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Discussion

Monitoring ecological consequences of efforts to restore landscape-scale connectivity

David M Watson[a,*], Veronica A J Doerr[b,c], Sam C Banks[d], Don A Driscoll[e], Rodney van der Ree[f,g], Erik D Doerr[b,c], Paul Sunnucks[h]

[a] Institute for Land, Water and Society, Charles Sturt University Albury, New South Wales, Australia
[b] CSIRO Land and Water Flagship, Black Mountain Laboratories, Canberra, Australian Capital Territory, Australia
[c] Research School of Biology, The Australian National University, Canberra, Australian Capital Territory, Australia
[d] The Fenner School of Environment and Society, The Australian National University, Canberra, Australian Capital Territory, Australia
[e] School of Life and Environmental Sciences and Centre for Integrative Ecology, Deakin University, Australia
[f] Ecology and Infrastructure International, Wantirna, Victoria, Australia
[g] School of BioSciences, The University of Melbourne, Melbourne, Victoria, Australia
[h] School of Biological Sciences, Monash University, Melbourne, Victoria, Australia

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ABSTRACT

Managing and restoring connectivity that enables wildlife movement through landscapes is the primary approach to reduce harmful effects of habitat loss and fragmentation. Improved connectivity is also increasingly invoked as a strategy to mitigate negative impacts of climate change by enabling species to track preferred environments and maintain evolutionary processes. Although initiatives to improve connectivity using restoration are becoming commonplace, we do not know how successful these actions are, nor which mechanisms underlie biotic responses.

Most ecological monitoring focuses on site condition or quality rather than those landscape-scale processes that connectivity is intended to facilitate. To assess biodiversity responses to connectivity initiatives, we argue that new monitoring approaches are needed that distinguish the roles of connectivity restoration from those of habitat augmentation or improvement.

To address this critical gap, we developed a conceptual model of the hypothesised roles of connectivity in complex landscapes and a linked framework to guide design of connectivity monitoring approaches in an adaptive management context. We demonstrate that integrated monitoring approaches using complementary methods are essential to reveal whether long-term landscape-scale goals are being achieved, and to determine whether connectivity management and restoration are the mechanisms responsible.

We summarize a real-world example of applying our approach to assist government develop a monitoring plan for a large-scale connectivity conservation initiative in the Australian Capital Territory. As well as highlighting the utility of the framework to help managers make informed choices about monitoring, this example illustrates the difficulties of convincing funding bodies to include monitoring in project budgets and the questions more likely to be answered with limited funds.

Synthesis and applications. Implementing an effective strategy to monitor connectivity conservation initiatives necessarily involves more work but we argue it is an essential investment rather than an additional cost. By optimizing allocation of limited monitoring resources, we can more effectively implement management that improves functional connectivity, and understand how changing connectivity affects population persistence.

1. Introduction

There has been a worldwide shift away from managing biodiversity within individual protected areas toward whole-of-landscape approaches (Worboys et al., 2010). This is partly because individual reserves are generally too small to support viable populations of many species, so multiple patches need to be connected by movements of individuals and genes to ensure persistence (Crooks and Sanjayan, 2006; Hilty et al., 2006). Moreover, with climates changing at unprecedented rates, the future of many ecosystems (even biomes; Moen et al., 2014) depends on the ability of species to adapt or track shifting regions of

* Corresponding author.
E-mail address: dwatson@csu.edu.au (D.M. Watson).

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habitat suitability. Adaptation to new climates and range-shifting are more likely if populations are functionally large and genetically diverse, both of which are facilitated by ecological connectivity (Sgrò et al., 2011; Driscoll et al., 2012).

This growing appreciation that effective conservation needs large, connected populations has led to landscape-scale connectivity initiatives (or 'connectivity conservation' initiatives; Worboys et al., 2010) proliferating in governmental and non-governmental programs (Fig. 1). Several countries base their national conservation strategies on large-scale connectivity (e.g., DeClerck et al., 2010), with concepts like 'defragmentation' and 'rewilding' being increasingly used to frame policy discussions (Fischman et al., 2014; Drenthen and Keulartz, 2014; Nogués-Bravo et al., 2016). Rather than being motivated by explicit research questions, the intent is usually to manage or restore structural connectivity (physical links between areas) to facilitate movement of individuals and/or genes through the landscape or support large-scale abiotic processes (Soulé et al., 2004). Connectivity is typically viewed in terms of structural measures of habitat (e.g., tree-cover) but such measures may not relate directly to

Fig. 1. Top: the Coto Brus valley on the Costa Rica-Panama border, a region where strategic restoration efforts have re-established connections between the Talamanca Range in the background and the Osa Peninsula, linking these two extensive reserves to the Mesoamerican Biological Corridor spanning eight countries. Large-scale monitoring is required to determine whether restoration of high elevation forests is more important for species persistence than augmenting extent of intervening lowland habitats. (Photo DM Watson). Bottom: Riparian corridor in farmland in south-eastern Australia, where revegetation efforts are focused on augmenting existing linear features in the landscape, increasing woodland habitats and facilitating animal movements as part of the continental-scale Great Eastern Ranges Initiative. Long-term monitoring is required to identify which species do not use linear features for movement, and may require targeted translocation to effect genetic interchange and minimise local extinctions (Photo M Crane, used with permission).

movement or permeability (Kadoya, 2009). That is, *structural* connectivity need not beget *functional* connectivity and the conditions required for movement by species vary widely, even within the same region (Amos et al., 2014; see 'Definitions of connectivity concepts' section, below). Furthermore, movement needed to support ecological and demographic processes may differ from that needed to support evolutionary processes (Lowe and Allendorf, 2010). Thus monitoring the ecological and evolutionary outcomes of attempts to enhance connectivity is critical to understand which approaches actually achieve their intended purpose.

A major impediment to monitoring connectivity conservation initiatives is that existing approaches to ecological monitoring focus on quantifying changes in metrics such as abundance of target species, species occurrence at patch scales (Worboys et al., 2010) or indirect measures such as habitat extent and configuration (Tischendorf and Fahrig, 2000). While these may be among the desired outcomes of connectivity management initiatives, such approaches do not quantify changes to connectivity nor their influence on biodiversity or ecological dynamics (including modified fire or flow regimes). Moreover, indirect measures of connectivity cannot distinguish proximate changes to populations and ecological processes from effects of habitat augmentation and/or improvement (Driscoll et al., 2014). Thus, conventional inventory- and habitat-based methods are often inappropriate for monitoring connectivity—misaligned with the immediate objectives of connectivity management and the spatial and temporal scales over which actions are expected to have desired effects (Kadoya, 2009; Gregory and Beier, 2014). New monitoring approaches are required to generate consistent and comparable measures of functional connectivity. An integrated approach is also critical to working across the spatial and temporal scales involved to inform on-ground management and restoration efforts in the context of landscape-scale conservation.

Implementing an effective strategy to monitor connectivity conservation initiatives necessarily involves more work but we argue that it is an essential investment rather than an 'added extra'. Currently, we have no way of judging which on-ground method has the greatest effect on a population, how to make methods work more effectively, or whether these interventions are addressing the long-term objectives of initiatives. In addition to generating information critical for reporting and evaluating effectiveness for particular projects, monitoring multiple initiatives using comparable approaches would enhance our generalized understanding of *how* connectivity affects populations. For example, are more connected populations necessarily more resistant to stochastic events; does increased connectivity across landscapes reduce the likelihood of invasion by exotic species and resultant changes to community dynamics? By measuring relevant response variables consistently at multiple scales across multiple systems, the mechanistic basis of observed patterns can be revealed, and generalized answers to these questions will emerge, improving our ability to make robust predictions and extrapolate projected outcomes to new sites, species or systems.

To improve connectivity monitoring strategies, we developed a process to guide decisions about what, where, when and how to monitor connectivity management and restoration. Rather than a generic "how to design a connectivity conservation monitoring strategy" or comparing the pros and cons of particular methods or objectives, we provide a novel framework for biologists, conservation managers and policy makers to align objectives of any initiative with planned actions, allowing them to determine how best to monitor the effectiveness of those actions in achieving the stated objectives. We build a conceptual model that makes explicit the many hypothesised links from on-ground connectivity management to organismal movement to the demographic parameters that define population processes and finally to the ultimate conservation outcomes intended. We embed this model within an adaptive management framework (Westgate et al., 2013) to provide a decision-support tool that links objectives to achievable monitoring goals, advising on the most appropriate methods to use for understanding, managing and reporting effects of connectivity restoration. We provide a real-world example of the mismatch between best-practice monitoring applying our approach and the actual approach adopted, comparing how the two strategies relate to aspirational and practical objectives. Our model and decision framework can be used to coordinate monitoring programs to yield generalisable conclusions from diverse conservation initiatives while addressing some of the most fundamental questions in ecology (Sutherland et al., 2013).

2. Definitions of connectivity concepts

Any discussion of connectivity must begin by clarifying terminology, as key terms have been variously used in the literature. In our conceptual model and decision framework, we use the following definitions:

Structural connectivity refers to the physical arrangement of habitats within a landscape, and is typically measured as a landscape pattern without regard to species-specific movement processes or habitat needs (Tischendorf and Fahrig, 2000). Some recent treatments of the concept account for heterogeneity in vegetation type and include landscape features that provide functional connectivity between populations without necessarily providing 'habitat' themselves (Doerr et al., 2014). For example, crossing structures installed to make roads more permeable to animal movement provide connectivity without changing the amount of habitat available (van der Ree et al., 2015).

Functional connectivity is a species-specific concept referring to the capacity of a landscape to facilitate effective movement by organisms (Tischendorf and Fahrig, 2000), including everyday movements and dispersal by individuals (Pe'er et al., 2011), and 'whole of population' movements such as migration.

'Everyday' or 'maintenance' movements relate to individuals, typically within an established home range, accessing resources required for survival. These movements are typically short-term events associated with behaviours like foraging, mating or social behaviour (Roshier and Reid, 2003). Thus, functional connectivity as it relates to everyday movements has implications for resource availability, social behaviour and reproductive success.

Dispersal is the movement of individuals away from an origin (Lowe and McPeek, 2014), commonly occurring as a discrete event in an animal's life, such as movement from birthplace to breeding location or from one breeding location to another. The spatial scale of dispersal events may overlap with the scale of everyday movements, but dispersal often occurs over larger scales within or among populations. Dispersal may be constrained by a lack of structural connectivity of landscapes (Doerr et al., 2010), with implications for demographic and genetic processes.

Gene flow is the movement of genes within and among populations (Slatkin, 1985; Neigel, 1997) facilitated by movement of individuals or gametes, such as mating forays leading to dispersal of gametes (Double and Cockburn, 2000) or pollen transfer in plants. Gene flow can influence demographic processes via inbreeding effects on survival and reproductive success (Keller and Waller, 2002), and evolutionary processes through effects on genetic diversity within populations, and adaptive differentiation among populations (Kawecki and Ebert, 2004).

Migration is used here to describe the regular (e.g., seasonal) or irregular movement of whole populations of animals, usually in response to environmental change or resource availability (Roshier and Reid, 2003; Dingle and Drake, 2007). Although migratory species are typically highly vagile and conservation actions commonly focus on habitat management at either end of the migration process (Martin et al., 2007), functional connectivity can be affected by the permeability of migratory pathways (Olsson and van der Ree, 2015) or threats to migration stopover sites (Mehlman et al., 2005).

Range shifts describe changes in the boundaries of species distributions, including contraction to a subset of an existing distribution and expansion into previously unoccupied regions (Dingle, 1996). In the context of connectivity conservation initiatives, the ability to colonise newly suitable habitat with changing environmental conditions is a major consideration (Opdam and Wascher, 2004).

3. Connectivity in complex landscapes

Landscape managers often assume that the relationships are relatively direct between on-ground actions to improve structural connectivity and long-term goals such as maintaining population viability and evolutionary potential, yet ecological theory suggests otherwise (Roshier and Reid, 2003; Bowler and Benton, 2005; Pierson et al., 2015 and references therein). Changes to connectivity are expected to have direct, proximate effects on movement processes, with the ultimate outcomes on population persistence and species richness over the longer-term depending on a complex suite of interacting intermediary population processes mediated via life history traits, demography and genetic variability (Fig. 2). Actions to manage or restore structural connectivity are undertaken with the intent of affecting population-scale movements which are then expected to influence births, deaths, immigration and emigration, resulting in population-level outcomes and other long-term aims of landscape-scale conservation initiatives. Note that each arrow in the diagram represents a hypothesis. For connectivity restoration to achieve the goals commonly desired, at least one full set of links between actions and long-term outcomes (a minimum of 4–5 hypotheses) must be true. In reality, connections between actions and outcomes may be indirect, diffuse, mediated via interactions or iterative feedbacks, or even non-existent. By integrating on-ground actions with long-term outcomes via population processes, the conceptual model makes ecological theory relevant for management, clarifying how changes to animal movements are thought to underpin population viability (Fig. 2). An explicit but simple representation like this can inform land managers and support development of appropriate and measurable monitoring targets to further our understanding of actual links between each level of the model (Westgate et al., 2013; Fischman et al., 2014).

In particular, our conceptual model makes it clear that no single monitoring method can assess which on-ground actions positively influence long-term landscape-scale goals. Rather, monitoring can be conducted at any level of the model depending on the objectives of the monitoring program (e.g., learning, improving, reporting), and each individual level reveals only part of the story. For example, consider two widely-used approaches in landscape-scale ecology: measuring movement and estimating occurrence patterns of a threatened species. Measuring movement through different types of managed or restored structural connections is an ideal way to learn about the immediate effectiveness of on-ground actions, thus enabling adaptive management. However, measuring movement provides no direct information about long-term goals related to improved population survival and thus cannot be used for reporting on long-term outcomes. Conversely, estimating occurrence at the landscape scale can serve a reporting function by tracking potential improvements in distributional extent and population size—common long-term goals (Mayer et al., 2005; Fleishman et al., 2006). Yet estimating occurrence cannot serve a learning function because it cannot determine whether connectivity actions were responsible for recorded improvements. Many on-ground actions will occur in a given landscape, so it is rarely possible to disentangle their individual effects. As a result, an ideal monitoring program would comprise multiple components collecting different data at different scales to assess the links between on-ground actions, movement, population dynamics, demography and genetics, and long-term conservation goals like persistence.

4. A decision framework for connectivity monitoring in the real world

Since funds are usually limited, the ideal monitoring program suggested by the conceptual model is unlikely to be achievable within any single connectivity initiative. In this real-world context, informed

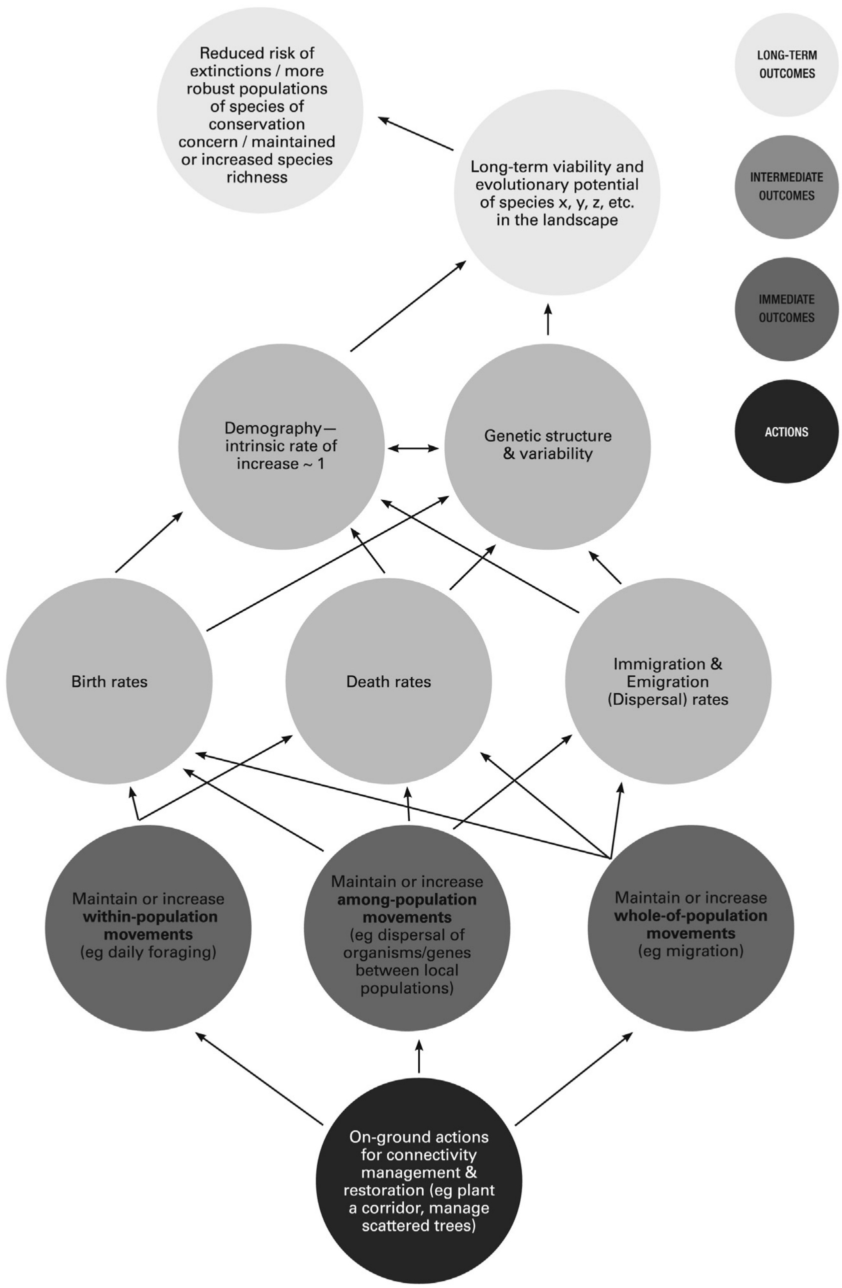

Fig. 2. Conceptual model of the pathways between on-ground actions to manage/restore connectivity and the long-term outcome currently desired by most landscape managers—persistence of diverse species in the landscape. Arrows represent mechanistic linkages (not necessarily positive, nor direct) for the organisms concerned (after Bowler and Benton, 2005; Pierson et al., 2015 and references therein), with three basic types of movement by organisms and their genes depicted: within-population, between-population, and whole-of-population movements. Within-population movements (also called maintenance or 'here and now' movements; Roshier and Reid, 2003) are the smallest-scale movements, relating to the normal ranging behaviour of organisms as they access resources. Among-population movements focus primarily on dispersal and mating forays by individuals, with a typical focus of connectivity management relating to dispersal between local populations in patchy landscapes, while whole-of-population movements include annual feeding/breeding migrations, nomadism and range shifts (Dingle, 1996). Monitoring at only one level of the model (e.g., movement, demography, genetic structure, species richness) necessarily assumes other cause-and-effect linkages in the network. Monitoring at a range of levels is ideal but in practice, managers may need to choose the level that provides the type of information most needed.

decisions need to be made about the type and scale of data that best match the monitoring goals (e.g., learning, improving, reporting) and, thus, which goals are achievable with available resources. We therefore modified an established adaptive management framework (Westgate et al., 2013) to provide a structured approach for using the conceptual model to make informed choices about how to monitor efforts at managing and restoring landscape connectivity (Fig. 3).

Our decision framework connects the multiple levels and relationships of the model with specific decisions about what and how to monitor, to ensure that selected monitoring approaches are feasible, yield sufficient information and align with program goals and monitoring aims. The framework begins with using the conceptual model as a set of hypotheses about how the landscape works to guide on-ground management objectives and actions (the pale and mid-grey components of Fig. 3). It highlights that monitoring ideally commences prior to implementation of on-ground actions, beginning with detailing the monitoring aims. This step is particularly crucial for connectivity conservation, as monitoring different links in our conceptual model (Fig. 2) involves different types of monitoring aims. If those aims are to learn about the immediate effectiveness of actions to manage and restore structural

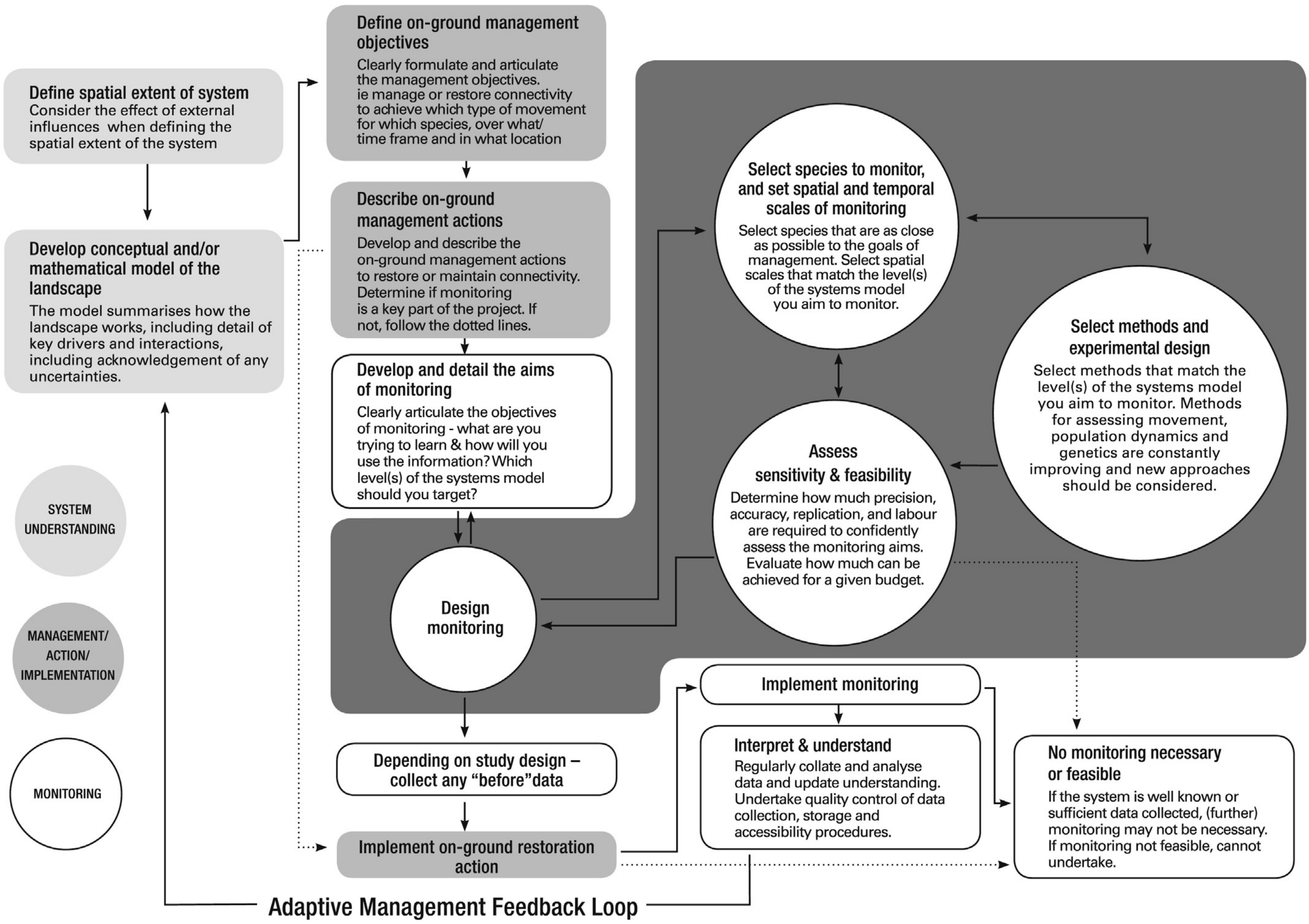

Fig. 3. A decision framework to align on-ground actions with meaningful monitoring in landscape-scale conservation initiatives. Unlike traditional adaptive management models, we integrate a landscape conceptual model with a focus on determining the goals of monitoring, because different goals usually require different approaches. Key features are the iterative process to design monitoring (shown in circles), considering methods that are specifically linked to the goals and scales of monitoring, and the potential need to revise monitoring aims or choose to not conduct monitoring whose goals are unfeasible.

connectivity, the focus is on the links between the bottom two levels of Fig. 2 (actions and immediate outcomes) and data will be required on movement (or a reliable surrogate of movement) at the scale of those individual on-ground actions. If the aim of monitoring is to improve the model itself, the greatest number of links and uncertainties in the relationships are in the middle sections of Fig. 2, suggesting that demographic data will be required at population scales. Finally, if the aim of monitoring is to report on long-term outcomes, the model suggests that data will be required on population viability for multiple species and evolutionary potential at landscape scales.

Clarity about the aims of monitoring leads to an iterative loop of aligning choices regarding species, scales and methods to fulfil those aims (white circles within the dark background in Fig. 3). In connectivity conservation, this step must be iterative because the sensitivity and feasibility of each method may mean that alternatives need to be selected, and even that the initial aims of monitoring require revision. It may not be possible to achieve any of the monitoring goals given available resources, and so the decision framework includes a possible end point that no monitoring be undertaken. If methods can be chosen that align with achievable and desirable monitoring goals, then monitoring can be implemented. The decision framework incorporates classic adaptive management steps to ensure monitoring data are interpreted and understood in order to implement more of the actions that were successful (if monitoring to learn), revise the conceptual model (if monitoring to improve), and/or report on outcomes (if monitoring to report).

Regardless of the specific monitoring choices made using the framework (Fig. 3), there are two basic monitoring design principles to which all connectivity monitoring programs should adhere. First, monitoring should include habitat-matched ‘do nothing’ control areas. To make defensible statements about relating ecological change to altered connectivity, there must be ‘do nothing’ areas where background changes are measured in the absence of management actions (Popescu et al., 2012). Convincing granting bodies and other authorities to devote resources to measure population processes outside the area of interest, particularly at landscape scales, may be challenging, despite its fundamental importance (Westgate et al., 2013).

A second fundamental monitoring design principle is to match the spatial and temporal scales of monitoring to objectives. Monitoring at each level of the conceptual model (Fig. 2) requires focus at different spatial scales. Movement is often best assessed between two sub-populations or two habitat patches as intervening connectivity characteristics can be explicitly identified (Doerr et al., 2010; Gregory and Beier, 2014). Intermediate outcomes are all at the population level and should thus be assessed over multiple sub-populations or patches (Harrisson et al., 2013; Amos et al., 2014). Long-term goals like maintaining or increasing the number of native species with viable populations should be assessed across the entire initiative. In addition, temporal scale should be considered explicitly—in terms of the timeframe of the initiative as well as projected change in ecological processes. Considering the generation time of resident organisms clarifies which taxa are more likely to have a measurable response within the time-scale of an initiative, and thus be instructive species to monitor.

5. Methods to monitor movement

Multiple methods are available for monitoring at each level of the model, with trade-offs between the complexity/expense of the method and the quality of the information/depth of understanding obtained. There is often an assumption that survey data on species occurrence (and thus tracking distributions and diversity for reporting purposes) are cheaper and easier to collect, making monitoring choices a foregone conclusion based on feasibility and cost. However, new methods for collecting data on movement and population demography are continually becoming available (Holland and Wikelski, 2009; Mennill et al., 2012; Kool et al., 2013; Bird et al., 2014; Driscoll et al., 2014). Thus, monitoring at any level of the model—to learn about actions, improve understanding, or report—is increasingly feasible.

Directly measuring movement using mark-release-recapture, genetic markers (assignment tests, parentage tests), radio telemetry, GPS and satellite tracking all provide different degrees of knowledge of movement paths. This provides the flexibility to tailor sampling efforts to balance available funding and the resolution required to make management decisions. GPS and satellite tracking can provide virtually continuous paths for animals large enough to carry tracking devices, providing insights into which landscape elements support movement (Krieger et al., 2012). Small animals and most plant propagules cannot yet be continuously tracked by GPS although high sampling rates using radio telemetry can provide reasonable approximations (Doerr and Doerr, 2005; Doerr et al., 2011). The main limitation of studies that attempt to observe dispersal directly is that, even for large animals, it is difficult to sample enough individuals over sufficiently long time periods and large enough spatial scales. Consequently, sporadic long-distance movements may go undetected and dispersal will be prohibitively difficult to estimate accurately (Kanno et al., 2014).

Genetic data can eliminate the need to recapture individuals and can be highly informative about dispersal. Landscape genetic approaches can provide information on the *relative* permeability of landscape elements to movement (Landguth et al., 2010a, but see Graves et al., 2013), and genetics can also provide estimates of *absolute* dispersal rates. The latter can be estimated with *direct* genetic approaches to detect individual dispersal, such as assignment tests or genetic mark-recapture (Stow and Sunnucks, 2004; Walker et al., 2006; Banks and Lindenmayer, 2014), and *indirect* approaches that use computational modelling (such as Approximate Bayesian Computation) to estimate the demographic rates underpinning observed genetic patterns (Jaquiéry et al., 2010). For indirect genetic approaches, it is important to understand the temporal scale (i.e., number of generations) for which the various genetic metrics are sensitive to dispersal (Broquet and Petit, 2009) and the potential lag in genetic pattern following changes in dispersal (which may differ if dispersal increases or decreases in response to management; Landguth et al., 2010b).

Large datasets of species presence/absence can inform indirect inference about how patch isolation, condition and landscape features like structural connectivity influence colonisation and extinction risk based on which patches are occupied and unoccupied. If collected consistently across multiple small-scale projects, occupancy and associated environmental data can be combined into larger analyses of movement and population trends (Doerr et al., 2011). A key limitation is that no direct information is available on the routes used, so inference on relationships between on-ground actions and movement can be drawn only where comparisons are made between different clearly identifiable types of structural connectivity.

Stochastic patch-occupancy models can explore immigration and emigration rates and simulation models can predict dispersal for species with well-understood mechanisms of movement, either by simulating larger landscapes based on smaller scale direct tracking (Severns et al., 2013) or by simulating movement of organisms that flow with wind or water (Cabral et al., 2011; Jacobi and Jonsson, 2011). Such modelling approaches could be used to evaluate expected changes in movement given particular management interventions, and to assess how movement influences population processes (Fig. 2).

In the absence of actual evidence about movement, it is tempting to rely on expert opinion or inferences based on species characteristics. Species traits can provide insight into how movement is influenced by changes in the landscape. Volant species, water-born propagules and other functional groups can be highly dispersive, enabling, for example, rapid recolonisation of degraded landscapes or restored areas (Moir et al., 2005; Barnes and Chapman, 2014; van Dijk et al., 2014). It may be possible to monitor changes in connectivity by combining trait information with targeted occupancy data. For example, arrival of species with traits associated with poor dispersal into areas where they were previously absent might indicate high connectivity (e.g., Razeng et al., 2016). Expert opinion might not improve movement estimates, and can make them worse (Seoane et al., 2005; Stevens et al., 2010; Zeller et al., 2012). These best guesses may be helpful in weighing up whether a management action is likely to improve or worsen connectivity, but predictions derived from expert opinion should be verified using other methods.

6. Our decision framework in practice

The Australian Capital Territory (ACT) government is consolidating and connecting over 60,000 ha of remnant box-gum grassy woodland along an urban to rural gradient. The ACT approached two of us (V. & E. Doerr) to develop a plan for monitoring the landscape-scale outcomes of this program of work with a particular focus on improvements in connectivity. We present this plan as a worked example of how our conceptual model and decision framework can inform choices about connectivity monitoring with limited resources, illustrating how to minimise this mismatch.

6.1. System understanding and management implementation (pale and mid-grey components of Fig. 3).

The extent of the system was defined by political boundaries. Our conceptual model (Fig. 2) represents what the ACT was aiming to achieve, including increases in all three types of species movements (which may vary among landscape-scale conservation initiatives). Both conceptual and spatial connectivity models had already been developed to clarify anticipated relationships between on-ground actions and movement of biota (Doerr et al., 2010; Barrett and Love, 2012). The ACT undertook strategic revegetation in areas identified in the models as having high connectivity value as well as in areas where the models suggested a small restoration of structural connectivity would result in large improvements to functional connectivity. Thus, on-ground management actions comprised plantings to enhance existing connections as well as plantings to create new connections between woodland remnants.

6.2. Develop aims of monitoring

Consultation revealed two primary aims for the monitoring program. First, information on the general persistence of native species and on overall landscape-level species richness was needed to help meet the ACT's mandated federal reporting obligations (i.e., data to track and report on long-term outcomes in Fig. 2). Second, assessment of the relative effectiveness of different management actions (enhancing vs. creating connections) to support movement (the link between the lower two levels in Fig. 2) was needed. Using Fig. 2 to guide this conversation assisted in clarifying various potential aims of monitoring and why complementary methods might be required for each.

6.3. Design monitoring using the iterative loop (circles with the dark grey background in Fig. 3)

We first explored ideal species, scales and methods for monitoring, and then engaged the ACT in a frank discussion of sensitivity and feasibility (including revisiting the monitoring aims) to settle on a final design. The ACT initially hoped to monitor birds, mammals, reptiles and plants at both whole-of-landscape and individual connection scales to meet their aims of landscape-level reporting on outcomes and learning about the effectiveness of different connectivity actions. However, assessments of sensitivity and feasibility identified multiple barriers to achieving each of these monitoring aims. Most importantly, an extremely limited budget for monitoring was stipulated by the external agencies funding the work. To assess landscape-scale aims with sufficient sensitivity would require at least a moderate number of replicate managed landscapes plus a complementary set of paired control landscapes. Only 3–4 landscapes are to be managed for connectivity improvement, so only large effects are likely to be detectable, and few (if any) landscapes are available where no on-ground works are planned. Similarly, the number of sites for monitoring movement through enhanced or created connections is limited by the number of participating land-owners. Furthermore, achieving both monitoring aims for all organismal groups would require long-term data, since tree and shrub plantings may not be sufficiently mature for 10–20 years to provide functional connectivity for species of interest. Thus, the feasibility assessment conducted in the context of the conceptual model and an explicit understanding of monitoring aims (learning and reporting) made it clear that only a subset of monitoring goals could be achieved with the available resources.

The decision framework thus helped to focus on a subset of achievable monitoring goals and methods. It also revealed significant opportunities to develop partnerships and alternative approaches for minimising the gap between ideal and achievable monitoring. Specifically, the ACT revised their monitoring aims to focus primarily on a qualitative approach to landscape-level richness for mandated federal reporting (i.e., description of observed trends without the robust sample sizes required for formal statistical analysis). That is, despite substantial investment in connectivity, they chose not to use their main resources to monitor the immediate outcomes of connectivity restoration in order to learn which actions were best, but rather to simply track the long-term landscape-level outcomes. Secondary aims, such as analysing determinants of species richness, estimating population persistence, and site-based monitoring to assess the relative effectiveness of different actions, were then planned to be addressed through partnerships.

6.4. Final design

To achieve the revised primary monitoring aim but still provide components to work toward achieving secondary aims, the adopted monitoring design involved four elements:

1. *Landscape-scale bird surveys to track species richness*. These could be performed by citizen scientists and summary statistics calculated to guide qualitative descriptions of landscape change (the long-term outcomes in Fig. 2) for reporting. The lack of fragmented landscapes where on-ground works were not conducted led to the use of reference landscapes (i.e., similar but largely unfragmented areas where management/restoration is not required) to provide an untreated comparison. This supports narrative reporting but is unable to indicate whether on-ground actions to enhance or restore connectivity lead to higher species richness. The use of the conceptual model and decision framework made that clear to the ACT government.
2. *Nested design to provide initial site-scale data for assessing effectiveness of connectivity management actions*. By placing some sampling sites for landscape-scale surveys within areas where connectivity actions were and were not undertaken, data on species presence in a limited number of connections can be obtained. Assuming that data on presence in connections can be used as a coarse surrogate for movement through those connections, these data will provide the building blocks for eventual analysis of the relationship between on-ground connectivity actions and their movement consequences (the bottom two levels of Fig. 2) once sufficient sample sizes are available.
3. *Influence existing partnerships to monitor persistence of additional species groups and build sample size of connectivity management sites and landscapes*. Our conceptual model (Fig. 2) provides a framework for discussions with the ACT's existing research partners about research projects that would effectively complement the base monitoring plan. It can also help guide partnerships with additional landscape-scale conservation initiatives to align monitoring toward a coordinated distributed experiment model (Beier and Gregory, 2012; Fischman et al., 2014), building sample sizes to transition to more formal, quantitative analyses.
4. *Use of space-for-time substitution to test connectivity management actions and update model*. We (Doerr et al., 2014) also studied bird occurrence and directionality of movement in areas of the ACT currently predicted to provide connectivity, as well as reference areas predicted not to provide connectivity. This provided a cost-effective alternative to updating the conceptual model without waiting a decade or more for new plantings to begin having an effect.

Overall, the specific choices and final monitoring plan of the ACT government reflect funding constraints, and the primary aim is to inform progress toward landscape-level goals using only a narrative rather than an analytical approach. Narrative approaches may be highly effective for reporting on broad landscape-level trends. The main limitation with this primary aim (which may be common given widespread funding constraints) is that it leaves substantial uncertainty over whether the program of on-ground actions to enhance and restore structural connectivity actually influences movement and is responsible for any changes in species occurrence. Partnerships are thus planned to fill that gap, including attracting new funding through research avenues rather than government land-management avenues. Nonetheless, the process of developing a monitoring approach using our decision framework linked to our conceptual model clarified trade-offs between potential primary aims and prompted new thinking about partnerships and alternative approaches to meet broader monitoring needs. Without our approach, the ACT's monitoring resources would likely have been spread too thinly over multiple aims and multiple species groups, with eventual belated realisation that insufficient information was available to address any monitoring goal.

7. Prospect

Limits to funding and resources may mean that managers themselves will only be able to monitor at one level of the model and likely only for a small range of species. Partnerships with researchers, community groups and citizen science initiatives can facilitate more comprehensive monitoring if explicitly linked (Bird et al., 2014). In particular, this allows comparison of a range of species with different dispersal abilities, helping discern relationships between management actions and multiple types of population dynamics, ultimately linking trends over landscape scales to particular management actions. While many of these types of data might traditionally be collected by researchers, it may be possible to include citizen scientists in the data collection (Watson and Watson, 2015), thereby building local capacity and the social license critical to any initiative's longevity.

As the number of connectivity conservation initiatives grows, so the learning opportunities expand regarding the sensitivity of particular organisms, permeability of particular landscape elements and efficacy of particular management actions. To date, any emergent understanding across initiatives has been informal. By increasing consistency and working toward a standard set of management practices, these initiatives can become progressively more experimental (Fischman et al., 2014). Each initiative need not employ the same design but, by adopting a common conceptual model and monitoring framework, multiple initiatives can collectively contribute to an improved systems-wide understanding. Such a collaborative effort could yield data necessary to address some of our most fundamental and long unanswered questions in ecology, such as how processes at the individual-level affect populations (Sutherland et al., 2013). Long-term archiving of data, metadata, analytical products and planning instruments is essential to maximise comparisons and allow for analyses that draw on multiple initiatives (Tingley et al., 2009). Ultimately, we envisage treating landscape-scale conservation efforts as an informal set of coordinated distributed experiments, collecting monitoring data and analysing it *across* initiatives, yielding improved understanding and more effective management (Beier and Gregory, 2012; Fischman et al., 2014).

Connectivity conservation is genuinely challenging, involving large financial commitments and a vision that extends beyond individual funding cycles, political boundaries, even the lifetimes of people involved in the conception and initial implementation. Because the benefits are potentially so great for safeguarding biodiversity and ecosystem processes over large areas, connectivity conservation should be subject to optimized investment. This must include investment in monitoring to discern whether management is having desired effects, integrating outcomes of these distributed experiments to improve the accuracy of the conceptual model and associated decision-support framework. Building monitoring into all aspects of connectivity conservation can ensure that we harness the scientific potential of the large-scale experiments that landscape restoration can represent, and thus learn how to maximise their on-ground benefits. At the same time, a structured approach as outlined here should promote realistic assessment of what can reasonably be concluded from information provided through monitoring. It can also stimulate new and creative thinking about how to close the gap between achievable monitoring and ideal monitoring that helps us learn about the effectiveness of our actions, improve our understanding, and track our long-term progress toward achieving the vision of connectivity conservation.

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References

Amos, N., Harrisson, K.A., Radford, J.Q., et al., 2014. Species- and sex-specific connectivity effects of habitat fragmentation in a suite of woodland birds. Ecology 95, 1556–1568.

Banks, S.C., Lindenmayer, D.B., 2014. Inbreeding avoidance, patch isolation and matrix permeability influence dispersal and settlement choices by male agile antechinus in a fragmented landscape. J. Anim. Ecol. 83, 515–524.

Barnes, A.D., Chapman, H.M., 2014. Dispersal traits determine passive restoration trajectory of a Nigerian montane forest. Acta Oecol. 56, 32–40.

Barrett, T., Love, J., 2012. Fine Scale Modelling of Fauna Habitat and Connectivity Values in the ACT Region. New South Wales Office of Environment and Heritage, Armidale.

Beier, P., Gregory, A.J., 2012. Desperately seeking stable 50-year-old landscapes with patches and long, wide corridors. PLoS Biol. 10, e1001253.

Bird, T., Lyon, J., Nicol, S., et al., 2014. Estimating population size in the presence of temporary migration using a joint analysis of telemetry and capture-recapture data. Methods Ecol. Evol. 5, 615–625.

Bowler, D.E., Benton, T.G., 2005. Causes and consequences of animal dispersal strategies: relating individual behaviour to spatial dynamics. Biol. Rev. 80, 205–225.

Broquet, T., Petit, E.J., 2009. Molecular estimation of dispersal for ecology and population genetics. Annu. Rev. Ecol. Evol. Syst. 40, 193–216.

Cabral, J.S., Bond, W.J., Midgley, G.F., Rebelo, A.G., Thuiller, W., Schurr, F.M., 2011. Effects of harvesting flowers from shrubs on the persistence and abundance of wild shrub populations at multiple spatial extents. Conserv. Biol. 25, 73–84.

Crooks, K.R., Sanjayan, M. (Eds.), 2006. Connectivity Conservation. Cambridge University Press.

DeClerck, F.A.J., Chazdon, R., Holl, K.D., et al., 2010. Biodiversity conservation in human-modified landscapes of Mesoamerica: past, present and future. Biol. Conserv. 143, 2301–2313.

Dingle, H., 1996. Migration: The Biology of Life on the Move. Oxford University Press, Oxford.

Dingle, H., Drake, V.A., 2007. What is migration? Bioscience 57, 113–121.

Doerr, E.D., Doerr, V.A.J., 2005. Dispersal range analysis: quantifying individual variation in dispersal behaviour. Oecologia 142, 1–10.

Doerr, V.A.J., Doerr, E.D., Davies, M.J., 2010. Does Structural Connectivity Facilitate Dispersal of Native Species in Australia's Fragmented Terrestrial Landscapes? Systematic Review No. 44. Collaboration for Environmental Evidence. http://www.environmentalevidence.org/SR44.html.

Doerr, V.A.J., Doerr, E.D., Davies, M.J., 2011. Dispersal behaviour of Brown Treecreepers predicts functional connectivity for several other woodland birds. Emu 111, 71–83.

Doerr, E.D., Doerr, V.A.J., Davies, M.J., Davey, C., Allnutt, J., 2014. Flyways and Byways: Guiding Restoration of Wildlife Corridors—Monitoring Connectivity Restoration in the Australian Capital Territory. A Report Prepared for the Australian Capital Territory Environment and Sustainable Development Directorate. CSIRO Climate Adaptation Flagship, Canberra.

Double, M., Cockburn, A., 2000. Pre-dawn infidelity: females control extra-pair mating in superb fairy-wrens. Proc. R. Soc. B 267, 465–470.

Drenthen, M., Keulartz, J. (Eds.), 2014. Old World and New World Perspectives on Environmental Philosophy: Transatlantic Conversations. Springer (236 pp.).

Driscoll, D.A., Felton, A., Gibbons, P., et al., 2012. Priorities in policy and management when existing biodiversity stressors interact with climate-change. Clim. Chang. 111, 533–557.

Driscoll, D.A., Banks, S.C., Barton, P.S., et al., 2014. The trajectory of dispersal research in conservation biology. Systematic review. PLoS ONE 9, e95053.

Fischman, R.L., Meretsky, V.J., Babko, A., et al., 2014. Planning for adaptation to climate change: lessons from the US national wildlife refuge system. Bioscience 64, 993–1005.

Fleishman, E., Noss, R.F., Noon, B.R., 2006. Utility and limitations of species richness metrics for conservation planning. Ecol. Indic. 6, 543–553.

Graves, T., Beier, P., Royle, J.A., 2013. Current approaches using genetic distances produce poor estimates of landscape resistance to inter-individual dispersal. Mol. Ecol. 22, 3888–3903.

Gregory, A.J., Beier, P., 2014. Response variables for evaluation of the effectiveness of conservation corridors. Conserv. Biol. 28, 689–695.

Harrisson, K.A., Pavlova, A., Amos, J.N., et al., 2013. Disrupted fine scale population processes in fragmented landscapes despite large scale genetic connectivity for a widespread and common cooperative breeder: the superb fairy-wren (*Malurus cyaneus*). J. Anim. Ecol. 82, 322–333.

Hilty, J.A., Lidicker, W.Z., Merenlender, A.M., 2006. Corridor Ecology: The Science and Practice of Linking Landscapes for Biodiversity Conservation. Island Press, Washington, D.C.

Holland, R.A., Wikelski, M., 2009. Studying the migratory behavior of individual bats: current techniques and future directions. J. Mammal. 90, 1324–1329.

Jacobi, M.N., Jonsson, P.R., 2011. Optimal networks of nature reserves can be found through eigenvalue perturbation theory of the connectivity matrix. Ecol. Appl. 21, 1861–1870.

Jaquiéry, J., Broquet, T., Hirzel, A.H., Yearsley, J., Perrin, N., 2010. Inferring landscape effects on dispersal from genetic distances: how far can we go? Mol. Ecol. 20, 692–705.

Kadoya, T., 2009. Assessing functional connectivity using empirical data. Popul. Ecol. 51, 5–15.

Kanno, Y., Letcher, B.H., Coombs, J.A., Nislow, K.H., Whiteley, A.R., 2014. Linking movement and reproductive history of brook trout to assess habitat connectivity in a heterogeneous stream network. Freshw. Biol. 59, 142–154.

Kawecki, T.J., Ebert, D., 2004. Conceptual issues in local adaptation. Ecol. Lett. 7, 1225–1241.

Keller, L.F., Waller, D.M., 2002. Inbreeding effects in wild populations. Trends Ecol. Evol. 17, 230–241.

Kool, J.T., Moilanen, A., Treml, E.A., 2013. Population connectivity: recent advances and new perspectives. Landsc. Ecol. 28, 165–185.

Krieger, J., Grandy, R., Drew, M.M., Erland, S., Stensmyr, M.C., Harzsch, S., Hansson, B.S., 2012. Giant robber crabs monitored from space: GPS-based telemetric studies on Christmas Island (Indian Ocean). PLoS ONE 7, e49809.

Landguth, E.L., Cushman, S.A., Murphy, M.A., Luikart, G., 2010a. Relationships between migration rates and landscape resistance assessed using individual-based simulations. Mol. Ecol. Resour. 10, 854–862.

Landguth, E.L., Cushman, S.A., Schwartz, M.K., McKelvey, K.S., Murphy, M.A., Luikart, G., 2010b. Quantifying the lag time to detect barriers in landscape genetics. Mol. Ecol 19, 4179–4191.

Lowe, W.H., Allendorf, F.W., 2010. What can genetics tell us about population connectivity? Mol. Ecol. 19, 3038–3051.

Lowe, W.H., McPeek, M.A., 2014. Is dispersal neutral? Trends Ecol. Evol. 29, 444–450.

Martin, T.G., Chades, I., Arcese, P., Marra, P.P., Possingham, H.P., Norris, D.R., 2007. Optimal conservation of migratory species. PLoS ONE 2, e751.

Mayer, P., Abs, C., Fisher, A., 2005. Baselines of biodiversity — the plant species richness of natural forests as a target for nature conservation. In: Marchetti, M. (Ed.), Monitoring and Indicators of Forest Biodiversity in Europe—From Ideas to Operationality. European Forest Institute Proceedings. European Forest Institute, Joensuu, pp. 393–404.

Mehlman, D.W., Mabey, S.E., Ewert, D.N., Duncan, C., Abel, B., Cimprich, D., Sutter, R.D., Woodrey, M., 2005. Conserving stopover sites for forest-dwelling migratory landbirds. Auk 122, 1281–1290.

Mennill, D.J., Battiston, M., Wilson, D.R., Foote, J.R., Doucet, S.M., 2012. Field test of an affordable, portable, wireless microphone array for spatial monitoring of animal ecology and behaviour. Methods Ecol. Evol. 3, 704–712.
Moen, J., Rist, L., Bishop, et al., 2014. Eye on the taiga: removing global policy impediments to safeguard the boreal forest. Conserv. Lett. 7, 408–418.
Moir, M.L., Brennan, K.E.C., Koch, J.M., Majer, J.D., Fletcher, M.J., 2005. Restoration of a forest ecosystem: the effects of vegetation and dispersal capabilities on the reassembly of plant-dwelling arthropods. For. Ecol. Manag. 217, 294–306.
Neigel, J.E., 1997. A comparison of alternative strategies for estimating gene flow from genetic markers. Annu. Rev. Ecol. Syst. 28, 105–128.
Nogués-Bravo, D., Simberloff, D., Rahbek, C., Sanders, N.J., 2016. Rewilding is the new Pandora's box in conservation. Curr. Biol. 26, R87–R91.
Olsson, K., van der Ree, R., 2015. Railways, roads, and fences across Kazakhstan and Mongolia threaten the survival of wide-ranging wildlife. In: van der Ree, R., Smith, D.J., Grilo, C. (Eds.), Handbook of Road Ecology. Wiley-Blackwell, London.
Opdam, P., Wascher, D., 2004. Climate change meets habitat fragmentation: linking landscape and biogeographical scale levels in research and conservation. Biol. Conserv. 117, 285–297.
Pe'er, G., Henle, K., Dislich, C., Frank, K., 2011. Breaking functional connectivity into components: a novel approach using an individual-based model, and first outcomes. PLoS ONE 6, e22355.
Pierson, J.C., Beissinger, S.R., Bragg, J.G., et al., 2015. Incorporating evolutionary processes into population viability models. Conserv. Biol. 29, 755–764.
Popescu, V.D., de Valpine, P., Tempel, D., et al., 2012. Estimating population impacts via dynamic occupancy analysis of before-after control-impact studies. Ecol. Appl. 22, 1389–1404.
Razeng, E., Moran-Ordonez, A., Box, J.B., Thompson, R., Davis, J., Sunnucks, P., 2016. A potential role for overland dispersal in shaping aquatic invertebrate communities in arid regions. Freshw. Biol. 61, 745–757.
Roshier, D.A., Reid, J.R.W., 2003. On animal distributions in dynamic landscapes. Ecography 26, 539–544.
Seoane, J., Bustamante, J., Diaz-Delgado, R., 2005. Effect of expert opinion on the predictive ability of environmental models of bird distribution. Conserv. Biol. 19, 512–522.
Severns, P., McIntire, E.B., Schultz, C., 2013. Evaluating functional connectivity with matrix behavior uncertainty for an endangered butterfly. Landsc. Ecol. 28, 559–569.
Sgrò, C.M., Lowe, A.J., Hoffmann, A.A., 2011. Building evolutionary resilience for conserving biodiversity under climate change. Evol. Appl. 4, 326–337.
Slatkin, M., 1985. Gene flow in natural populations. Annu. Rev. Ecol. Syst. 16, 393–430.
Soulé, M.E., Mackey, B., Recher, H.F., et al., 2004. The role of connectivity in Australian conservation. Pac. Conserv. Biol. 10, 266–277.
Stevens, V.M., Turlure, C., Baguette, M., 2010. A meta-analysis of dispersal in butterflies. Biol. Rev. 85, 625–642.
Stow, A.J., Sunnucks, P., 2004. High mate and site fidelity in Cunningham's skinks (*Egernia cunninghami*) in natural and fragmented habitat. Mol. Ecol. 13, 419–430.
Sutherland, W.J., Freckleton, R.P., Godfray, H.C.J., et al., 2013. Identification of 100 fundamental ecological questions. J. Ecol. 101, 58–67.
Tingley, M.W., Monahan, W.B., Beissinger, S.R., et al., 2009. Birds track their Grinnellian niche through a century of climate change. Proceedings of the National Academy of Sciences USA. 106, pp. 19637–19643.
Tischendorf, L., Fahrig, L., 2000. On the usage and measurement of landscape connectivity. Oikos 90, 7–19.
van der Ree, R., Smith, D.J., Grilo, C. (Eds.), 2015. Handbook of Road Ecology. John Wiley & Sons Ltd., Oxford, UK.
van Dijk, W.F.A., van Ruijven, J., Berendse, J.F., de Snoo, G.R., 2014. The effectiveness of ditch banks as dispersal corridor for plants in agricultural landscapes depends on species' dispersal traits. Biol. Conserv. 171, 91–98.
Walker, F.M., Sunnucks, P., Taylor, A.C., 2006. Genotyping of 'captured' hairs reveals burrow-use and ranging behavior of southern hairy-nosed wombats. J. Mammal. 87, 690–699.
Watson, D.M., Watson, M.J., 2015. Wildlife restoration: mainstreaming translocations to keep common species common. Biol. Conserv. 191, 830–838.
Westgate, M.J., Likens, G.E., Lindenmayer, D.B., 2013. Adaptive management of biological systems: a review. Biol. Conserv. 158, 128–139.
Worboys, G., Francis, W.L., Lockwood, M. (Eds.), 2010. Connectivity Conservation Management—A Global Guide. Earthscan, London.
Zeller, K.A., McGarigal, K., Whiteley, A.R., 2012. Estimating landscape resistance to movement: a review. Landsc. Ecol. 27, 777–797.