (Pe'er et al. 2011; Pliscoff et al. 2020). Spatially explicit models such as species distribution models (Elith et al. 2011), least-cost path mapping (Sawyer et al. 2011a), models based on electric circuit theory (McRae et al. 2008), and various toolkits for GIS (Correa Ayram et al. 2016), are increasingly applied in designing regional scale corridors for various taxa and ecosystems (Braaker et al. 2014; Naidoo et al. 2018; Pliscoff et al. 2020). Readily available data such as topographic data (elevation, aspect, slope), soil and vegetation type, can be used to model habitat suitability and a matrix of habitat suitability for multiple species can then be combined to predict a corridor pathway that benefits multiple species (Elith et al. 2011; Brodie et al. 2015; Petsas et al. 2020; Pliscoff et al. 2020; Miranda et al. 2021).

Despite the prolific use of numerical modelling to identify corridor connectivity networks at regional scales, these corridor network models are rarely validated for their actual use by the target species (Kilbane et al. 2019). Landscape connectivity requires ground-truthing because of the limitations associated with ecological modelling. Some limitations include accounting for threatening processes and the presence of key resources that cannot be provided in continuous spatial layers. This is particularly relevant for species with obligate habitat requirements, such as tree hollow availability. Thus, on-ground assessments of habitat suitability of modelled corridors are essential for conservation managers, so as to effectively manage and prioritise their management actions.

In this study, a fragmented landscape impacted by agriculture and urbanisation, we used a multiple-species methodological framework (Pliscoff et al. 2020) to identify the most cost effective corridor pathway for targeted conservation activities. This study used species distribution modelling, electric circuit-based modelling, and a consensus of suitability, to quantify

the functional connectivity of eight semi-arboreal and arboreal species. The central focus of the corridor was to connect an endangered species and isolated population of greater gliders (*Petauroides volans*) with contiguous landscape across nine kilometres of fragmented habitat. Evaluation of the modelled corridor was performed via ground-truthing the habitat suitability for all eight species and monitoring artificial crossing structures over and underneath the highway. This assessment of the corridor meant that data driven recommendations could be made for strategic conservation management purposes.

Materials and methods

Study site

Our study area focused on the fragmented agricultural landscape surrounding the township of Berry, in New South Wales (NSW), located 111 km south of Sydney, Australia (Fig. 1). This area is the location of a Great Eastern Ranges (GER) wildlife corridor project called the ‘Berry Bush Links’ (GER 2021). The Berry wildlife corridor aims to create additional habitat and connect the fragmented Seven Mile Beach National Park (SMBNP) with contiguous habitat 9 km to the west of the park (known as the ‘Illawarra Escarpment’). The area is characterised by mostly cattle and dairy farming, and low density rural residential properties. A major highway (up to 80 m wide) runs between the Illawarra Escarpment and Seven Mile Beach National Park (Fig. 1). The species identified as a priority for the corridor’s creation is the endangered greater glider. The population of greater gliders at Seven Mile Beach National Park (Fig. 1) was listed as an endangered population, primarily due to its isolation from other populations found locally and regionally (NSW Scientific Committee 2016). The geographical boundaries used in this study was the natural barrier of the Shoalhaven River (see southern end of map in Fig. 1), and the furthest northern end of Seven Mile Beach National Park (Fig. 1).

Connectivity model parameters

Our study used five key steps in producing an all-species corridor for the study landscape (Fig. 2). Using

occurrence and environmental data, species distributions were first created. The probability of a species presence was then used to calculate a resistance surface, used in modelling connectivity models. A consensus map for connectivity for all species was then analysed using a least cost path to produce a final all species corridor (Fig. 2).

Species data

This study focused on a group of eight native, arboreal marsupials (Table 1). The species ranged from those heavily reliant on trees and canopy for movement (gliding species) to more generalist species such as brown antechinus, ringtail possums, brushtail possums and southern bobucks (Table 1). Presence data was obtained using three different methods.

Firstly, empirical data was collected and primarily targeted small mammals (Gracanin et al. 2022). This involved live trapping and camera trapping at 164 sites, between August to November 2019, for a total of 4592 camera trap nights and 1148 live trap-nights (Gracanin et al. 2022). Further data was utilised from a long-term camera trap study in the landscape as well, that spanned over one year (November 2019–November 2020) and added up to 6517 camera trap nights (Gracanin and Mikac 2022a, b).

Secondly, spotlighting surveys were conducted for ringtail possums, brushtail possums, southern bobucks, greater gliders, feathertail gliders and eastern pygmy possums (Davey 1990; Wintle et al. 2006; Vinson et al. 2020a). This involved walking 100–500 m transects, depending on site size and private property limitations, with an AceBeam H30 4000 lm head torch. Spotlighting surveys were conducted by one observer (A.G.), walking at a speed of 5 min per 100 m, scanning for eyeshine in the canopy, mid-storey, and understorey. A pair of 8 × 40 pair of binoculars (Avalon 10 × 42 PRO HD) were used to aid in identifying species. The GPS coordinates of the animal were recorded by standing beneath where the animal was first sighted. All spotlighting surveys commenced one hour after last light. As feathertail gliders and eastern pygmy possums are often difficult to detect in dense forests such as rainforests, water stations were placed in trees (n = 8) for over a year to aid in detecting their presence (Mella et al. 2019). Water was used as “bait” for these species as they are rarely attracted



◀**Fig. 1** The study landscape near the township of Berry, NSW. The blue outline is the focus area of the Berry Bush Links project for the Berry wildlife corridor (GER 2021)

to traditional small mammal baits of peanut butter, honey and oats (Huang et al. 1987; Tasker and Dickman 2001). The third method used for obtaining species occurrence data was through downloading records from the online database BioNet (NSW Government 2022). BioNet are validated records of species from qualified observers and uploaded to a central database as per NSW Scientific Licensing requirements. Data was downloaded from this database for all eight species, from 1980 to 2021.

Species distribution models

We used a multivariate approach, maximum entropy (Maxent), to correlate species presence and environmental variables to predict the distribution of species across the landscape (Elith et al. 2011). The distribution of all eight species were modelled with maximum entropy algorithm (Maxent) with the R package: ‘maxnet’ (Phillips et al. 2017). A ‘block’ partition scheme ($k=4$) was selected for all analyses. The regularisation multiplier was set to between 1 and 5 (with steps of 0.5), and all feature classes (L, LQ, H, LQH, LQHP; L=linear, Q=Quadratic, H=hinge, and P=product) were selected. In total, 45 different models were built, run, and tested for each species. The model selection was based on the lowest delta corrected Akaike information criterion (AICc) (Supplementary 1). Occurrences were partitioned for training (70% of the total) and testing (30%) and pseudoabsences (10,000 background points) were randomly distributed across the study area. Five environmental variables were used in the modelling: elevation, slope, aspect (DCS Spatial Services 2022), soil (DPIE NSW 2020) and vegetation type (DPIE NSW 2013). Vegetation type was manually updated by comparing it to recent satellite imagery, and relevant habitat was added (with vegetation type validated in the field) or removed (where development had occurred). The spatial layer for vegetation type also included categories for agricultural land and urban land. All environmental layers were at a spatial resolution of 25 m.

Connectivity models

We employed circuit theory to identify potential corridors linking core areas within the landscape, using the software Circuitscape 4.0.5 (McRae and Shah 2009). Circuit theory links populations through multiple pathways, with connectivity potential increasing according to the density of pathways (McRae et al. 2008). The models produced from Maxent were converted by inverting the values of habitat suitability so that each pixel represented a resistant value ranging from 0 to 1 (higher values indicating more resistance). Using expert opinion, literature reviews, and field data (Zeller et al. 2012), the resistant values for rope bridges, underpasses, highways, and rivers, were manually changed to better reflect their impact as barriers (Supplementary 2). Values for highways and rivers wider than 25 m, were manually changed to better represent the barrier they pose for each species. For each species, the wildlife underpasses and rope bridges along the highway were assigned a resistant value that was calculated using the average resistance values from urban areas. This was because urban areas represent the closest surface type in similarity (e.g. concrete surfaces, wooden poles, street lights), and thus reflect a more appropriate value than using a value based on expert opinion alone (Zeller et al. 2012). Core habitat (nodes) were selected based on fragment size ($>50\text{Ha}$) and the conservation status of the habitat. We selected core habitat that was either a large patch within the landscape, or sections representing a larger continuous landscape. Seven nodes were selected, and each were protected by government (NSW National Parks and Wildlife Service estate or local council reserves) or were private properties with conservation agreements. These nodes also represented the goal of the Berry Wildlife Corridor to connect the larger continuous landscape of the Illawarra Escarpment and surrounds, with the isolated Seven Mile Beach National Park. A graph-based connectivity metric, the Index of Integral Connectivity (IIC), was calculated for each model using Conefor Sensinode 2.6 (Saura and Torné 2009) to compare connectivity between species.

All species corridor

A consensus current map was created by averaging the eight normalised current maps for each species

Fig. 2 Key methodological steps used in the study to estimate the movement corridors for each of the eight species. Methodological framework was adapted from (Plissock et al. 2020)

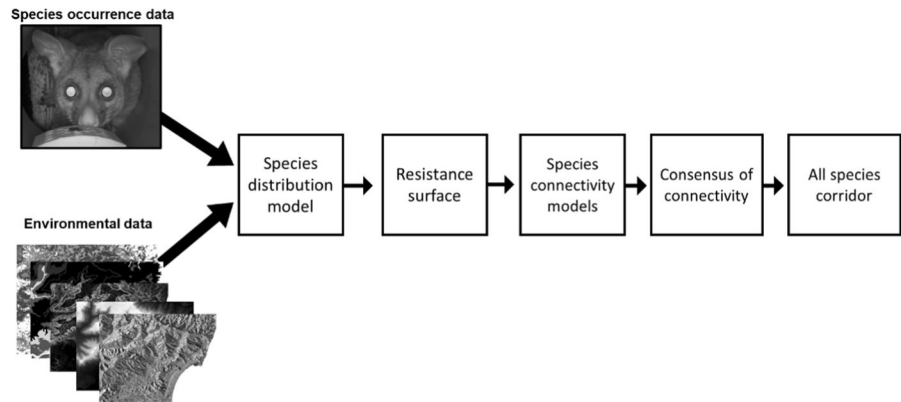


Table 1 Summary of arboreal marsupial species found in the study’s landscape

Species	Weight (g)	Movement methods	Conservation listing
Feathertail glider (<i>Acrobates pygmaeus</i>)	12	Gliding, climbing	Not listed
Brown antechinus (<i>Antechinus stuartii</i>)	28	Climbing, moving on ground	Not listed
Eastern pygmy possum (<i>Cercartetus nanus</i>)	40	Climbing, moving on ground	Vulnerable in NSW
Sugar glider (<i>Petaurus breviceps</i>)	130	Gliding, climbing, sometimes on ground	Not listed
Common ringtail possum (<i>Pseudocheirus peregrinus</i>)	860	Climbing, moving on ground	Not listed
Greater glider (<i>Petauroides volans</i>)	1300	Gliding, climbing	Endangered in NSW and Nation- ally
Common brushtail possum (<i>Trichosurus vulpecula</i>)	2400	Climbing, moving on ground	Not listed
Southern bobuck (<i>Trichosurus caninus</i>)	3100	Climbing, moving on ground	Not listed

from Circuitscape (Monsimet et al. 2020; Petsas et al. 2020; Miranda et al. 2021). A least cost path analysis was performed on the all-species conductance map using Linkage Mapper (McRae and Kavanagh 2022).

Evaluation of proposed corridor

The final corridor network produced was evaluated by ground-truthing key habitat requirements for all eight species. Key habitat variables measured were: (1) feed tree composition; (2) noxious weed coverage; and (3) hollow availability for size classes < 5 cm, 5–10 cm and > 10 cm. Habitat surveys were performed at points along the final corridor network, that were spaced on average, 100 m apart. Each variable had a

weighted value in terms of its relative importance for each species, so that the sum of values equated to a final index of suitability that ranged from zero (not suitable) to 1 (highly suitable) (Supplementary 3). We gave variables a higher weight if expert opinion, literature reviews, and field data were in agreement that the variable was highly influential in determining habitat value. Variables thought to be less important by experts or indicated by field data we gave a lower weight. From this, weighted habitat rankings for the segments of the final corridor for each species were calculated to indicate its value as both habitat and as movement corridors.

The monitoring of two rope bridges (between 18/4/2020 and 18/4/2022) and two underpasses

(between 16/6/20 and 19/8/21) was also undertaken using motion sensor cameras (Fig. 3). Qualified tree climbers accessed rope bridges found over the highway and installed motion sensor cameras at each end (Spypoint Link S Cellular Solar Trail Camera). These cameras were solar powered (charging an internal lithium battery) and cameras uploaded photos daily to a server. This ensured continued, uninterrupted monitoring of two rope bridges. In the two underpasses, cameras (Browning Tail Cameras BTC-7-4 K) were positioned on the ceiling on either end of the passages and left to record the underpass floors for over one year. Additional cameras were positioned on wooden poles to face wooden bridges inside the underpasses (Fig. 3).

Results

Species distribution models

More generalist species had a greater and consistent coverage of habitat suitability, compared to more specialist species such as the greater glider, eastern pygmy possum and feathertail glider (Fig. 4). Both

eastern pygmy possums and feather tail gliders had greater suitability at high elevations in more topographically diverse terrain, particularly favouring Illawarra Subtropical Rainforest. Ringtail possums, brushtail possums, antechinus, and sugar gliders, all had medium to high suitability values for most of the vegetation throughout the landscape. The southern bobuck showed a distinct preference for higher elevation habitat, and the greater glider had moderate to low suitability in available vegetation with most suitable habitat occurring along the Illawarra Escarpment.

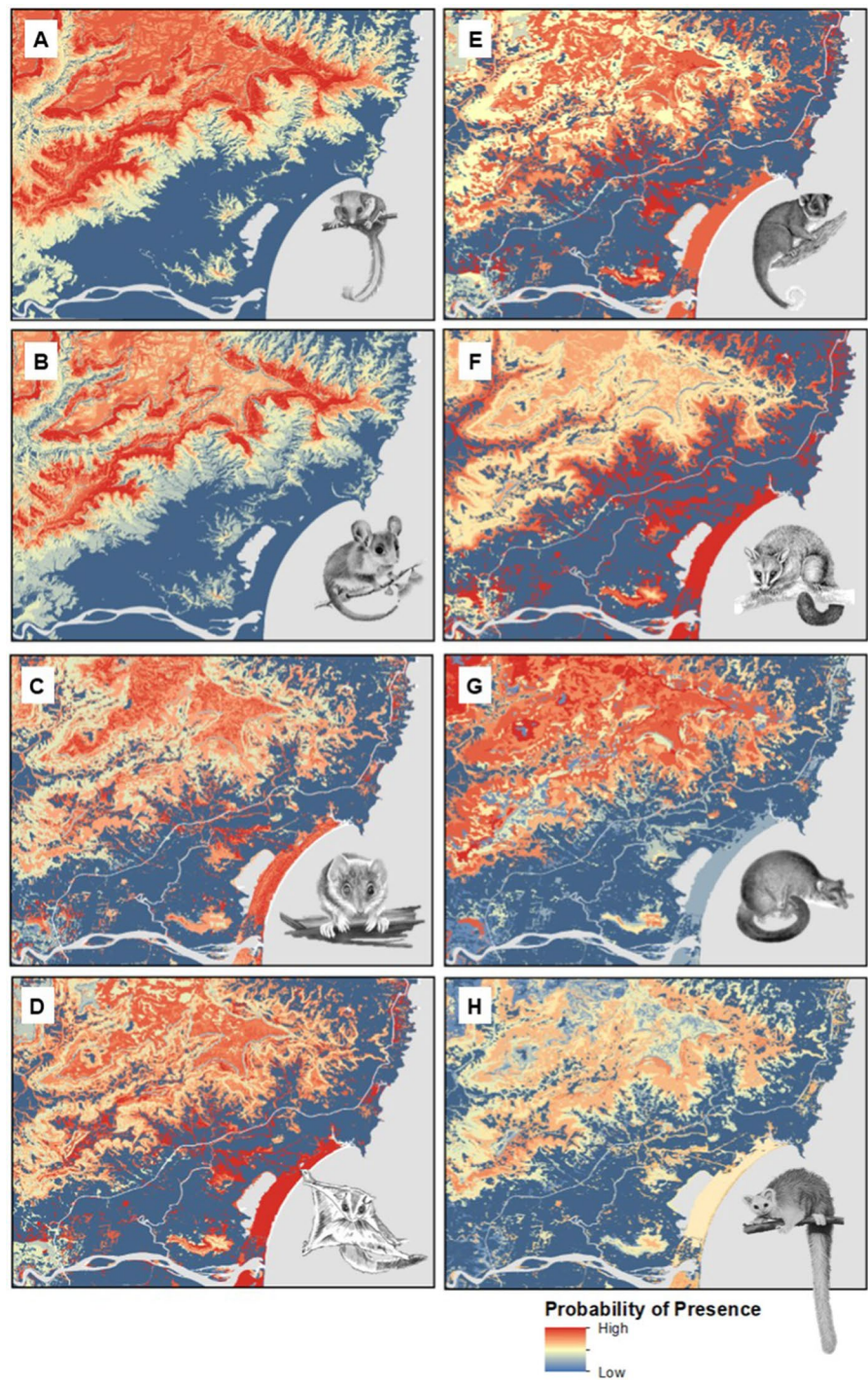
Potential connectivity models

For each species, connectivity models differed in the amount of area in the potential connectivity network (Fig. 5). Feathertail gliders and eastern pygmy possums were restricted to movements along and within the Illawarra Escarpment and surrounding national parks. Whereas ringtail possums, brushtail possums, antechinus, and sugar gliders, all had high levels of connectivity, with higher values in the IIC index. The greater glider had the least amount of connectivity of all the species.

Fig. 3 Motion sensor cameras (A) used to monitor usage of the rope bridges (B) to cross over the Princes Highway. Cameras were also installed to monitor underpass tunnels and wooden bridges inside (C, D)



Fig. 4 MaxEnt species distribution maps for **A** Feathertail glider *Acrobates pygmaeus*; **B** Eastern pygmy possum *Cercartetus nanus*; **C** Brown antechinus *Antechinus stuartii*; **D** Sugar glider *Petaurus breviceps*; **E** Ringtail possum *Pseudocheirus peregrinus*; **F** Brushtail possum *Trichosurus vulpecula*; **G** Southern bobuck *Trichosurus cunninghami*; **H** Greater glider *Petauroides volans*

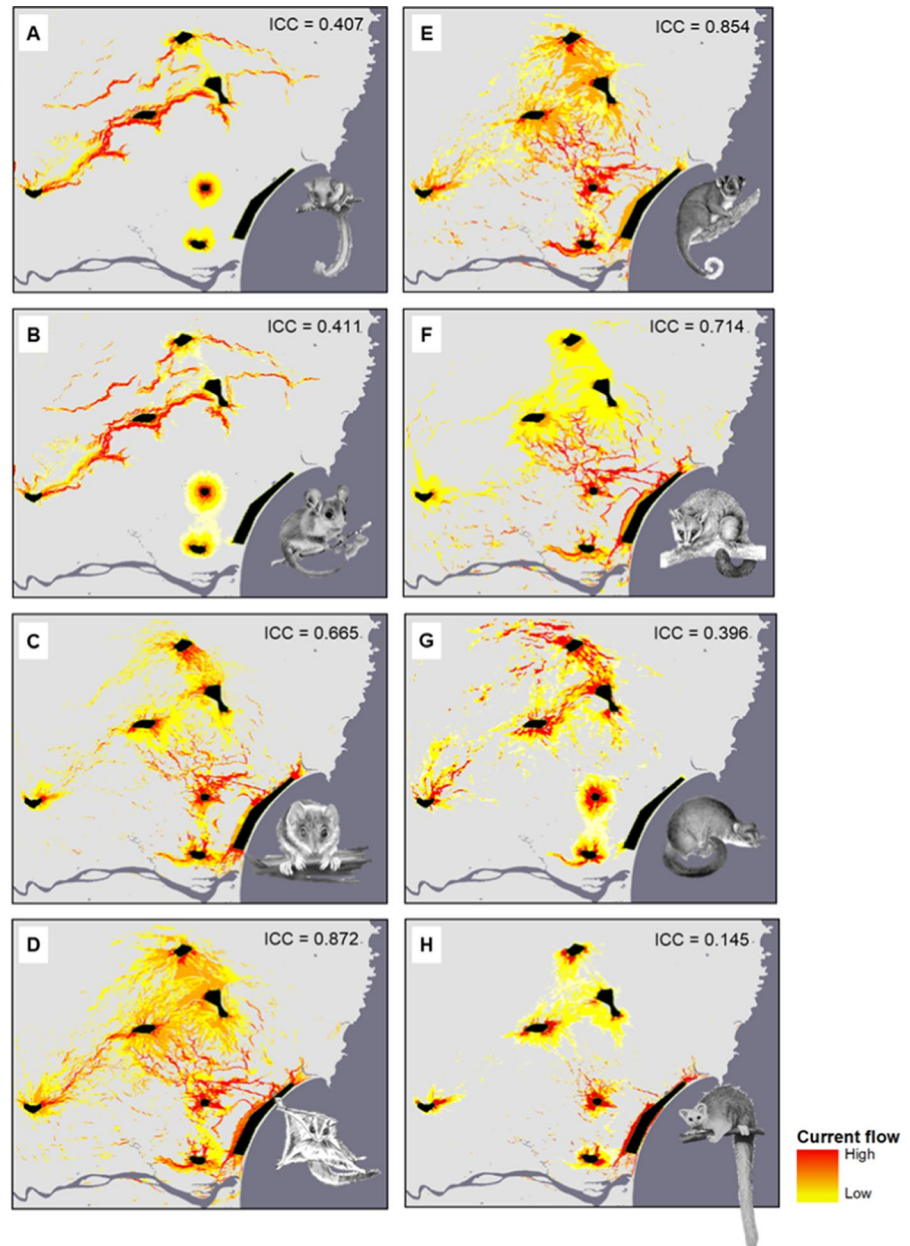


All species corridor

The final corridor as defined through least cost path analyses, focused on connecting all species between

Seven Mile Beach National Park (SMBNP) and the Illawarra Escarpment (Fig. 6). The impact of the highway and river as strong barriers to movement were evident. The corridor identified did not utilise

Fig. 5 Potential connectivity analysis for wildlife species within the study's fragmented landscape, as based on circuit theory corridor implemented using Circuitscape. Focal fragments are shown in black, with yellow (low flow) and red (high flow) showing corridor flow intensity. **A** Feathertail glider *Acrobates pygmaeus*; **B** Eastern pygmy possum *Cercartetus nanus*; **C** Brown antechinus *Antechinus stuartii*; **D** Sugar glider *Petaurus breviceps*; **E** Ringtail possum *Pseudocheirus peregrinus*; **F** Brushtail possum *Trichosurus vulpecula*; **G** Southern bobuck *Trichosurus cunninghami*; **H** Greater glider *Petauroides volans*. Upper left corner values show Integral Index of Connectivity (IIC) from Conefor Sensinode 2.6



steppingstone fragments of habitat, instead riparian corridors and roadside habitat were selected. Sections of these thin linear corridors, and the rope bridges and underpasses, were identified as pinch points (Supplementary 4).

Rope bridge and underpass usage

Of the two underpasses only cameras from one underpass were not stolen, and this underpass recorded

arboreal mammal species utilising the underpass. *Trichosurus* species was recorded crossing on 24 occasions in this underpass, however distinguishing features were difficult to discern on cameras. Based on nearby observations (less than 100 m away), *T. vulpecula* and *T. cunninghami* have been recorded in the area, thus the possums recorded on camera using the underpass are likely to be both species. Each possum record was of it using the floor, and not the wooden bridge installed inside the underpass for



Fig. 6 Final corridor for all species based on a least cost path analysis connecting Seven Mile Beach National Park with the Illawarra Escarpment. Segments highlighted in white (1–4) were ground-truthed for their suitability for all eight species

arboreal species. On two occasions, brown antechinus were recorded using the underpass tunnels.

Of the two rope bridges only two arboreal mammal species were recorded using the bridges (Fig. 7). Bridge one recorded one occasion where a sugar glider used the bridge. The second bridge recorded 68 sugar glider crossing events and one ringtail possum crossing.

Evaluation of proposed corridor network

Ground-truthing the final modelled corridor pathways was performed for approximately 35% of the

corridor network. Permission to access some of the pathways was limited due to private properties or terrain access. Upon evaluation, the species that had the most suitability across all corridor segments was the ringtail possum, followed closely by the sugar glider (Table 2). The least amount of suitability was found for the greater glider, feathertail glider and pygmy possum (Table 2). The segment that performed best in terms of corridor and habitat suitability for all species was segment four, along Woodhill Mountain Road, followed closely by segment one, Beach Road.

Fig. 7 Sugar glider (*Petaurus breviceps*) (left) and ringtail possum (*Pseudochiurus peregrinus*) (right) recorded using rope bridges to cross the highway



Table 2 Weighted habitat rankings (0–1) from ground truthing segments of the all-species corridor modelled

Species	Segment 1	Segment 2	Segment 3	Segment 4	Total
Feathertail glider	0.36	0.24	0.14	0.36	1.10
Pygmy possum	0.36	0.24	0.14	0.36	1.10
Antechinus	0.44	0.44	0.24	0.44	1.57
Sugar glider	0.64	0.47	0.17	0.47	1.74
Ringtail possum	0.64	0.18	0.06	0.88	1.76
Brushtail possum	0.53	0.11	0.01	0.70	1.35
Bobuck	0.53	0.11	0.01	0.70	1.35
Greater glider	0.52	0.06	0.01	0.52	1.10
Total	4.04	1.84	0.76	4.43	

Discussion

Our results show a clear trend where generalist species (brown antechinus, sugar gliders, ringtail possums, brushtail possums) had greater connectivity than more specialist species (feathertail gliders, pygmy possums, southern bobucks, and greater gliders). Despite the few species presence records in the fragmented landscape for these specialist species, we have identified areas that with further habitat restoration, are more likely to facilitate the movement of these species.

Species distribution models

Species resistant to human disturbance and considered more generalist, had a greater distribution across the study landscape. Common brushtail possums, ringtail possums, sugar gliders and brown antechinus, all had presence observations spread throughout the entire landscape in both small fragments of habitat and in all the reserves. These species are known to occupy and utilise such habitat despite threats posed in the matrix of cleared land (Laurance and Laurance

1999; van der Ree 2000; Marchesan and Carthew 2008; Malekian et al. 2015; Gracanin et al. 2019; Gracanin and Mikac 2022a). Recent genetic analyses confirmed the ability of sugar gliders to move effectively in our study’s fragmented landscape as they had high gene flow and limited genetic structure (Gracanin et al. 2023). Additionally, we have shown in our other work that sugar gliders are highly mobile (Gracanin and Mikac 2022a) and able to move on the ground (Gracanin et al. 2019).

For more specialist species, predicted distribution was more restricted as observations were limited east of the highway. The southern bobuck was predicted to have higher probability of presence along the Illawarra Escarpment, at higher elevations in forested habitat. Observations of the southern bobuck in this study were restricted to the west of the highway. Despite being highly forest-dependent, other studies have detected bobuck populations in linear roadside remnant vegetation (Martin et al. 2007). Long term monitoring in the study landscape did not detect bobucks in areas west of the highway (Gracanin and Mikac 2022b). However, monitoring of underpass tunnels indicates the possibility of bobucks using the

tunnels to cross the highway, and that the species may be present east of the highway. Only two observations were found east of the highway for the eastern pygmy possum and feathertail glider, both at David Berry Memorial Hospital. At this site, the habitat is comprised of Illawarra Lowland Subtropical Rainforest, a critically endangered ecological community. This remnant forest likely represents the type of forest that was historically widespread across most of the study landscape, and that these species are possibly restricted to this site and other wet sclerophyll forest nearby.

Potential connectivity pathways

Dispersal is an important consideration for population dynamics and to maintain viability over time (Doak et al. 1992; Stow et al. 2001; Schtickzelle et al. 2006; Fletcher et al. 2018). Our study found connectivity pathways were numerous and highly conducive to more generalist species, which included the common brushtail possum, ringtail possum, sugar glider and brown antechinus, as these species not only readily move through remnant linear fragments but are also known to reside permanently in such habitat (van der Ree 2000; Wilson et al. 2007; Marchesan and Carthew 2008; Taylor and Rohweder 2013; Molloy and Davis 2017; Gracanin and Mikac 2022a). More specialised and cryptic species, including the feathertail glider, eastern pygmy possum, and greater glider, all had limited connected pathways between focal nodes as both cleared habitat and unsuitable habitat limited the intensity or existence of conductance pathways. It is important to note the limitations of the final models as the friction values manually changed are based on a combination of expert opinion and literature, and thus conductance at barriers (highways and rivers) and linkages (underpasses and rope bridges) may not accurately represent a species capacity for movement at these areas. However, many studies utilise this approach and to overcome these limitations is to conduct field-validation which this study performed on rope bridges and underpasses, as well as conducting habitat assessments of pathways (Sawyer et al. 2011b).

All species corridor

In other studies, the utilisation of an umbrella species, often a threatened species, have priority for conservation planning purposes (Roberge and Angelstam 2004; Mortelliti et al. 2009; Thornton et al. 2016). There were several different pathways for more common, generalist species in our landscape (Fig. 5), however, the all-species corridor created through a least cost path analysis was then constrained by the highly specialised greater glider. This pathway starting from SMBNP, follows medium and large *Eucalyptus* dominated roadside habitat before utilising less suitable habitat along riparian corridors and a rope bridge for crossing the highway. By using existing connected pathways, and the shortest distance of resistance to movement, targeted restoration efforts can take effect following ground-truthing. One other study into habitat connectivity for greater gliders at SMBNP failed to consider Beach Road (Segment 1; Fig. 6) as a corridor (Vinson et al. 2020b). The study was more hypothetical in their approach by drawing potential corridors, and they recommended the installation of glider poles within the large Coomonderry Swamp as well as reforestation efforts along the boundary of this swamp (Vinson et al. 2020b). However, there are logistical challenges, such as that the swamp and surrounding swamp edge, is subject to regular intense flooding. Furthermore, greater gliders have high site fidelity and dispersal appears to be limited (Suckling 1982; Taylor et al. 2007), and thus are unlikely to use glider poles compared to other, more mobile species (Taylor and Goldingay 2013; Taylor and Rohweder 2020).

Highways present significant barriers for arboreal species, including common, generalist species (Russell et al. 2009, 2013; Soanes et al. 2016; McCall et al. 2017). The all-species corridor modelled identifies one of the rope bridges acting as a pinch point for movement, and through the data collected at these rope bridges, they may provide limited connectivity for all species. Similar to other studies, the sugar glider was readily able to utilise the rope bridge crossing (Goldingay et al. 2013; Soanes et al. 2015, 2017a; Goldingay and Taylor 2017). These studies have also recorded extensive use of these bridges by ringtail possums, brushtail possums and feathertail gliders. There is some evidence of rope bridge usage by a species of pygmy possum, *Cercartetus caudatus*,

however this was for smaller roads and not highways (Weston et al. 2011). There have been no records of greater gliders using rope bridges, though other large gliding species such as the yellow-bellied glider readily use glider poles as steppingstone movement pathways across highways (Taylor and Rohweder 2020).

The greater glider is generally considered a relatively poor disperser, with high site fidelity and has a low reproductive rate (Maloney and Harris 2008). Thus, the species is vulnerable to barriers to movement, however a population viability analysis found that even low dispersal rates could prevent extinctions of populations separated by roads (Taylor and Goldingay 2009). Therefore, through habitat restoration (further discussed below), it is possible that greater gliders could overcome the barrier posed by the highway dissecting the study location.

Management recommendations

Through ground-truthing surveys, limitations in corridors to act as habitat and facilitate movement of species were identified. For all segments surveyed and their surrounding habitat, an increase in hollows is recommended for all species though in particular for the greater glider. This is through both artificial carving of existing hollows in their early stages of formation and nest box installation. A widening of the corridors is needed, through planting a diversity of *Eucalyptus sp.*, though in particular *E. pilularis* a preferred feed and habitat tree of the greater glider population at Seven Mile Beach National Park (Vinson et al. 2020b). Additional feed trees include *Acacia*, *Banksia* and *Callistemon* species (Lindenmayer 2002). At segment three, a large density of *Lantana camara* posed a large issue for arboreal mammal usage of the habitat. Removal of weeds in this riparian area is needed, as well as subsequent revegetation with preferred trees.

For all common species, connectivity was apparent, and the least cost path corridor identified the shortest area to target revegetation and habitat restoration efforts. This pathway also utilised a rope bridge over the highway. Though not detected using rope bridges in this study, feathertail gliders have been recorded using artificial structures to cross highways in other areas of Australia (Goldingay et al. 2013, 2018). For the eastern pygmy possums and brown antechinus, further revegetation at

underpasses may improve the species propensity to use them, especially for smaller, narrower drainage culverts (between 50 and 100 cm wide) that were not monitored in this study (Yanes et al. 1995; Chen et al. 2021). Unfortunately, of the two underpasses monitored for over a year, cameras from one of the underpasses were stolen. This is a limitation for our interpretations about the usage of the underpasses in this area along the Princes Highway, as other species besides *Trichosurus* species and brown antechinus, may have used this other underpass.

The endangered population of greater gliders at SMBNP, the focus of the corridor connectivity efforts, is very limited in terms of obtaining functional connectivity in the landscape and is significantly genetically differentiated from other populations (Knipler et al. 2023). A least cost path analysis identifies the shortest, and least costly path, for a wildlife corridor, so that conservation managers can be cost effective with limited funding. For greater gliders, intense reforestation efforts are required to widen linear corridors to at least 100 m wide. If the recommended reforestation efforts and habitat improvements are made along the modelled corridor, the final issue of the highway remains a significant barrier. The gliding threshold for the species is limited by the highway width and the limited ability of greater gliders to use artificial crossing structures (Taylor and Goldingay 2009). However, three scenarios are available to help the greater gliders persist at SMBNP. Firstly, a habitat bridge (wildlife-dedicated land or green bridges; Plaschke et al. 2021; Corlatti et al. 2009; Taylor and Goldingay 2010; Gužvica et al. 2014) would be the long-term effective solution for overcoming the barrier of the Princes Highway, although the most expensive. Secondly, increasing available habitat accessible to greater gliders east of the highway would allow for the population to increase and be more resilient to stochastic changes (Lande et al. 2003; Reed 2004; Frankham et al. 2010; Ovaskainen and Meerson 2010). In this scenario, segment one of the modelled corridors (Beach Road) presents the best opportunity to allow gliders to disperse into larger fragments of habitat at Hartley Hill Reserve and Moeyan Hill Reserve. Thus, efforts should focus on thickening the habitat on this road and increasing the number of appropriate hollows for the species (Hofman et al. 2022). A third scenario is to translocate greater gliders individuals to SMBNP,

to increase genetic diversity of the isolated population (Knippler et al. 2023). However, this requires detailed assessment of genetic data from nearby populations to determine how a program would operate to ensure success (Batson et al. 2015; Weeks et al. 2015; Knippler et al. 2023).

Conclusions

Through a multiple species methodological framework, we identified networks of connected habitat for each species before identifying a final corridor for all species. Spatial models are limited in their ability to capture ecological data, such as hollow availability. Hollow availability was critical for seven of the eight species in this study, as they are reliant on them for denning and for raising young. We found that ground-truthing the all-species corridor was critical to identify actions needed to restore habitat. In addition, artificial structures meant to improve the movement of arboreal mammals over the highway, were found to be limited. Our study exemplifies the importance of ground-truthing in connectivity conservation studies to ensure conservation outcomes are realised.

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Author contributions AG and KM conceived the ideas; AG designed the methodology; AG collected the data; AG analysed the data; AG led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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Data availability The datasets generated during and/or analysed during the current study are available from the corresponding author on reasonable request.

Declarations

Conflict of interest The authors declare no conflicts of interest.

Ethical approval This work was conducted under NSW DPIE Scientific Licence 101968 and UOW Animal Ethics protocol AE1902.

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