Sarawak Wildlife Corridors
**EXECUTIVE SUMMARY**

Wildlife corridors are essential for long-term conservation. Most national parks and other protected areas are too small on their own to support viable populations of large animals, so it is important that animals are able to disperse among parks in order to find food and mates, avoid inbreeding, and shift locations in response to climate change. Wildlife corridors facilitate this dispersal, and can prevent wildlife populations from becoming increasingly isolated in national parks, which could lead to extinction and the loss of some of Sarawak’s world-renowned biodiversity. We have analyzed the habitat selection of several Protected and Totally Protected wildlife species in Sarawak and surrounding areas using camera trap data and metapopulation models. Our goal was to identify the most important wildlife corridors in Sarawak—the ones that contribute the most to preventing the extinction. Our analysis shows that the most important dispersal route is between Kayan Mentarang and Betung Kerihun. Protecting intact forest habitat along that route would greatly enhance wildlife persistence. Our camera trapping shows that the Hose Mountains are a very important wildlife area, with mammal diversity and abundance among the highest anywhere in Malaysian Borneo. Gazetting the Hose Mountains and Batu Laga National Parks remains a critical priority. Other important corridors in Sarawak are those connecting the Hose Mountains to Betung Kerihun and connecting Gunung Mulu, Ulu Temburong, and Usun Apau to Kayan Mentarang.

**RINGKASAN EKSEKUTIF**

I. Goal
To protect wildlife corridors to help ensure that protected and charismatic animals in Sarawak are not reduced to isolated populations with reduced gene pools or driven extinct. Wildlife corridors are areas of forest that are long and wide enough, and are properly managed, to link national parks and other protected areas into a network. This will enable animals to disperse amongst these protected areas to find habitat, food, and mates.

II. Justification
Sarawak has some of the highest biodiversity on earth, including many rare, beautiful, and iconic species. The state also has several important protected areas where threatened wildlife can live. However, many mammals and birds in tropical rainforests live at low population density – meaning that even in pristine habitat, the abundance of the animals will be relatively low. For example, the Sunda clouded leopard (Neofelis diardi), the largest predator in Sarawak and a species only found in Borneo and Sumatra, is so rare that only around 2 individual leopards occur per 100 km² (Brodie and Giordano 2012, IUCN 2015). Based on these estimated population density, this means that even large protected areas such as Gunung Mulu National Park and Lanjak Entimau Wildlife Sanctuary could only support about 10 and 36 clouded leopards, respectively. Orangutans are similarly limited – their average population density is higher than that of clouded leopards but their distribution is much smaller (Husson et al. 2008). Decades of research in conservation biology have shown that it is generally necessary to have hundreds or thousands of individuals of a given species to ensure their long term survival – any fewer and the species has a high probability of going extinct. Therefore, even though Sarawak has several important, large protected areas, each of these places is too small on its own to support populations of large wildlife species into the future.

Animals need to move around to find new spaces to live in, find mates, and to have “escape routes” from certain areas that become unsuitable, for example too hot, from climate change. If the protected areas in Sarawak could be linked (with each other and with those in Kalimantan and Brunei) into a network, wildlife could move among the various parks and would be much less likely to go extinct than if the animals become confined to parks that are becoming increasingly isolated by conversion of surrounding lands. Proper management is also essential to ensure that protected areas and also wildlife corridors are safe from overhunting and illegal encroachment.

We have used camera traps to study wildlife in Sarawak, to determine the habitat needs of different mammal species. We used these data in cutting edge analyses to estimate animal dispersal from every protected area in Sarawak to every other through the complex, heterogeneous landscapes in between.

The 43 protected area complexes in Sarawak have approximately 900 possible wildlife corridors between them (Appendix A). It is probably infeasible to protect all of those wildlife corridors, so it is important to prioritize them. We used newly developed, cutting-edge analysis to determine which corridors are the most important to wildlife persistence. We present here the prioritization of wildlife corridors, focusing on the most important corridors. We propose that legal protection measures are needed to protect these critical corridors. This will help ensure that wildlife in Sarawak does not go extinct or become isolated populations.
Protecting landscape connectivity in these areas will also support Sarawak’s commitment to:


(ii) The Convention on Biological Diversity (Target 11; https://www.cbd.int/sp/targets/rationale/target-11/), to which Malaysia is a signatory.

(iii) The Heart of Borneo Tri-National agreement, to which Malaysia is a signatory.

(iv) The Sarawak Government’s target of achieving 1 million hectares of Totally Protected Area in the State.

III. METHODS

We used motion-triggered “camera traps” to study the ecology of wildlife in 15 study areas across Sarawak (as well as Sabah), inside and outside of protected areas, in logged and unlogged forest, in hunted and unhunted areas, and across elevations from sea level to 1800 m. This took many years; altogether the data provide an unparalleled picture of how different wildlife species respond to natural and human-caused variation in habitat conditions.

We then used new algorithms to estimate animal dispersal across complex landscapes. Recently, ecologists have begun to use mathematical models developed for electrical circuit theory to predict the flow of dispersing animals. Such models were developed to understand the path that electrical current would take as it flows across a complex surface from a battery to a ground. These models can predict the relative proportion of current that would follow one possible route versus another, and how changing the resistance of the surface would affect the current flow (e.g. Brodie et al. 2015a). Clearly animals are not electrons, and an individual animal might behave in complex and unpredictable ways. But when considering hundreds or thousands of individuals together (for jungle mammals and even people), current flow models can predict average behaviour very well. These models have been verified with genetic data for both mammals and plants (McRae and Beier 2007). The approach is analogous to economics –individual people might make irrational choices, but on average people’s financial decisions tend to follow predictable patterns. So these models allow us to quantify the numerous and various paths that animals leaving one national park might take to get to another national park. They also help us understand how changing the quality of the habitat in between the parks will affect the total number of dispersing animals that can successfully complete the trip. We mapped all of the protected areas in Sarawak >100km² in size and also the large parks on the Sarawak border in Indonesia and Brunei. We used the circuit-based algorithms discussed above to estimate the routes that animals leaving each of these protected areas would travel to get to every other protected area (Figure 1; more details on these methods are provided in the Appendix).

But how do we decide which of the possible linkages between protected areas are most important? It is probably infeasible to legally protect all of the possible wildlife corridors among large protected areas in Sarawak, and it might not even be necessary to do so. Some of the wildlife corridors are probably much more important than others. We developed a method to prioritize wildlife corridors based on how much each corridor would contribute to the long-term persistence of the Protected and Totally Protected mammal species in Sarawak. To do this, we used a branch of ecology called
“Metapopulation Theory”. A metapopulation is a group of populations; for example, all of the clouded leopards living in Gunung Mulu National Park would be one population, and those living in Ulu Temburong another population. The metapopulation includes those two populations, plus all the others in the state (and nearby parks on the Sarawak border), and dispersal among these populations. We used our field-data-based dispersal models to look at how much the protection of each individual wildlife corridor would reduce the probability of extinction of the entire metapopulation. Then we did this for every species. We ended up with an ordered list of wildlife corridors, ranked in terms of how much each corridor will reduce the loss of wildlife from Sarawak.

Protecting the corridors that we identify as the most important will greatly reduce the chances of extinction for wildlife, and showcase Sarawak’s commitment to long-term conservation based on the best-available science.

Land use change affects every species differently. Some species rely very heavily on undisturbed forest, such as many carnivores (Brodie et al. 2015b). If wildlife corridors are not established, the dispersal of these species may be severely reduced. Other species such as orangutan might still disperse through selectively logged forest (Husson et al. 2008), but their dispersal rates are much lower in disturbed habitat, so corridors of intact forest could greatly improve their chances of long-term persistence in Sarawak. Other species persist perfectly well in disturbed habitat (Brodie et al. 2015b), and so do not need wildlife corridors. Importantly, our analysis integrates across all of these species, and so our recommendations are based on management options that will have the best outcome for the most Protected and Totally Protected species in Sarawak.

IV. Findings

Based on the analyses described above (with more details provided in the Appendix), we ranked the potential wildlife corridors across Sarawak (Figure 2). Our analysis showed that the most important areas for wildlife connectivity are:

1. Linking Lanjak Entimau and Betung Kerihun to Kayan Mentarang
2. Linking the Hose Mountains to Betung Kerihun
3. Linking Pulong Tau and Ulu Temburong to Kayan Mentarang
4. Linking Usun Apau to Kayan Mentarang

Habitat conditions on the ground in these proposed corridors are variable. Most have already been selectively logged. However, our previous results demonstrate that if logged forests are allowed to recover without additional logging, they provide suitable habitat for many mammal species (including some Protected and Totally Protected species) relatively quickly.

V. Proposed Actions

1. Gazette the proposed Hose Mountains and Batu Laga National Parks, as these are key areas for connectivity and wildlife conservation at the state-wide scale. Our camera trapping work demonstrates that even though portions of these parks have been heavily logged, the areas support some of the highest mammal diversity and abundance in all of Malaysian Borneo – on par with the famous Danum Valley and Maliau Basin Conservation Areas in Sabah. Habitat protection here is essential, and could also help provide a refuge for animals affected by the Bakun Dam impoundment. Combined with the spectacular scenery, these parks have a vast and untapped ecotourism potential (Figure 3).
(2) The most urgent connectivity need in Sarawak—indeed in all of Borneo—is for habitat connection that link Kayan Mentarang to the transboundary protected area complex composed of Betung Kerihun and Lanjak Entimau (Finding 1 above). This could be accomplished in several ways (Figure 4):

**(Option 2.1 –Most ambitious)** Establishment of a new protected area (e.g. National Park or Conservation Area) between Hose Mountains, Betung Kerihun, and Kayan Mentarang National Parks. This would address both Findings 1 and 2, above. Ideally this protected area would include both ridgelines and river courses; this is important because many dispersing animals follow ridges for travel while other species (particularly riparian specialists) avoid ridges but instead prefer to move along rivers. A park such as this would add ~6000 km² of protected area to the state.

**(Option 2.2 –Ambitious)** The new national park that has been proposed by the Sarawak government, Baleh, could be expanded to provide linkage between Kayan Mentarang, Betung Kerihun, and the Hose Mountains, but provide less direct linkage from the Hose Mountains to Kayan Mentarang. This would still address Findings 1 and 2 but require less land area than Option 1.1, adding 2400 km² of protected area to the state (in addition to the 670 km² of the proposed Baleh National Park).

**(Option 2.3 –Less Ambitious)** Establishment of wildlife corridors linking Kayan Mentarang to Betung Kerihun and, separately, Hose Mountains to Betung Kerihun. This would still address Findings 1 and 2 but require still less land area than Option 1.2. Narrow corridors would be less effective for sustaining dispersal be multiple species because it will be difficult for a single corridor to encompass both ridgelines and riparian areas. This would add 750 km² of protected area to the state (in addition to the 670 km² of the proposed Baleh National Park).

(3) Establish legally protected wildlife corridors in northern Sarawak that link Gunung Mulu, Ulu Temburong, Pulong Tau, and Kayan Mentarang National Parks. This addresses Finding 3 above. WWF has undertaken a corridor to link Mulu, Pulong Tau, and Kayan Mentarang via Layun and the Kubaan Puak Forest Management Unit—if this could be extended to also include a corridor between Mulu and Ulu Temburong, it would achieve this proposed action (Figure 5). Surrounding these corridors are sustainably managed forests. The corridors, alongside the surrounding sustainably managed landscapes, also help to conserve ecosystem services.

(4) Establish a legally protected wildlife corridor that links Usun Apau and Kayan Mentarang National Parks. This addresses Finding 4 above. Usun Apau is a high plateau, and so likely does not contain many riparian specialists—therefore the corridor that we propose follows a ridgeline running between the two parks rather than river courses (Figure 6).

VI. WILDLIFE CORRIDORS IN THE WIDER CONSERVATION CONTEXT

The habitat connectivity proposals made here should be viewed as part of the broader Systematic Conservation Planning (SCP) exercise led by WWF-Malaysia in collaboration with UNIMAS, and the Sarawak Forest Department. The SCP has considered a suite of attributes and used MARXAN algorithms to identify priority areas for conservation. The wildlife corridors proposed here are implemented to the SCP via a post-MARXAN analysis. As discussed above, most of the priority corridors identified here have also been identified by the SCP analysis as areas important for conservation based on species representation and other ecological attributes.
VII. CONTACT INFORMATION

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Figure 1: Predicted dispersal routes for wildlife moving between the Hose, Usun Apau National Park, and Kayan Mentarang National Park, based on circuit theory algorithms. Yellow are areas that many animals will travel through, while blue are areas that few animals will use.
Figure 2: Possible habitat corridors between protected areas (brown) in Sarawak and adjoining areas ranked from most important (red) to important (pink) to less important (yellow). Green background shows the extent of forested area. Note that importance values in the histogram (bottom panel) are on a log scale, so that corridor 1 is actually 700 times more important than corridor 3 in terms of supporting long-term wildlife persistence.
Figure 3: Wildlife and scenery in the proposed Hose Mountains and Batu Laga National Parks, demonstrating the importance of this area for conservation and its ecotourism potential.
Figure 4: Three options for landscape connectivity between Hose Mountains, Betung Kerihun, and Kayan Mentarang National Parks. Option 2.1 (top; ~6000 km²) secures the entire region between the three parks, including both river courses and ridge lines, to support dispersal by different species. Option 2.2 (middle; ~3000 km²) secures a smaller area; Option 2.3 (bottom; ~1400 km²) only adds habitat corridors to the proposed Baleh National Park. Hose Mountains, Betung Kerihun, and Kayan Mentarang National Parks shown in brown, and the proposed Baleh National Park in light blue. Elevation ranges from 100 m (black) to 1600 m (white); rivers shown in blue.
Figure 5: Location of the ongoing WWF-Malaysia corridor project to link Gunung Mulu, Pulong Tau, and Kayan Mentarang National Parks. We propose here adding an additional linkage (shown in red) connecting Mulu to Ulu Temburong.

Figure 6: Close-up of the corridor that we propose here (in red) to link Usun Apau National Park in Sarawak to Kayan Mentarang National Park in Kalimantan (both parks shown in brown) along a ridgeline between the two areas.
APPENDIX A –Technical details of the analytical methods

A.I. Justification (taken from Brodie et al., “Connecting science, policy, and implementation for landscape-scale habitat connectivity”, In Press, Conservation Biology)

A.I.a. Which potential wildlife corridors are most important?
The fragmented nature of many landscapes means that numerous habitat patches exist, and the number of possible wildlife corridors between patches becomes vast as the number of patches increases. The 43 protected area complexes in Sarawak, for example, have 903 possible corridors between them. (Connecting each of \( N \) patches to every other patch in a network requires \( (N^2 - N)/2 \) links.) Given so many options for corridors, and limited funding and political capital available to provide them all with legal protection and on-site management, we need to prioritize which potential corridors are most important.

In some cases the patches that need to be connected are determined politically. In Sabah, for example, forested habitat between the two large parks in the west, Mt. Kinabalu (754km\(^2\)) and the Crocker Range (1,399km\(^2\)), was lost decades ago, leaving them effectively isolated. The Sabah Parks department instigated the EcoLinc project (Table 1) to reestablish connectivity. Likewise, the Sabah Forest Department wanted to maintain connections between the three flagship conservation areas of central Sabah (Imbak Canyon, Maliau Basin, and Danum Valley). Although not specifically stated as the driver for this decision, scientists involved with Danum Valley Conservation Area had emphasized the ecological importance of the elevational gradient represented by the Silam-Danum-Maliau-Imbak forest complex (spanning 0 – 1600 m elevation) to support possible range shifts in response to climatic changes. In Singapore, the hourglass-shaped Eco-Link wildlife bridge was constructed across a major expressway to re-connect two nature reserves that were fragmented in 1985 (Chong et al. 2010).

But in other cases, determining which habitat patches warrant connection by protected forests is not as easy. Planning for the Central Forest Spine (CFS) Masterplan in West Malaysia revealed 6,119 forest fragments in Peninsular Malaysia. Prioritization of linkages between these patches was done with expert opinion, based on fragment size, elevation, and known wildlife habitats. In Sarawak, there is less direction as to how to prioritize linkages - many protected areas still have forest habitat between them (Gaveau et al. 2014), and it is not clear which linkages are most important to metacommunity persistence.

The problem of corridor prioritization has received substantial attention, usually in terms of each corridor’s contribution to overall connectivity of the landscape – the proximate goal of the connectivity strategy. Prioritizations often employ graph theory, a branch of mathematics based on the analysis of information flow across networks of nodes (ecologically analogous to patches) and links between the nodes (i.e., corridors; e.g., Urban et al. 2009, Rayfield et al. 2011). Using graph theory, corridors can be ranked in terms of the contribution of each to overall connectivity (Urban et al. 2009, Rayfield et al. 2011) or gene flow (Rozenfeld et al. 2008). However, several problems with these approaches limit their utility. For example, rankings based on the contribution of each patch or corridor to landscape connectivity are very sensitive to the connectivity metric used (Laita et al. 2011, Ziolkowska et al. 2014), and many of the connectivity measures have divergent and counterintuitive model behaviors (Laita et al. 2011). Overall, connectivity measures derived from graph theory tend to focus on the dynamics of
immigration and local extinction and not on regional population size or persistence (Moilanen 2011).

Corridors could also be prioritized based on their relative contributions to the long-term persistence of metapopulations of the focal species (Nicholson et al. 2006, Webb and Padgham 2013), thereby addressing the ultimate goal of the connectivity strategy. This can be problematic, however, due to inconsistencies and difficulties in estimating metapopulation persistence. Spatially-explicit population models are data and computation intensive, making optimization across multiple species difficult (Burgman et al. 2001). Instead, many studies use surrogates of metapopulation persistence rather than direct estimations of persistence itself (Webb and Padgham 2013). Such surrogates include species occurrence probabilities (Williams and Araujo 2000) or the proportion of habitat occupied (Urban and Keitt 2001). Rankings based on the contribution of each link to overall connectivity in a metapopulation context are also highly sensitive to the extinction and colonization parameters (Gilarranz and Bascompte 2012), so their utility may be limited for focal species whose demography is poorly known.

A.I.b. Where should the corridors be located?
Once we determine which habitat patches are to be connected, we need to determine where exactly the wildlife corridors between them should go. The science is well advanced for this issue and powerful modeling tools are available for determining optimal corridor locations. For example, some models estimate the “least-cost path” between two patches, which is a measure of potential connectivity (Beier et al. 2008). Other models use electrical circuit algorithms to determine the paths of maximum dispersal from one patch to another (McRae et al. 2008); these simulate random-walk dispersal by numerous individuals of the focal species and determine how many dispersers pass through each landscape pixel, thereby providing information on functional connectivity. These models are often data intensive, and the necessary habitat selection information may or may not be available at the outset of a corridor designation process. The ongoing connectivity planning in Sarawak is based on camera-trapping-based assessments of habitat quality for the various focal species (Brodie et al. 2015a, Brodie et al. 2015b). The CFS Masterplan did not have explicit maps of habitat quality, but accumulated a number of different proxy datasets (e.g., known wildlife habitats, human-wildlife conflicts, fragment size) and then the final designation of corridor locations was determined via a multi-criteria prioritization process and fine-tuned by expert opinion (FDTCP 2010). In this case, a major focus was to reconnect fragmented major forest blocks; hence, rough locations for the linkages were largely clear.

Expert estimation may be used where direct habitat selection information is unavailable. In Singapore, least-cost path analysis has been carried out based on vegetation structural analysis and expert estimation of habitat requirements of moderate specialist small mammal, amphibians and reptiles, bird and butterfly species. The proposed maps have been validated for presence or absence of species at selected patches (Abdul Hamid and Tan 2014). However, it has to be kept in mind that specialist and generalist species require different solutions for connectivity with short range corridors for specialists to habitat and resource stepping stones for generalists (Dennis et al. 2013).

A.II. Analysis (taken from Brodie, Mohd-Azlan, and Schnell, “How individual links affect network stability in a large-scale, heterogeneous metacommunity”, In Review)
We studied an incipient metacommunity on the island of Borneo (~743,000 km²), which straddles the equator and was, until the mid-twentieth century, almost entirely covered by humid tropical rainforest (Bradshaw et al. 2009). Past and ongoing forest clearance mean that the protected areas (e.g., national parks, wildlife reserves) on Borneo, as in many parts of the world, are becoming increasingly isolated (Gaveau et al. 2014). We examined two scenarios for the ongoing formation of a metacommunity from a previously continuous community consisting of the 30 forest mammal species detected through previously published, intensive, and wide-scale camera-trapping efforts (Brodie et al. 2015a, Brodie et al. 2015b). In the first (“deforested matrix” scenario), we assumed that protected areas (hereafter “patches”) would remain, or recover to, tall rainforest while the intervening landscape matrix would be deforested, strongly reducing dispersal permeability for all of the mammal species. In the second (“heterogeneous matrix” scenario), we assumed that the landscape matrix would remain a heterogeneous mixture of selectively logged forests and cleared areas (Gaveau et al. 2014), with impacts on dispersal that varied among the mammal species (see below for how we estimated species-specific dispersal).

As we do not account for species interactions in determining patch composition, ours is a neutral metacommunity model (Logue et al. 2011). Neutral models are not meant to imply that species interactions do not occur, but the models provide interaction-less approximations that can estimate diversity patterns and dynamics relatively precisely in a range of systems (Hubbell 2001, Kalyuzhny et al. 2015). In some of the few mammal-mammal interactions studied in Borneo, trophic impacts of large predators do not appear to influence occurrence or local abundance of prey or mesopredators (Brodie and Giordano 2013).

Habitat patches in our system ranged from ~100 – 39,000 km². Long-term persistence of large-bodied species in the smaller patches is almost inconceivable without emigration due to low population densities (Brodie and Giordano 2012). Though the metacommunity is still forming via ongoing habitat loss and degradation in the matrix and increasing isolation of the protected areas, we model dynamics of the metacommunity once it has reached colonization-extinction equilibrium (sensu Hanski 1994). We note that such equilibrium assumptions are the rule rather than the exception in many types of modeling studies (Williams et al. 2011).

The links in our network are potential dispersal routes between pairs of adjacent patches. The strength of each link, proportional to the number of dispersers able to successfully move between the patches, varied depending on whether there was a strip of intact tall forest (i.e., a “corridor”) between the patches versus only matrix habitat. We estimated link locations by determining the least-cost paths between each pair of adjacent patches using Linkage Mapper software (McRae and Kavanagh 2011). We buffered these paths by 2.5 km on either side and assumed that the 5 km wide wildlife corridors would remain, or recover to, tall rainforest. Our previous research in the system suggests that mammal diversity recovers rapidly after the cessation of logging (Brodie et al. 2015b), and that 5 km wide corridors substantially enhance dispersal for multiple mammal species (Brodie et al. 2015a).

We then employed circuit-theoretical analysis (McRae et al. 2008) to estimate the resistance distance between each pair of patches in both of the landscape matrix scenarios, for all species, with and without wildlife corridors, using Circuitscape software (McRae and Shah 2009). The resistance distance between any two patches is the minimum movement costs between them, accounting for multiple dispersal pathways including through the wildlife corridor itself (when present) and also through the
surrounding landscape matrix (McRae et al. 2008). We set the resistance of a given 1 km² landscape pixel to 1 in forest habitat (in patches as well as corridors) and to higher values in selectively logged forest based on species-specific responses to selective logging from their standardized regression coefficients in a previously published measure of logging impacts (Brodie et al. 2015b). We set the resistance in deforested matrix to 100; this value is higher than, but within the same order of magnitude as, the resistance value in selectively logged forest for the most logging-sensitive species.

We used metapopulation capacity models to assess how much the presence of a wildlife corridor at a given link affected long-term metapopulation persistence. The importance of link \(i\) to long-term metacommunity stability \(I_i\) in an assemblage with \(S\) species was:

\[
I_i = \sum_{s=1}^{S} m_{s,i} - m_s
\]

where \(m_{s,i}\) and \(m_s\) are the metapopulation capacities for species \(s\) with and without (respectively) a corridor at link \(i\). Metapopulation capacity is the leading eigenvalue of the matrix \(M\), calculated as \(f(D_{ij})A_jA_i^{0.5}\) for all patches where \(j \neq i\), and a 0 value for \(j = i\). \(A_i\) is the areas of patches \(j\) providing colonists to \(i\), and distances \(D_{ij}\) with a colonization ‘survival’ function \(f\) applied to it; this is a proxy for the persistence probability of the overall metapopulation (Hanski and Ovaskainen 2000). In its original formulation, metapopulation capacity led to illogical values for large-scale landscapes, giving 0 capacity values to single patch scenarios, no matter how large the patch, and even penalizing the connecting of patches in networks (Schnell et al. 2013). We accounted for this by incorporating into our models the within-patch recolonization term of Schnell et al. (2013), i.e., \(f(D_{ij}) = 1\) when \(j = i\).

To generate matrices of between-patch disperser survival probabilities for each species, needed as input for the metapopulation capacity models, we assumed a decay in the survival of dispersing individuals with increasing resistance distance. To determine where survival became zero, we used a power law function for maximum dispersal distances based on body size in mammals (Santini et al. 2013), and then determined average resistance distances corresponding to these Euclidian distances.

Dispersal rates and disperser survival are poorly known (at best) for most species, and unknown for the taxa in our system. Therefore, to assess whether potential errors in our estimated dispersal matrix biased our conclusions, we performed another analysis with a 5-fold increase in maximum dispersal distance for all species and determined the correlation between these and the original results. We also assessed link importance via removing individual corridors from a network where all adjacent patches were joined ("removal model") and compared estimated link importance values to those generated using the "addition" method outlined in Equation 1.

Finally we examined how traits of the links related to their importance to metacommunity stability. We used linear models to assess how the importance of links varied with their length (measured as Euclidian distance between the two patches at either end, cost-weighted distance, least-cost path length, or resistance distance), centrality to the network (measured as current-flow centrality in circuit-theoretical models; McRae 2012), the sizes of the patches they connected, and interactions among these factors. We generated a set of models corresponding to all possible combinations of the factors (each standardized to mean = 0 and variance = 1) and ranked them using AIC-based model selection. Traits or interaction terms were considered to significantly affect link importance if the 95% confidence intervals of their model-averaged regression coefficients did not include zero.
APPENDIX B – Literature Cited


