Connecting science, policy, and implementation for landscape-scale habitat connectivity

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ABSTRACT

In an increasingly fragmented world, networks of habitat corridors are critical to support movement of organisms between habitat patches and the long-term persistence of species. The science of corridor design and the policy of corridor establishment are developing rapidly, but often independently. Here we assess the links between the science and policy of habitat corridors, to better understand how corridors can be effectively implemented, with a focus on a suite of landscape-scale connectivity plans in tropical and sub-tropical Asia. Our synthesis suggests that the process of corridor designation may be more efficient if the scientific determination of optimal corridor locations and arrangement is synchronized in time with the achievement of political buy-in and policy direction for corridor designation. Land tenure and the intactness of existing habitat in the region are also critical factors – optimal connectivity strategies may be very different if there are few, versus many, political jurisdictions (including commercial and traditional land tenures) and intact versus degraded habitat between patches. We identify financing mechanisms for corridors, and also several important gaps in our understanding of effective corridor design including how corridors, particularly those managed by local communities, can be protected from habitat degradation and unsustainable hunting. Finally, we point to a critical need for quantitative, data-driven models that can prioritize potential corridors or multi-corridor networks based on their relative contributions to long-term metacommunity persistence.

INTRODUCTION

Natural habitats in many parts of the world are increasingly fragmented. Maintaining or re-creating connections between fragments is critical to maintain movement of organisms and genes between them (Prugh et al. 2008) and to support the long-term persistence of metapopulations (Nicholson et al. 2006). Indeed, a fundamental conservation strategy is the establishment of large-scale (i.e., landscape- or continental-scale) habitat networks consisting of core habitat patches linked by habitat corridors (Soule & Terborgh 1999).

Landscape-scale habitat connectivity plans have been, or are being, developed in many parts of the world (Beier et al. 2008; Beier et al. 2011). The quantitative science of corridor design and assessment is also progressing rapidly (Beier et al. 2011). Here we use the term "corridor" to mean a strip of habitat that links two habitat patches; corridors can be retained when surrounding lands are cleared or restored through habitat rehabilitation. In some cases it may be possible to create corridors by increasing the structural complexity of the agricultural matrix, and thus its permeability to dispersing wildlife (Yue et al. In press). The proximate goal of a corridor is to promote "functional connectivity" (Fagan & Calabrese 2006), or the movement of organisms, across it in order to maintain gene flow between the patches and increase resilience to a range of pressures (e.g., climate change, extreme weather events, hunting); the ultimate goal of the corridor is, or should be, to support the long-term persistence of metapopulations of native species. While there are few examples to date of connectivity plans enhancing metapopulation persistence, corridors have been shown to be effective at increasing movement and gene flow across the landscape (e.g., Sawaya et al. 2014) and ecological processes such as seed dispersal (e.g., Levey et al. 2005).

As with many conservation arenas, however, in landscape connectivity it remains unclear what the relative influence of science and policy are, and how best to link them (Berger & Cain 2014). Here we assess the linkages between science and policy in the design and implementation of habitat corridors, focusing on case studies in tropical and sub-tropical

Asia, a biodiversity hotspot region with some of the highest biodiversity (Myers et al. 2000) and rates of habitat loss (Hansen et al. 2013) in the world. We assess the scientific analysis, policy framework, and implementation details of six connectivity projects in Asia, spanning a range of spatial scales and biological and socio-political settings (Table 1). Several conclusions emerge from our assessment of the science and policy of landscape-scale habitat corridor strategies that have not been well highlighted in the literature to date. We present some findings from our synthesis and also identify areas where overcoming important gaps in our knowledge could greatly improve the efficacy of corridor strategies.

CORRIDOR SCIENCE

Once the goals of a given connectivity project have been established, for example to connect two or more natural areas, a series of scientific questions will help guide the strategy and implementation:

What are the focal taxa?

We have no data on the ecological requirements of most of the taxa in many communities, particular in hyper-diverse regions such as tropical Asia. Moreover, species differ immensely in their responses to anthropogenic disturbances and, thus, their need for corridors in the first place. Therefore, habitat corridor strategies often focus on a few priority taxa. The identity of these taxa is often determined subjectively, for example by focusing on large-bodied, charismatic “flagship species”. For example, the Central Forest Spine (CFS) Masterplan (FDTCP 2010a) in Peninsular Malaysia focused on tigers (*Panthera tigris*), tapirs (*Tapirus indicus*), and elephants (*Elephas maximus*), as these were endangered and expected to garner public support for the connectivity strategy. In Central Sabah, considerable weight was given to the habitat requirements of orangutan (*Pongo pygmaus*) and elephants, despite there being little evidence that these species use the area. Either implicitly or explicitly, focusing on priority taxa assumes that such taxa will be umbrella species, in that promoting habitat connectivity for them will also ensure connectivity for other sympatric species. If priority taxa are chosen explicitly to be umbrella species, they should be wide-ranging organisms with low population density that are specialized on intact habitat, such as many large-bodied carnivore species (Beier et al. 2008). Indeed connectivity strategies in Asia often focus on tigers (Wikramanayake et al. 2011) or, in places where they do not occur, such as Sarawak, Sunda clouded leopard (*Neofelis diardi*) and sun bear (*Helarctos malayanus*). Research suggests that these species will be effective umbrella species for other species that are intolerant of intense habitat disturbances (Brodie et al. 2015a).

Priority taxa could also be those critical to ecosystem function. Loss of important seed dispersing animals, for example, could inhibit forest regeneration, so large-bodied frugivores could serve as priority taxa for conservation in order to maintain the ecological process of seed dispersal (McConkey et al. 2012). Connectivity strategies could also focus on smaller insects and birds that provide important pollination services. In Singapore, for example, an abandoned rail corridor is used by the globally vulnerable straw-headed bulbul (*Pycnonotus zeylanicus*) and the CITES-listed common birdwing butterfly (*Troides helena* *cerberus*) (Ho et al. 2011), thereby potentially increasing exchange of both animals and animal-pollinated plants between the connected habitat patches.

Which potential habitat corridors are most important?

The fragmented nature of many landscapes means that numerous habitat patches exist, and the number of possible habitat 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*(N-1))/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 CFS Masterplan 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., Rayfield et al. 2011; Urban et al. 2009). Using graph theory, corridors can be ranked in terms of the contribution of each to overall connectivity (Rayfield et al. 2011; Urban et al. 2009) 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 & 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 & Padgham 2013). Such surrogates include species occurrence probabilities (Williams & Araujo 2000) or the proportion of habitat occupied (Urban & 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 & Bascompte 2012), so their utility may be limited for focal species whose demography is poorly known.

Where should the corridors be located?

Once we determine which habitat patches are to be connected, we need to determine where exactly the habitat 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 2010a). 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 & 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).

CORRIDOR POLICY

Maintaining effective landscape connectivity will often require consideration of the availability and spatial arrangement of habitat patches across state or national boundaries. This requires innovative mechanisms for cross-boundary spatial planning because land is owned by the states. Peninsular Malaysia, comprising 11 of the country's 13 states, has federally mandated National Physical Plans (NPPs) that provide top-down justification for spatial planning, mobilized through the National Physical Planning Council chaired by the Prime Minister (Taib & Siong 2008). The East Malaysian states of Sabah and Sarawak are not currently subject to the federal NPPs. Cross-border connectivity planning in those states, however, is guided by the vision for the Heart of Borneo Initiative, a tri-country program seeking to protect and link the forests of the island of Borneo through sustainable land uses (WWF 2007). At small scales involving multiple stakeholders, innovative measures of land use need to be developed. The National Parks Board of Singapore has been pro-active in connecting its fragmented habitats by constructing corridors along city's streetscape with bird and butterfly friendly plantings (Jain et al. 2014).

Several policy issues must be considered for connectivity strategies either within or between states.

Legal mechanisms for corridor designation

The protection of habitat corridors may occur via numerous mechanisms. The simplest is when the corridor locations are managed by a single private group or government agency amenable to connectivity planning. In North America, for example, The Nature Conservancy often purchases land outright to serve as habitat corridors, or works with landowners to implement conservation easements on corridors (Kiesecker et al. 2007). The CFS connectivity establishment in Peninsular Malaysia also requires a significant amount of land acquisition or gazettement of protected areas, given that most of the corridors are landscapes with multiple types of land tenure including forest reserves, state-owned forests, plantation areas, and villages. The central Sabah corridor is on land effectively controlled by the state via the Sabah Foundation, and required a re-designation of permitted land use activities rather than additional land purchases or multi-stakeholder management plans. For important corridors, management prescriptions can be recommended to ensure the long-term protection of these linkages. In contrast, the Sabah EcoLinc corridor is community-owned and so required extensive consultations with the local communities to determine the degree and extent of habitat protection (Vaz & Agama 2013). Bhutan's biological corridor network is unique in that the initial designation in 1999 was by Her Majesty the Queen Mother Ashi Dorji Wangmo Wangchuck as a "Gift to the Earth from the People of Bhutan", and designated under the 1995 Forest and Nature Conservation Act of Bhutan (WCD 2010). The conservation status of biological corridors in Bhutan is higher than that of forest reserves but lower than that of protected areas (WCD 2010).

Long-term maintenance of political buy-in and leadership

Achieving political buy-in for landscape-scale connectivity and conservation plans will often be difficult and time-consuming (Schwabe et al. 2015). It also cannot be a one-time activity – political buy-in must be maintained continuously. Habitat corridors that required extensive political capital to designate could easily become “paper corridors”, heavily influenced by illegal deforestation and hunting, without continued political support leading to effective enforcement (Jain et al. 2014). Moreover, without continued political support, often both at the federal level for leadership and the state level for implementation, future re-evaluations of spatial plans could reverse current gains. Under strong political pressure for economic development, parks and corridors could be de-gazetted (Bernard et al. 2014) or simply ignored and cleared for agriculture or industry (Hedges et al. 2013; Heng 2012).

Probably the most effective way to achieve long-term political buy-in is for conservation scientists to work with government agency staff to co-produce connectivity plans (Beier 2008; Beier et al. 2015). The persistence of corridor networks in Singapore since the year 1991 (Tan 2006) and their recent unprecedented increase in the form of “Nature Ways”, only seems possible by continued political support and funding to build and maintain such corridors. Such political will is necessary for the long term success of any corridor network. Many of the “Nature Ways” in Singapore have engaged the communities by providing gardening opportunities of bird and butterfly friendly plants. Public participation has reinforced political support of such corridors.

Commitment to implementation and enforcement

The designation of corridors, even if habitat protection is ensured into perpetuity, is not sufficient to ensure that the corridor will provide functional connectivity for the focal taxa (Jain et al. 2014). It is essential to ensure emplacement of a robust management structure and enforcement mechanisms on the ground for the corridors to fulfil their intended functions. Corridors can be degraded via encroachment from unplanned or poorly planned development (Jain et al. 2014). Unsustainable hunting, for local subsistence or markets, is also a major threat to vertebrates in most tropical areas (Milner-Gulland et al. 2003), and could be particularly severe in narrow corridors that provide easy access to hunters (Brodie et al. 2015b). Several corridors in the CFS receive or have received strong poaching pressure, reducing their effectiveness at supporting wildlife movement (Clements et al. 2010). It is even possible that overhunted corridors could become attractive sinks or "ecological traps" that reduce population viability. According to recent surveys, the most important hurdles to effective enforcement of conservation regulations (such as hunting prohibitions) in Malaysia are, in order of decreasing importance, (i) insufficient resources and capacity for enforcement, (ii) little determent due to weak sentences upon conviction of offenders even though the prevailing laws have high penalties, and (iii) jurisdictional boundaries, and lack of coordination among agencies at both Federal and State level (Nagulendran et al. 2014). We note that, while weak sentences may be insufficient to deter illegal hunting, very harsh sentences may be unlikely to be enforced by authorities –it may be that moderate sentences with an emphasis on restoring the ecological damage are optimal (WCD 2010).

Similarly, implementation of corridors has been difficult in Bhutan. Boundaries are not demarcated on the ground and most corridors do not have a management plan, although these are required under the 2007 Rules on Biological Corridors. In the absence of corridor management plans, many forest management units and community forests were established and infrastructure such as construction of roads, transmission lines have been placed in corridor areas (WCD 2010). Some urgent tasks include establishment of decentralized governance and management systems for individual corridors, integration of corridors into local land use plans and practices, hiring and training of staff, and securing financial resources. Capacity and resources for corridor management on the part of the governments and communities need urgent enhancement. With the high poverty rate (12%), the Bhutan government is striving to improve living standards. Given limited financial and human resources in the government, there is a need for achieving an integrated approach to advancing national and local development along with landscape connectivity for biodiversity conservation.

AWARENESS ABOUT THE IMPORTANCE OF CONNECTIVITY

Awareness on the part of the public and government officials about the need for landscape-scale habitat connectivity is required for legislators to commit political and financial capital to designating corridors. Awareness among local communities, key government agencies with jurisdictions relevant to corridor areas (e.g., ministries of agriculture, forestry, and land planning), and industry stakeholders is particularly critical. In Peninsular Malaysia, the first National Physical Plan required significant awareness-raising and outreach (FDTCP 2010b). There is also a greater need to create cross-sectoral awareness, for example to ensure that the objectives of the National Tiger Conservation and Action Plan in Peninsular Malaysia do not conflict with those of the National Highway Network Development Plan.

Educating the public and policy-makers about the need for landscape-scale connectivity is also important to help overcome potential antagonism towards corridors. Antagonism can stem from different sources. In some cases local communities feel disaffected and disenfranchised from past conservation actions (e.g., the designation of national parks or forest reserves on lands that they claimed traditional title to). In the Sabah EcoLinc, for example, communities resented the nearby Kinabalu National Park, and so the corridor plan involved no new designation of forest reserves but instead relied on community-managed forest instead. Long-term monitoring is needed to ensure the efficacy of such management. Antagonism can also arise at the other end of the economic spectrum, from developers who point to the often massive opportunity costs of corridor designation in the form of lost opportunities for industrial agriculture (Nantha & Tisdell 2009).

Recent surveys suggest that the biggest hurdles to conservation awareness in Malaysia are (i) lethargy and lack of passion among the Malaysian public on biodiversity and environmental issues (ii) the lack of champions or personalities to promote and garner support for conservation, and (iii) lack of training and capacity of officers in charge of public awareness programs to effectively execute their duties (Nagulendran et al. 2014). A conservation group called Borneo Futures has addressed the second point by pairing researchers with a popular Sabahan musician as the public spokesman for the conservation goals. As with political buy-in, awareness can also be greatly improved and maintained by co-production of connectivity plans by conservation scientists and government agency staff (Beier 2008; Beier et al. 2015).

FINANCING CONNECTIVITY PLANS

In addition to political capital, providing legal protection for corridors requires financial capital in order to effectively manage the corridors, purchase the land outright, or defray the opportunity costs incurred by preventing land conversion. Financing plans are too often lacking in corridor schemes. This is particularly true in Malaysia, where state governments have the rights over lands and natural resources including timber, mineral, and water and depend on them for revenue (Clements et al. 2010).

The bulk of the funding for corridor management often comes directly from governments. The CFS initiative implementation is envisaged to run into the end of the 12^{th} Malaysian Plan (2025) and is expected to cost over US $1 billion (MNRE/UNDP 2014). Long-term funding requires the establishment of sustainable financing mechanisms. Some examples of such national-level financing mechanisms exist around the world. Belize and Palau have added conservation fees and green fees respectively to departure taxes payable by visitors upon leaving the country. The fund generated is allocated for conservation (UNDP 2012). Certain areas where development is limited for other reasons, such as in the UNESCO World Heritage city of Melaka (Malaysia) have “bed taxes”, or governmental fees for hotel accommodations. This model could be applied for conservation, whereby a small addition to the existing accommodation tax can be pulled together to create a fund to support protected area and corridor management. “Wildlife bonds”, analogous to Development Impact Bonds and Social Impact Bonds (Warner 2013), could raise money for corridors, as could conservation-fee vehicle license plates, which can generate substantial funding for wildlife conservation in the US (MDJ 2015). None of these, which could systematically and sustainably generate millions of dollars of new funding per year, to our knowledge, have yet been tried for habitat connectivity fund raising in tropical Asia.

In some cases it may also be possible to use payments for ecosystem services to offset the costs of corridor management. Protecting tropical forests for the carbon they store, embodied by the Reduced Emissions from Deforestation and Degradation Plus (REDD+) program, could also be used to help fund habitat connectivity. At a national and regional scale, the location of REDD+ projects is essentially haphazard from the point of view of spatial habitat planning. But there is no reason that REDD+ projects could not be specifically situated to serve as habitat corridors (Brodie et al. 2012). For example, the Central Sabah corridor may be effectively doubled in width and overall extent by the protection of the 1140 km^2 Kuamut Forest Reserve funded by carbon trading. Moreover, based on its on-going project to calculate the nation’s forest carbon stocks (Ngo et al. 2013), the Singapore government could earmark a significant part of the income from emission reduction for protected area and corridor management costs to maintain the ecosystem services (i.e., carbon sequestration) that generate credits for the country.

Finally, we note that refinement of certain certification policies could create mechanisms to generate new habitat corridors without the need for additional funding. Both the Forest Stewardship Council and the Roundtable on Sustainable Palm Oil require the assessment and designation of “high conservation value” (HCV) patches in order to certify timber or palm oil, respectively. But HCV assessments do not operate at a landscape level - the unit of assessment is the estate, forest concession, or plantation. If certification rules were revised to require a consideration of landscape-scale processes, HCVs could be situated so as to act as “stepping stone corridors”, providing broad-scale habitat linkage. A proposed initiative to approach Round Table on Sustainable Palm Oil (RSPO) certification at a jurisdictional level, using Sabah (Malaysia) as a pilot case, would allow HCV assessments at the level of the state (D. Webber, RSPO Secretary General, pers. comm.). This would allow decisions to be made about connectivity at the landscape scale and, through associated compensatory mechanisms, fund forest protection and restoration including the reconnection of key protected areas through the establishment of new corridors.

LESSONS LEARNED

The importance of synchronizing the timing of corridor science and policy

Science and policy are generally performed by different groups and proceed at different paces. This means that if a time comes when there is sufficient political capital to launch a habitat connectivity strategy but there are not enough ecological data to inform the decision-making, the process could be delayed or opt to rely on expert opinion rather than objective analysis. In the CFS and the Sabah EcoLinc projects, for example, the political decisions to designate corridors were made before relevant data were available on where the corridors would best be located. Thus these projects had to devote time and resources to consolidating available data (CFS) or collecting field data de novo (EcoLinc). In Sarawak the reverse occurred –objective analyses of focal species habitat selection for use in corridor planning had been underway for several years during which the state government had little to no interest in conservation (Brodie et al. 2015a; Brodie et al. 2015b). In 2014, under a new government, conservation planning (including large-scale habitat connectivity strategies) has commenced via a collaboration between non-governmental organizations, government agencies, and academic institutions. In general, communication and collaboration via long-term relationships among scientists, policy-makers, and land managers, would reduce delays in enacting corridor plans and their implementation.

Land tenure is a crucial input variable to corridor analysis

Assessments of landscape-scale connectivity and plans for habitat corridors almost always include land use maps (e.g., delineating forest versus agriculture) as inputs to the decision-making process. Land tenure maps, however, may be equally important. The differences between the Sabah EcoLinc and the central Sabah corridor project are illustrative. The EcoLinc, while connecting two government-owned parks, had to pass through areas controlled by local communities who were reluctant to give up their agricultural areas so the corridor had to pass through a narrow bottleneck of remnant intact forest. In central Sabah, the corridor lands were all owned by a single government agency (the Forest Department); when that agency decided to set aside corridors it could do so by executive fiat. Such land tenure information, when publically available (which is by no means always the case in

Asia), could be easily incorporated into circuit-theoretical or other connectivity models, providing target areas for corridors that are much more feasible to enact politically.

The intactness of the region determines optimal corridor design, location and management approach

Land use strongly influences animal dispersal paths (McRae et al. 2008), so optimal corridor locations will differ depending on if the landscape is already degraded (and needs restoration) or still intact but facing imminent degradation. The CFS Masterplan included construction of wildlife underpasses because many of the necessary connections were already severed by roads (FDTCP 2010a). Most of Sarawak has been selectively logged but not yet converted to agriculture (Gaveau et al. 2014), so old-growth forest corridors are generally unavailable but logged forest corridor options are plentiful.

Different types of the corridors require different physical and socioeconomic management approaches

Different corridor management approaches need to be considered depending on the land tenure and land use and socioeconomic situation on the ground. In most cases, a mix of physical and socioeconomic measures are necessary to create functional corridors, as most of corridors are inhabited multiple use areas. Physical measures include measures such as new protected areas as done in the case of Sabah, creation of riparian reserves to secure wildlife corridors and protect water resources, and building of wildlife crossing overpasses and viaducts in critical ecological corridor facing infrastructural barriers as done in some of the CFS corridors, and rehabilitation of degraded forest. Most importantly, these physical measures require long-term management plans if the corridors are effective. Socioeconomic approaches are critical in developing countries in particular, and include ecotourism development and promotion to realize economic benefits from conservation oriented land uses for local communities and enhancement of sustainability of community non-timber forest product harvests, and improvement of plantation estate design and operation to maintain wildlife movement and ecosystem services. In places, socioeconomic measures may need to include actions to abate human-wildlife conflicts. This can include compensation schemes, improvement of farming and land use practices to mitigate human wildlife conflict, awareness programs and community involvement and empowerment.

Evaluating outcomes

The connectivity plans that we evaluated did not include specific desired outputs, making it difficult to monitor their success at achieving their outcomes. Ideally, connectivity plans would include a outputs related to species-specific processes of dispersal and population dynamics, incorporating environmental change and stochasticity (Nicholson et al. 2006), and evaluated with a single "currency" that is transparent, understandable to scientists and managers alike, and addresses the ultimate goal of the connectivity strategy. Perhaps the best such currencies are the long-term probability of metapopulation persistence (Bakker & Doak 2009) or the minimization of long-term extinctions in metacommunities (Nicholson et al.

2006). It may, however, take a long time for extinctions to occur, so landscape-level gene flow could serve as a useful medium-term metric of connectivity (Gregory & Beier 2014).

KNOWLEDGE GAPS

Ranking and prioritizing corridors

Currently there are few standardized, quantitative ways to prioritize the contribution of individual corridors to metacommunity persistence (Nicholson et al. 2006), or to compare the importance of corridors versus other conservation actions, for example setting aside new protected areas. Strategic Conservation Planning (e.g., Fajardo et al. 2014), can be used to rank protected areas (or potential new protected areas) in terms of their contribution to species representation, but cannot assess the probabilities that those species will persist over the long-term. For example, even large, high-quality habitat patches (which have high conservation value on their own) will contribute little to meta-population persistence if they are too isolated, and would thus be of low value for connectivity. If the ultimate goal of a landscape connectivity plan is to ensure long-term metapopulation or metacommunity persistence, individual corridors must be prioritized using metapopulation or metacommunity models.

Determining optimal corridor widths

There are multiple methods (discussed above) for determining locations for corridors to ensure optimal connectivity. But many of these only provide the optimal corridor route – corridors, for example, may be situated to follow "least-cost paths" – but these are one-dimensional lines and it is unclear how far on either side of the line the actual corridor should extend (Beier et al. 2008; Brodie et al. 2015a). Corridors that are too narrow will be highly accessible to hunters as well as vulnerable to edge effects such as fire, wind, and increased mortality of canopy tree species. But wide corridors may be expensive to procure or manage. Moreover, limited political and financial capital may entail tradeoffs between the number of corridors that can be established and the dimensions of each one. Objective tools to determine the optimal widths of a series of corridors in a network are highly needed.

Identifying optimal land use patterns in corridor areas to improve corridor efficacy and socioeconomic benefits

Many corridors are in multiple-use areas with mixtures of production and conservation land uses. In developing nations, governments' top priorities are often poverty reduction, so for corridors to function on the ground stakeholders at national and local levels need to be convinced of corridors' benefits. Given this, a range of socioeconomic research would be useful for corridors, including economic assessments of different land use patterns in corridor areas and comparing scenarios in terms of long-term economic values derived from the area while accounting for biodiversity and ecosystem services values. The Sabah Forest Department is developing an economic model to establish the optimal land use patterns of a multiple use forest landscape to optimize economic and biodiversity conservation benefits of a landscape.

Identifying the optimal mix of "top-down" versus "bottom-up" influence in corridor design and implementation

Some corridors are enacted by simple governmental decree ("top-down" designation), such as the corridors in Bhutan and central Sabah. Others, such as the CFS, are federal administrative approaches that have to be followed through by the states to actually designate corridors. Other plans may be driven by local communities ("bottom-up"); in the Sabah EcoLinc, the planning process was started and driven by a state government agency (Sabah Parks), but most of the land involved belonged to local communities who demanded that no new forest reserves be designated and the management of the corridor be left to the communities (Vaz & Agama 2013). Most connectivity strategies will have at least some mixture of top-down and bottom-up influence. A critical question is, how do different mixtures or types top-down versus bottom-up enactment strategies affect the long-term effectiveness of the corridor? Future monitoring of the various corridors we discuss here will allow us to assess the long-term success of top-down versus bottom-up corridors.

There is some evidence that involving non-governmental organizations (NGOs) in corridor science, policy and implementation can yield positive results. NGO led corridor initiatives may also provide a mix of top-down and bottom-up approaches. For example, Panthera is developing a comprehensive strategy to link core jaguar populations from

Northern Argentina to Mexico under the Jaguar Corridor Initiative through multilateral partnerships, government support and local buy-in (Panthera 2015).

Identifying the optimal mixture of expert opinion versus objective data

The vast majority of habitat connectivity plans rely on expert opinion at some stage of the process, often embedded into otherwise objective quantitative analyses (Beier et al. 2008). The human brain is very good at synthesizing disparate types of data, and it may be that subjective determinations of corridor priorities and optimal corridor locations are just as effective as completely objective data. Or not. Monitoring and future comparisons of the long-term effectiveness of corridors designed with a range of subjective versus objective approaches would provide important insights into optimal corridor design strategies.

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TABLE 1

Information on the six connectivity plans assessed here.

Connectivity plan	Country	Year of establishment	Priority taxa (if any)	Data analyses on which the plan was based	Legal designations and governance	Land tenure & Land use patterns
Biological corridors	Bhutan	1999	Five threatened carnivore species and six threatened ungulate	Satellite imagery and land use maps were used to sketch 14 potential corridors to link existing 10 protected areas.	Designation the Queen under the 1995 Forest and Nature Conservation Act. Rules on Biological Corridors	Predominantly national forest areas with a limited number of villages and settlements

			species	Assessment of the potential corridors was done based on wildlife abundance, topography, fire frequency, forest condition, and human disturbance	2007 provides framework for corridor governance and management	
Central Forest Spine Masterplan	Malaysia	2010	Elephant (*Elephas maximus*), tapir (*Tapirus indicus*), tiger	Data on existing and planned land use, known wildlife habitats, legal status of the land, size of forest	State governments not legally bound to implement because it is a federal government plan;	Most of the land between forest fragments are forest reserves that have been selectively logged, although some have been

			(*Panthera tigris*), and gaur (*Bos gaurus*)	fragments, and areas with human-wildlife conflicts	funding provided by the federal government	legally clear-felled for plantations
Sabah EcoLinc	Malaysia	2014	None	1 year field data collection on wildlife, flora, human communities and infrastructure, and human-wildlife conflicts	Mixed	Mixed
Central Sabah	Malaysia	2012	Elephants and	Elephant and large	Class I Protection	Part of Sabah's permanent

Corridor			other large mammals (also to improve ecological resilience in the face of climate warming)	mammal surveys. Long term research programme in the Danum Valley Conservation Area	Forest Reserves (buffered by Class II Commercial Forest Reserves)	forest reserve. Area under total forest cover.
Sarawak Landscape Connections	Malaysia	Pending	Six threatened carnivore species	Habitat selection data from widespread camera-trapping was used in circuit-	To be determined; initial proposals to call for land reclassification (to	Most of the land between protected areas state-owned (albeit with numerous unresolved

				theoretical animal dispersal models, in turn used to parameterize meta-population persistence models	increased protection status) by the state	native land claims) and leased as timber concessions (mostly already selectively logged) or other extractive uses
NatureWays and Eco-Link	Singapore	2013	Birds, butterflies, and small mammals	Habitat selection data gathered from camera trapping and visual surveys; corridor locations designated by expert estimation, though National	No legal protection; current government has expressed commitment to conserve for as long as possible	Roadside plantings and wildlife overpass

				Parks Board Singapore may have unpublished least-cost path analysis		