

Reintroduction modelling: A guide to choosing and combining models for species reintroductions

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Abstract

1. Species reintroductions are high-investment ecological interventions that require careful planning. Predictive models are useful tools for managing reintroductions.
2. We provide an overview of habitat suitability, dispersal, population dynamics and interspecies models, considering potential uses and limitations of established methods for reintroductions. Furthermore, we include a guide for integrating one or more model types to predict reintroduction outcomes and answer specific management questions.
3. Model utility will be maximized by considering the goals of the reintroduction, attributes of the reintroduced species, threats to persistence and the quality of available data.
4. *Synthesis and applications.* Our synthesis of state-of-the-art ecological models outlines how key ecological models can be applied to reintroductions. Our review can aid practitioners undertaking reintroductions to assess and quantify their data and modelling needs in line with their management goals.

KEYWORDS

biodiversity conservation, conservation management, conservation planning, ecological data, ecological models, predictive models, reintroduction, species management

1 | INTRODUCTION

Conservation reintroductions are the deliberate movement of organisms from one site, for release into its indigenous range from which it has disappeared (IUCN/SSC, 2013). They are a key component of biodiversity conservation (Seddon, Griffiths, Soorae, & Armstrong, 2014). Decisions as to when, where and how to reintroduce are frequently based on limited empirical data. Reintroductions create novel conditions with unexpected dynamics and reintroduced populations out of equilibrium (Roy et al., 2016). Some of these dynamics might be predicted before investing in a reintroduction by applying ecological models using knowledge of species' ecology and conditions in the reintroduction area (Sun et al., 2016). However, as new ecological models are constantly under development, there is an expanding, even bewildering, diversity of approaches available to practitioners.

Effective reintroduction planning often requires more than empirical field data. It is usually impractical to collect the data required to predict accurately how reintroduced species will react to alternative management actions (Duffy et al., 2007) and experimental manipulation can be applied rigorously only in controlled and simplified systems (Giometto et al., 2015). This has resulted in the widespread use of ecological models which combine the best available data with an understanding of ecological mechanisms and a degree of pragmatism to provide useful predictions (Aben et al., 2014). Here, we present a 'shoppers guide' for practitioners interested in applying ecological models to reintroductions, providing a conceptual comparison of models. We review the types of models that might be applied to reintroductions, compare strengths and weaknesses, and discuss how models of different aspects of species ecology can be combined to answer focused management questions. This overview provides a starting point for practitioners to enable them to 'get

their bearings' in the deep, and somewhat murky waters of the ecological modelling literature.

There are four key components to be considered when modelling reintroductions (Figure 1; Guisan & Thuiller, 2005):

1. Habitat suitability: to predict the ability of an area to support reintroduced populations (Gutt et al., 2017).
2. Dispersal processes: to predict the spread of founders from release sites (Aben et al., 2016).
3. Population dynamics: to predict population growth in reintroduction areas (Sewell, Baker, & Griffiths, 2015).
4. Interspecies interactions: to predict impacts of other species, for example, predators, prey, competitors, on reintroduced populations (Laperriere, Brugger, & Rubel, 2016).

We cover these four main components, but acknowledge other factors to consider when modelling reintroductions. For example, disease commonly causes reintroduction failure and models of disease mechanics can identify disease mitigation strategies (Sharkey, 2011). However, disease is not a factor universal to all reintroductions, so we focus on the factors important to all reintroduction programmes.

Advances in computation, data processing and simulations allow the combination of components as nested, interacting aspects of a species' ecology (Aben et al., 2016). Complex feedbacks between components can thus be represented (Zurell, 2017), although some

management questions can be addressed without the need for all areas to be fully nested (see Figure 1).

2 | HABITAT MODELS

In any reintroduction, a typical first step is to identify the quality and spatial attributes of candidate release sites, such as the size and location of habitat patches (Stone & Guy, 2017). Overall habitat quality is often not the primary reason a site is selected (other criteria might include absence of human disturbance or competition from invasive species) but the release site must be able to support an establishing population. Habitat modelling can also provide parameter estimates for other models (e.g. carrying capacity for population models) based on resource availability. Data requirements vary between habitat models, but all require spatially explicit data for attributes such as land cover, altitude, rainfall or temperature, which determine the habitat suitability.

The term 'habitat' is applied vaguely and inconsistently in ecological studies (Stadtman & Seddon, 2018). For simplicity, we use the term to denote the geographical area providing abiotic and biotic conditions for species persistence but omit trophic interactions such as predation. This definition is a geographical projection of a species' fundamental niche, the entire set of conditions under which an animal can survive and reproduce, as factors limiting access to this fundamental niche are best considered in models interacting with the habitat model (Figure 1; Pulliam, 2000).

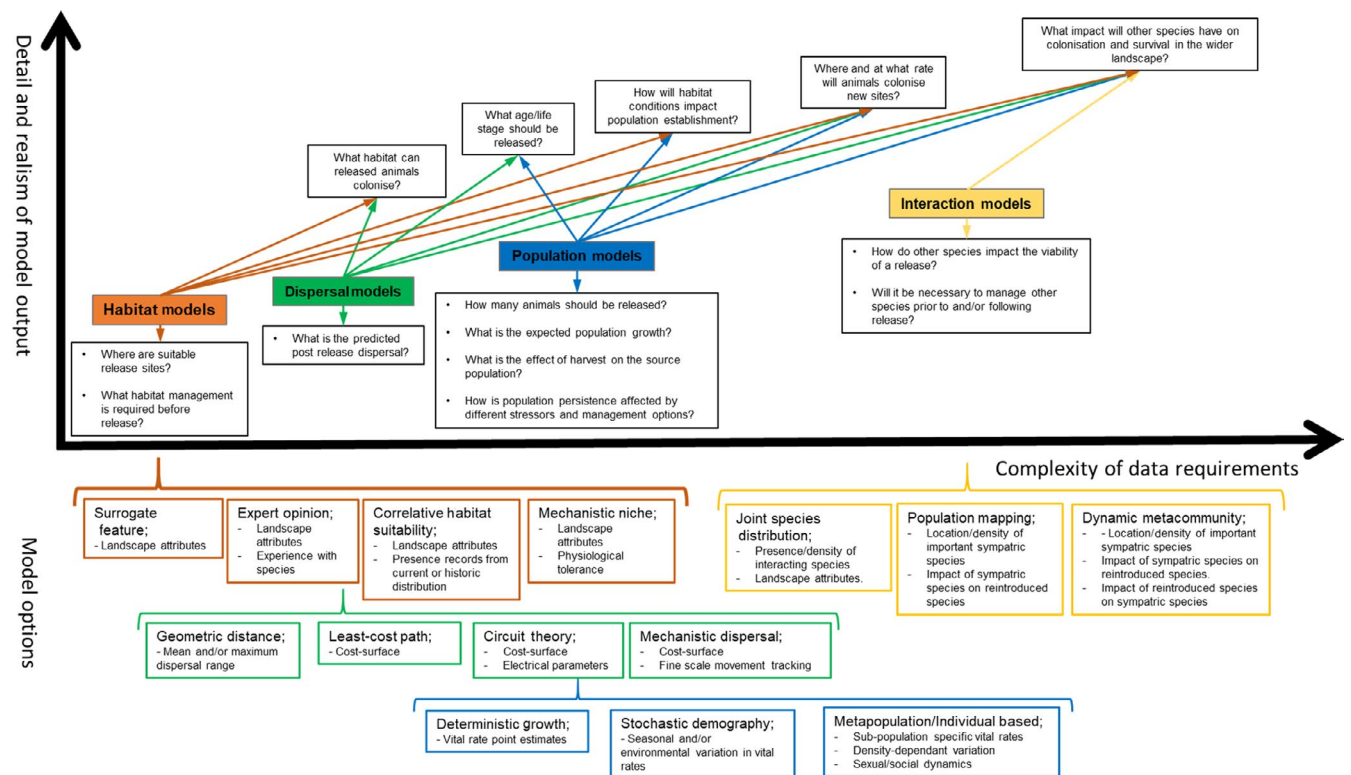


FIGURE 1 Groups of ecological models and key questions for the management of reintroductions they can inform. Arrows indicate which kind of model, or combinations of models, is required for each question. Boxes below the axis identify specific models and their data inputs

The simplest method for estimating habitat structure (location and extent of habitat patches) uses a single landscape attribute as a surrogate, such as the extent of dominant vegetation. For example, grassland extent can be used as a habitat surrogate for grazers, and forest cover for browsers (Zanin, Tessarolo, Machado, & Albernaz, 2017). While surrogates are computationally straightforward, they are also ecologically simplistic and exclude many factors that determine habitat suitability (Stadtman & Seddon, 2018). Surrogates are unlikely to provide enough detail to predict landscape use beyond coarse classifications.

Correlative habitat suitability models provide a more nuanced prediction of habitat structure (Sun et al., 2016). These consider multiple landscape attributes and species location records (e.g. presence-absence data or presence-only data from surveys or observations) to identify habitat based on correlations between local conditions and species distributions (Austin, 2007). Correlative models are commonly used to predict habitat distribution at large spatial scales, and shifts in distribution under climate change (Keith et al., 2008; Phillips, Anderson, & Schapire, 2006). These models assume that the populations from which presence records are drawn are in equilibrium, limited from spreading only by climatic and landscape factors. As this assumption is not upheld for reintroduced populations at establishment and growth stages, care must be taken in selecting species records and explanatory landscape attributes. Correlative models might otherwise mis-identify the dynamic range boundaries of expanding populations as niche limitations (Jiménez-Valverde et al., 2011).

Alternatively, expert opinion can be used to map the occurrence of suitable conditions (Larson, Thompson, Millspaugh, Dijk, & Shifley, 2004). Although lacking statistical rigour, expert-based models can outperform statistical models for some reintroductions as datasets for focal species commonly lack records from locations analogous to release areas. Landscape change since species extirpation often means the release area is a novel environment for the reintroduced species. Thus, correlative models will likely underestimate habitat availability in proposed release locations if the habitat is good quality but outside the range of training data (Jiménez-Valverde et al., 2011). Experts in the ecology of the reintroduced species can provide the knowledge lacking in formalized datasets to make appropriate inferences when quality data are limited. However, the subjectivity of models based on 'opinion' means that comparison between species and landscapes, as well as defining appropriate scaling and thresholds, becomes problematic.

Mechanistic niche models can be used in reintroduction planning to estimate niche requirements from first principles. They infer environmental tolerances from the physiological and biophysical attributes of a species to map their fundamental niche (Peterson, Papeş, & Soberón, 2015). Although these models can overcome the subjectivity of expert opinion, and errors associated with correlative models, their required data are rarely available. Where physiological and biophysical data are available, it is usually only for a few specimens, meaning individual-level variability

is overlooked when inferring population-wide patterns (Peterson et al., 2015).

Current habitat modelling methods provide insight into the spatial properties of habitat for a reintroduced species but assume that landscape and climate attributes are static. Temporal dynamics, including seasonality, succession and climate change, alter the size, location and quality of habitat. This variability has been addressed in some studies by modifying habitat model outputs, mostly with reference to anthropogenic climate change predictions (Dullinger et al., 2012). Creating more realistic, dynamic habitat models remains a challenge because data to detect temporal changes are limited. Metrics such as rainfall and temperature are commonly calculated as long-term averages (Fick & Hijmans, 2017), whereas surveys of attributes such as vegetation and land cover are conducted too infrequently to detect short-term dynamics (Leathwick et al., 2002).

For habitat models to be useful, the spatial resolution of habitat data must be relevant to the scale at which the modelled species exhibits habitat preferences. Ecologically relevant scales often do not overlap with the scale of landscape data recording, or the scale of human modification. Animals can also respond to separate landscape attributes at different scales, so considering a single scale can introduce bias (McGarigal, Wan, Zeller, Timm, & Cushman, 2016). To address this issue, models often choose a spatial resolution by compromising between an estimated functional scale for the species and pragmatic use of available data (Austin, 2007). The development of multi-scale niche models is at the cutting edge of this issue (DeCesare et al., 2012).

Habitat models can identify potential reintroduction sites when applied at national or international scales. Subsequently, they can be used at local scales to identify release sites and lower quality habitat within release areas that might require active management, such as supplementary feeding. Nüchel, Bøcher, Xiao, Zhu, and Svenning (2018) apply a correlative habitat suitability model using contemporary and historical records to identify potential suitable range, a first step in screening for reintroduction sites.

3 | DISPERSAL MODELS

Dispersal is the process of individuals or propagules (e.g. seeds, spores or larvae) moving between patches of habitat. Dispersal mode is a key determinant of habitat use following reintroduction (Ziółkowska, Perzanowski, Bleyhl, Ostapowicz, & Kuemmerle, 2016). In order to map accessible resources for reintroduced populations, dispersal must be considered (Holloway, Miller, & Gillings, 2016). For example, a 'habitat map' might identify high-quality reintroduction areas based on large areas of habitat (Corlett, 2016) but, if dispersal barriers exist, the site could be a poor choice, as founders would be unable to colonize the landscape (Moraes et al., 2018).

In the long term, dispersal also determines how reintroduced species establish metapopulation dynamics, influencing

population viability and determining gene flow across the landscape (Hanski, 1999). Thus, reintroduction programmes should consider long-term and short-term dispersal patterns as these determine population establishment and persistence (IUCN/SSC, 2013).

In the simplest approach, geometric distance models, only the straight-line distance between habitat patches, limits dispersal. These distances are easily calculated (Raines, 2002) but do not consider the way animals move through landscapes. Dispersing animals will choose relatively hospitable areas and avoid dangerous ones; they might use small habitat patches as 'stepping-stones', or follow linear connecting elements (e.g. riverbanks, hedgerows). Failure to account for these processes leads to inaccurate predictions, though there will likely be broad correlation as nearby habitat patches are generally easier for dispersing animals to find and colonize. Population-scale dispersal patterns can be incorporated into spatial distance models using dispersal kernels, distributions describing the range of distances potentially travelled by any individual, where levels of dispersal decline more rapidly with increasing distance between patches (Slone, 2011). As these do not consider structure in the inter-habitat matrix, the areas that are not habitat for the focal species, they are likely to produce poor estimates of dispersal in landscapes with significant structural variation (Keller, Van Strien, & Holderegger, 2012).

Cost-distance models have been developed to account for the structure of the landscape matrix and how this affects the movement of animals (Graves, Chandler, Royle, Beier, & Kendall, 2014). To calculate cost-paths between habitat patches, the landscape is modelled as a cost-surface, where features are scored according to their resistance to movement. The least-cost path is then the route between two habitat patches with the lowest resistance, and dispersal frequency is inversely proportional to this least-cost path. However, least-cost models are structural models and have been criticized for not taking into account the cognitive processes of dispersing animals (Simpkins, Dennis, Etherington, & Perry, 2018). Their main drawback is that cost-distance models assume dispersers have perfect knowledge of the landscape and take detours or pass through bottlenecks to reach certain patches. This can be reasonable, for example where animals use paths marked by conspecifics or follow established migration routes, but often it is not (Mateo-Sánchez et al., 2015). Other methods take more account of the cognitive processes involved in dispersal, but still rely on a cost-surface to quantify the impacts of matrix structure in directing movements. A variety of methods are used to estimate cost-surfaces, including expert opinion (Graves et al., 2014), animal tracking (Cushman, Lewis, & Landguth, 2014), genetic distances (Zeller et al., 2018) and inverting habitat suitability (Keeley, Beier, & Gagnon, 2016). The cost-surface should capture the resistance of matrix elements to species movements to ensure models generate useful predictions (Keeley, Beier, Keeley, & Fagan, 2017). Creating a cost-surface for a reintroduction is likely to face data-limitation issues, like those of habitat models. Landscape resistance must be often inferred from data collected outside of the

release area (from currently occupied areas) and novel landscape features cause issues.

Circuit theory models use the analogy of electrons moving in an electrical system to represent the movement of animals across the landscape (Hanks & Hooten, 2013). Habitat patches are represented as nodes, connected by a resistance surface. When a voltage is placed across the model landscape, this stimulates movement from a point of origin, a power source in the analogy, to a destination, an earth (Cowley, Johnson, & Pocock, 2015). The advantage of circuit theory models over cost-distance models is that rather than modelling dispersal via a single pathway, all routes between two nodes are considered. Use of pathways is weighted according to conductivity (inverse resistance), predicting relative use of all available pathways during dispersal and population radiation (Mateo-Sánchez et al., 2015). The electronics analogy can hamper parameterization and interpretation of the dispersal model, possibly leading to inappropriate model set-up and reduced impact of outputs due to confusion over the meaning of input parameters and output metrics (Hanks & Hooten, 2013).

Another group of advanced models are mechanistic dispersal models, which simulate how individuals make dispersal decisions and interact with landscape features (Bocedi, Zurell, Reineking, & Travis, 2014). These models incorporate knowledge of the landscape by considering dispersal as semi-random diffusion based on erratic motion (Codling, Plank, & Benhamou, 2008). Refinements recognize that animals do not move entirely randomly, with correlated random walk models incorporating a tendency to maintain a consistent heading (Byers, 2001). The most cutting-edge mechanistic models explicitly model movement decisions as having random elements, but influenced by directional consistency, sensory range and a cost-surface (Coulon et al., 2015). Such models require difficult factors such as directional persistence and perceptual range to be estimated (Bocedi, Palmer, et al., 2014). These models are process-based with predictions emerging from species' fundamental traits, rather than population-level inferences. As such, mechanistic models might better predict dispersal patterns in a novel landscape.

Considered in isolation, dispersal models can predict release site-fidelity, aiding managers in determining an appropriate release cohort size for establishment. This utility can be enhanced by incorporating demographic and life-history factors, such as seasons when animals disperse (Hinderer, Litt, & McCaffery, 2017), and incorporating information from habitat models. This can provide specific predictions of how much habitat is available via dispersal. For example, Peters et al. (2015) use coupled habitat and dispersal models for brown bears *Ursos arctos* to identify post-release habitat use.

4 | POPULATION MODELS

Habitat and dispersal models predict the habitat accessible to a founder population, and how they might colonize the wider landscape. But colonization depends on the founder population

providing new dispersers through population growth (Adams et al., 2015). Modelling population dynamics can improve predictions of post-release establishment and spread (Larson et al., 2004; Schurr et al., 2012). Through population modelling, complex processes can be represented, such as metapopulation source–sink dynamics (Hanski, 1999; Lee & Bolger, 2017). These models can predict where stable populations might establish, estimate population growth in different patches and identify where dispersal might establish a sub-population or inter-breeding in a metapopulation (Walker, Marzluff, & Cimprich, 2016).

Population models must be capable of predicting the realized population growth rate in a given setting. The main challenge is identifying factors determining survival and breeding success (Akçakaya, 2000). The simplest population model for most species would use observed population rates for mortality and fecundity in a deterministic linear population growth equation that ignores variation in landscape and environmental conditions. Incorporating factors such as carrying capacity and density-dependent feedbacks require making inferences from census data (Stubben & Milligan, 2007). Further, mortality and fecundity data from a relict range might not reflect post-release responses, as factors constraining population growth might differ between areas. For example, if the relict population persists in suboptimal conditions, the reintroduced population might be freed from environmental constraints (Panfylova, Bemelmans, Devine, Frost, & Armstrong, 2016).

More complex population models express vital rates, that is, birth, death and dispersal, as random (stochastic) responses to local environmental conditions and population density, with the parameters for response functions inferred from census data (Bocedi, Palmer, et al., 2014). These models can also incorporate individual (age, sex, phenotype, personality) and local population effects on vital rates and predict demographics of establishing populations. For a reintroduced population, density is likely to be lower than in the current range, so a response function from that range could yield inaccurate predictions, for example, due to Allee effects (Xia et al., 2013).

Complex population models include metapopulation models and individual-based models (MacPherson & Gras, 2016; Mestre, Cánovas, Pita, Mira, & Beja, 2016). Both can incorporate the effects of local conditions, population density and individual traits when predicting population growth and structure. They differ in the scale at which equations are applied; metapopulation models apply functions at the level of subpopulations, whereas individual-based models simulate every animal within a metapopulation. While metapopulation models are computationally less intensive, the abstraction of patterns to a population scale can make them less intuitive than individual-based models where such patterns arise from individual interactions (Akçakaya, 2000). Both groups of models can be used to predict population growth, as long as factors determining survival, fecundity and dispersal are appropriately represented. Individual-based models are an intuitive choice, as reintroductions will typically involve small populations.

BOX 1 Modelling the reintroduction of the Meadow Brown butterfly *Maniola jurtina* in South West Finland (Heikkinen et al., 2015)

The Meadow Brown butterfly *Maniola jurtina* is a dry grassland specialist in its northern range margin in South West Finland. Dispersal limitation has prevented the species from tracking changing climate conditions. Making it a candidate for assisted colonisation northwards.

Habitat model

The authors determined habitat suitability using correlative niche models (generalized linear models, generalized additive models and generalized boosting method). They refined this climatic suitability to habitat cover using grassland landcover classes. Twelve sites were chosen as release sites for simulations (shown in Figure 2).

Dispersal model

A dispersal kernel was used with a density-independent dispersal rate to simulate radiation from the release sites.

Population model

A female-only individual based model with non-overlapping generations was used to simulate stochastic growth dynamics. Using growth rate (r_{max}) and carrying capacity (K) estimates from a literature search, surveys and expert opinion.

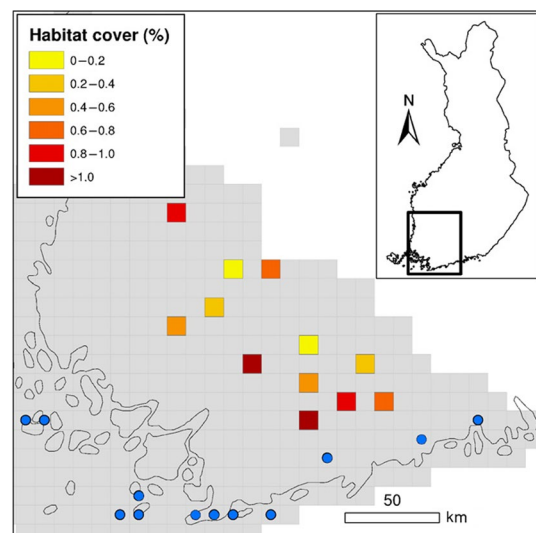


FIGURE 2 From Heikkinen et al. (2015). Distribution of the selected twelve 10 km × 10 km grid cells ('10 km × 10 km landscapes') used in the modelling of translocation potential of *Maniola jurtina* in SW Finland. Cover of suitable habitat in the selected 10 × 10 km cells is shown using a six-level scale. Grey shading indicates climatically suitable area for the species and blue dots (midpoints of 10 × 10 km grid cells) indicate known occurrences in 2001–2010

BOX 1 (Continued)**Integration**

Habitat, dispersal and population simulations were combined using the RangeShifter v1.0 software (Bocedi, Palmer, et al., 2014), to create a spatially-explicit, dynamic metapopulation model to simulate post-release dynamics following the release of 40 females to each of the 12 reintroduction sites.

Results

Simulations highlighted the importance of population growth rate and use of multiple release sites for successful establishment, providing recommendations for management of the proposed reintroduction. Authors highlighted the need for long-term population dynamic data to validate model outputs and for further development of models considering individual variation and genetic effects.

Population models can determine the size of release cohort required for population establishment, with more detailed models also indicating the ideal age/gender balance of this release cohort. Incorporating effects of stressors and management options such as supplementary feeding can give insight into the best management options. When founder animals come from wild sites population models can identify the maximum sustainable harvests for source populations (Dimond & Armstrong, 2007). Combining population models with predictions of habitat quality in the release area allows predictions of local condition impacts on population growth; adding dispersal allows predictions of the rate and pattern of population expansion. For example, Ovenden, Palmer, Travis, and Healey (2019) use an individual-based population model and a mechanistic dispersal model for Eurasian lynx *Lynx lynx* to simulate reintroductions with different founding populations (Also see Box 1 for an example of these models in practice).

5 | INTERSPECIFIC INTERACTIONS

By combining models of habitat, dispersal and population dynamics, temporally and spatially explicit predictions can be made (Adams et al., 2015). While these incorporate details of reintroduced species attributes, they ignore interactions with other species (Dormann et al., 2018). In reintroductions, interactions with introduced species, parasites and humans are often significant and negative (Adams et al., 2015; Corlett, 2016). Combining spatially dynamic models for multiple species is rarely considered due to technical challenges and data requirements and these models remain at the forefront of computational capacity. Nevertheless, they represent the next major development for ecological simulations, and warrant some consideration here.

One developing method that might enable identification of species interaction effects is joint species distribution modelling. These use presence or abundance data for multiple species and

landscape data to identify patterns of co-occurrence not explainable by differences in habitat requirements (Tikhonov, Abrego, Dunson, & Ovaskainen, 2017). However, such patterns are correlational, so these models do not identify causal mechanisms and many processes can produce similar patterns (Dormann et al., 2018). Additionally, correlations in species co-occurrence may also be explained by a responses to an unmeasured variable (Ovaskainen, Rybicki, & Abrego, 2019). They assume species interactions are consistent across all areas, which is often not the case, especially since reintroductions might create novel species interactions (Ovaskainen, Roy, Fox, & Anderson, 2016). Consequently, joint species distribution models should be interpreted with care, and perhaps be used for hypothesis generation rather than directly predicting interactions in release areas (Pollock et al., 2014).

The simplest species interaction models require a population map of interacting species and an estimate of interaction impacts (e.g. on mortality, fecundity and dispersal). Estimates are often uncertain and might not be generalizable (Ovaskainen et al., 2019), or are based on theoretical assumptions (Thompson, Rayfield, & Gonzalez, 2017). These responses can be binary (based on presence/absence) or continuous (based on the population density of interacting species). Numerous interactions can be modelled, including predation, parasitism and competition. This has the drawback of being one-directional and non-dynamic, as interacting species are mapped according to survey or habitat data and would not be influenced by the introduced species (Hale & Koprowski, 2018). Going beyond one-way impact requires much greater modelling effort.

Mechanistic models with two-way species interactions need separate models for each interacting species considered. Prey, competitors, predators and parasites require modelling to the same level as the reintroduced species, and spatial and temporal aspects of interactions must be incorporated (Viljugrein, Lingjærde, Stenseth, & Boyce, 2001). This requires the formulation of complex, interaction terms between each model constructed. Data availability and computational power will limit such spatially explicit metacommunity modelling. Nevertheless, they could provide the most accurate, explicit and useful predictions.

Interspecific models identify how other species will affect the viability of a reintroduction, with more detailed models providing specific predictions of tolerable population sizes for coexistence and indicate the intensity of control required for other species to enhance reintroduction outcomes. When combined with other models to form spatially explicit metacommunity models detailed and specific reintroduction management plans can be identified across large areas and time-scales (Thompson et al., 2017).

6 | PRACTICAL RECOMMENDATIONS

The components of a holistic model to manage species reintroductions have been discussed. We have reviewed the methods available for each submodel (Summarized in Table 1) and described how these could be combined to predict reintroduction dynamics

TABLE 1 Summary of predictive models applied to reintroductions. Cited references are published examples of each model type applied in a reintroduction context

Model group	Model	Strengths	Weaknesses	References
Habitat models	Surrogate feature	Can be applied with limited data (e.g. one landcover class) Analytically simple Suitable for specialized species	Often ecologically simplistic Unsuitable for species with complex or flexible habitat requirements	Rendall, Coetsee, and Sutherland (2018)
	Correlative habitat suitability	Statistically rigorous Based on niche theory and empirical data	Requires data from stable populations to reliably identify niche boundaries for reintroductions	Stone and Guy (2017)
	Expert opinion	Can make inferences beyond limited datasets	Difficulty comparing species and landscapes Inferring beyond broad categorization dubious	Dolný, Šigutová, Ožana, and Choleva (2018)
	Mechanistic niche	Predicts the species niche from first principles Potentially accurate in novel settings	High and specific data requirements Impractical in most cases	
Dispersal models	Geometric distance	Easy to calculate Identifies fragmentation of habitat	Does not consider matrix structure	Howell, Muhs, Hossack, Sigafus, and Chandler (2018)
	Least-cost paths	Considers effects of matrix directing species movement	Does not consider dispersal behaviours Calculation of costs is critical	Alexander, Olib, Bly, and Restani (2016)
	Circuit theory	Enables simultaneous consideration of available dispersal pathways	Parameterization and outputs can be obscure	Hinderer et al. (2017)
	Mechanistic dispersal	Detailed consideration of species behaviour during dispersal	Requires knowledge of perceptual range and turning frequency	Haydon et al. (2008)
Population models	Deterministic linear growth	Computationally simple Direct extrapolation from census data	Does not consider feedbacks, for example, habitat quality and density dependence	Lalas and Bradshaw (2003)
	Stochastic demography	Can incorporate numerous feedback mechanisms affecting vital rates	Requires detailed understanding of demography	Panfylova et al. (2016)
	Metapopulation	Computationally efficient at large population sizes	Population-level equations less intuitive than individual level	Howell et al. (2018)
	Individual based	Simulates individual interactions leading to metapopulation patterns Sound analogue for ecological processes	Computationally intensive, especially with large populations High data requirements	Sun et al. (2016)
Interspecific interactions	Joint species distribution	Relatively simple inputs required Identifies patterns in species co-occurrence	Correlational, no mechanistic understanding Assumes interactions are consistent	Magory Cohen and Dor (2019) ^a
	Population mapping	Incorporates impact of sympatric species on reintroduction Impact could be mediated via effects on habitat quality	Assumes that interacting species do not respond to the reintroduced species	Berger and Gese (2007) ^b
	Dynamic metacommunity	Enables consideration of dynamic interactions between multiple species	Extremely high levels of data required for multiple species and their interactions Computationally intensive	Hale and Koprowski (2018) ^c

^aSpecies invasion, analogous to a reintroduction.

^bPattern based, non-dynamic, empirical study that could be the basis of a model.

^cReview highlighting the lack of metacommunity considerations in species reintroductions.

(Figure 1; Guisan & Thuiller, 2005). In many cases, it will not be necessary to combine all submodels, as a single model (e.g. a habitat model) can address key management questions. Depending on the question and the data available, using simpler model structures might be the best option. While integrating more data and considering more parameters and processes adds to the potential realism of models, it also adds to the uncertainty of model outputs. As each parameter measurement has associated error, the more parameters in a model, the greater the cumulative uncertainty of model outputs (Conlisk et al., 2013).

Simpler models often hide statistical uncertainty behind unrealistic assumptions and will not yield good predictions because the uncertainty stated in their outputs is low. To avoid constructing advanced models of little practical benefit, or models that are inaccurate due to poor input data, both the research question and the quality of available data must be considered. In most cases, it is recommended that the simplest accurate model be used to aid in the understanding of the model and to increase the transparency of recommendations. However, identifying this 'simplest accurate model' is not straightforward, as tests of predictive accuracy cannot be performed until independent data are available after the reintroduction has commenced.

Choosing between model options is complicated as methods are rarely compared directly, and when they are they tend to produce conflicting outputs (Simpkins et al., 2018; Zeller et al., 2018). Model choice is often based on personal preference and ease of application, rather than evaluation of accuracy (Mateo-Sánchez et al., 2015). Model validation is therefore a crucial, but often neglected, stage in the modelling process, necessary for model selection based on performance (McClure, Hansen, & Inman, 2016). Reintroductions provide a unique opportunity for model validation. As reintroduced populations are small and localized compared with most naturally occurring populations, less effort is required for surveys (Mihoub, Jiguet, Lécuyer, Eliotout, & Sarrazin, 2014). Standard monitoring methods should provide sufficient data to validate predictions made by each submodel, and the overall predictions of combined models (Cagnacci, Boitani, Powell, & Boyce, 2010).

We recommend the following: (a) reintroduced populations should be appropriately monitored to provide a dataset against which model predictions can be evaluated; (b) predictions of submodels and combined models should each be validated to identify effects of cumulative uncertainty and (c) model validation is used to improve models and parameter estimates, rather than as a requirement to 'finish' a study. Effective validation allows the most accurate model to be identified and refined, to inform if, where and how reintroductions should occur.

7 | CONCLUSIONS

We have provided a digestible overview of the options available for predictive modelling of reintroductions and indicated how different models can be combined to create nuanced predictions of post-release patterns. This will enable non-modellers to get their bearings

in the vast literature on ecological models, although further research into specific models will be necessary.

We provide rules of thumb to be considered throughout the modelling process; from conception to evaluation attention should be paid to:

- The overall aims of the reintroduction.
- Specific management questions that the models seek to answer.
- The attributes of the focal species.
- Major threats/stressors to the species within its native range and whether these are expected to be different in the reintroduced area.
- Quality and type of data available.

These factors determine which modelling options are preferable and will guide choices between options. We recommend that effort is invested in model validation so that models can be applied with confidence based on their predictive accuracy and can be refined or developed further as necessary.

AUTHORS' CONTRIBUTIONS

J.H.-A., P.J.S., M.R.R. and R.O. conceived the idea and scope of the work; J.H.-A. reviewed the literature and led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

Data have not been archived because this article does not use data.

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REFERENCES

- Aben, J., Bocedi, G., Palmer, S. C. F., Pellikka, P., Strubbe, D., Hallmann, C., ... Matthysen, E. (2016). The importance of realistic dispersal models in conservation planning: Application of a novel modelling platform to evaluate management scenarios in an Afrotropical biodiversity hotspot. *Journal of Applied Ecology*, 53(4), 1055–1065. <https://doi.org/10.1111/1365-2664.12643>
- Aben, J., Strubbe, D., Adriaensen, F., Palmer, S. C. F., Travis, J. M. J., Lens, L., & Matthysen, E. (2014). Simple individual-based models effectively represent Afrotropical forest bird movement in complex landscapes. *Journal of Applied Ecology*, 51(3), 693–702. <https://doi.org/10.1111/1365-2664.12224>
- Adams, V. M., Petty, A. M., Douglas, M. M., Buckley, Y. M., Ferdinands, K. B., Okazaki, T., ... Setterfield, S. A. (2015). Distribution, demography and dispersal model of spatial spread of invasive plant populations with limited data. *Methods in Ecology and Evolution*, 6(7), 782–794. <https://doi.org/10.1111/2041-210X.12392>
- Akçakaya, H. R. (2000). Viability analyses with habitat-based metapopulation models. *Population Ecology*, 42(1), 45. <https://doi.org/10.1007/s101440050008>
- Alexander, J. L., Olimb, S. K., Bly, K. L. S., & Restani, M. (2016). Use of least-cost path analysis to identify potential movement corridors

- of swift foxes in Montana. *Journal of Mammalogy*, 97(3), 891–898. <https://doi.org/10.1093/jmammal/gyw032>
- Austin, M. (2007). Species distribution models and ecological theory: A critical assessment and some possible new approaches. *Ecological Modelling*, 200(1–2), 1–19. <https://doi.org/10.1016/j.ecolmodel.2006.07.005>
- Berger, K. M., & Gese, E. M. (2007). Does interference competition with wolves limit the distribution and abundance of coyotes? *Journal of Animal Ecology*, 76(6), 1075–1085. <https://doi.org/10.1111/j.1365-2656.2007.01287.x>
- Bocedi, G., Palmer, S. C. F., Pe'er, G., Heikkinen, R. K., Matsinos, Y. G., Watts, K., & Travis, J. M. J. (2014). RangeShifter: A platform for modelling spatial eco-evolutionary dynamics and species' responses to environmental changes. *Methods in Ecology and Evolution*, 5(4), 388–396. <https://doi.org/10.1111/2041-210x.12162>
- Bocedi, G., Zurell, D., Reineking, B., & Travis, J. M. J. (2014). Mechanistic modelling of animal dispersal offers new insights into range expansion dynamics across fragmented landscapes. *Ecography*, 37(12), 1240–1253. <https://doi.org/10.1111/ecog.01041>
- Byers, J. A. (2001). Correlated random walk equations of animal dispersal resolved by simulation. *Ecology*, 86(6), 1680–1690. [https://doi.org/10.1890/0012-9658\(2001\)082\[1680:CRWEOA\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2001)082[1680:CRWEOA]2.0.CO;2)
- Cagnacci, F., Boitani, L., Powell, R. A., & Boyce, M. S. (2010). Animal ecology meets GPS-based radiotelemetry: A perfect storm of opportunities and challenges. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, 365(1550), 2157–2162. <https://doi.org/10.1098/rstb.2010.0107>
- Codling, E. A., Plank, M. J., & Benhamou, S. (2008). Random walk models in biology. *Journal of the Royal Society, Interface*, 5(25), 813–834. <https://doi.org/10.1098/rsif.2008.0014>
- Conlisk, E., Syphard, A. D., Franklin, J., Flint, L., Flint, A., & Regan, H. (2013). Uncertainty in assessing the impacts of global change with coupled dynamic species distribution and population models. *Global Change Biology*, 19(3), 858–869. <https://doi.org/10.1111/gcb.12090>
- Corlett, R. T. (2016). Restoration, reintroduction, and rewilding in a changing world. *Trends in Ecology & Evolution*, 31(6), 453–462. <https://doi.org/10.1016/j.tree.2016.02.017>
- Coulon, A., Aben, J., Palmer, S. C. F., Stevens, V. M., Callens, T., Strubbe, D., ... Travis, J. M. J. (2015). A stochastic movement simulator improves estimates of landscape connectivity. *Ecology*, 96(8), 2203–2213. <https://doi.org/10.1890/14-1690.1>
- Cowley, D. J., Johnson, O., & Pocock, M. J. O. (2015). Using electric network theory to model the spread of oak processionary moth, *Thaumetopoea processionea*, in urban woodland patches. *Landscape Ecology*, 30(5), 905–918. <https://doi.org/10.1007/s10980-015-0168-6>
- Cushman, S. A., Lewis, J. S., & Landguth, E. L. (2014). Why did the bear cross the road? Comparing the performance of multiple resistance surfaces and connectivity modeling methods. *Diversity*, 6(4), 844–854. <https://doi.org/10.3390/d6040844>
- DeCesare, N. J., Hebblewhite, M., Schmiegelow, F., Hervieux, D., McDermid, G. J., Neufeld, L., ... Musiani, M. (2012). Transcending scale dependence in identifying habitat with resource selection functions. *Ecological Applications*, 22(4), 1068–1083. <https://doi.org/10.1890/11-1610.1>
- Dimond, W. J., & Armstrong, D. P. (2007). Adaptive harvesting of source populations for translocation: A case study with New Zealand Robins. *Conservation Biology*, 21(1), 114–124. <https://doi.org/10.1111/j.1523-1739.2006.00537.x>
- Dolný, A., Šigutová, H., Ožana, S., & Choleva, L. (2018). How difficult is it to reintroduce a dragonfly? Fifteen years monitoring *Leucorrhinia dubia* at the receiving site. *Biological Conservation*, 218(August 2017), 110–117. <https://doi.org/10.1016/j.biocon.2017.12.011>
- Dormann, C. F., Bobrowski, M., Dehling, D. M., Harris, D. J., Hartig, F., Lischke, H., ... Kraan, C. (2018). Biotic interactions in species distribution modelling: 10 questions to guide interpretation and avoid false conclusions. *Global Ecology and Biogeography*, 27(9), 1004–1016. <https://doi.org/10.1111/geb.12759>
- Duffy, J. E., Cardinale, B. J., France, K. E., McIntyre, P. B., Thébault, E., & Loreau, M. (2007). The functional role of biodiversity in ecosystems: Incorporating trophic complexity. *Ecology Letters*, 10(6), 522–538. <https://doi.org/10.1111/j.1461-0248.2007.01037.x>
- Dullinger, S., Gattringer, A., Thuiller, W., Moser, D., Zimmermann, N. E., Guisan, A., ... Hülber, K. (2012). Extinction debt of high-mountain plants under twenty-first-century climate change. *Nature Climate Change*, 2(8), 619–622. <https://doi.org/10.1038/nclimate1514>
- Fick, S. E., & Hijmans, R. J. (2017). WorldClim 2: New 1-km spatial resolution climate surfaces for global land areas. *International Journal of Climatology*, 37(12), 4302–4315. <https://doi.org/10.1002/joc.5086>
- Giometto, A., Altermatt, F., Fronhofer, E. A., Massie, T. M., Hammes, F., Klecka, J., & Petchey, O. L. (2015). Big answers from small worlds: A user's guide for protist microcosms as a model system in ecology and evolution. *Methods in Ecology and Evolution*, 6, 218–231. <https://doi.org/10.1111/2041-210X.12312>
- Graves, T., Chandler, R. B., Royle, J. A., Beier, P., & Kendall, K. C. (2014). Estimating landscape resistance to dispersal. *Landscape Ecology*, 29(7), 1201–1211. <https://doi.org/10.1007/s10980-014-0056-5>
- Guisan, A., & Thuiller, W. (2005). Predicting species distribution: Offering more than simple habitat models. *Ecology Letters*, 8(9), 993–1009. <https://doi.org/10.1111/j.1461-0248.2005.00792.x>
- Gutt, J., Zurell, D., Bracegridle, T. J., Cheung, W., Clark, M. S., Convey, P., ... Grimm, V. (2017). Correlative and dynamic species distribution modelling for ecological predictions in the Antarctic: A cross-disciplinary concept. *Polar Research*, 31(1), 11091. <https://doi.org/10.3402/polar.v31i0.11091>
- Hale, S. L., & Koprowski, J. L. (2018). Ecosystem-level effects of keystone species reintroduction: A literature review. *Restoration Ecology*, 26(3), 439–445. <https://doi.org/10.1111/rec.12684>
- Hanks, E. M., & Hooten, M. B. (2013). Circuit theory and model-based inference for landscape connectivity. *Journal of the American Statistical Association*, 108(501), 22–33. <https://doi.org/10.1080/01621459.2012.724647>
- Hanski, I. (1999). *Metapopulation ecology*. Oxford, UK: Oxford University Press.
- Haydon, D. T., Morales, J. M., Yott, A., Jenkins, D. A., Rosatte, R., & Fryxell, J. M. (2008). Socially informed random walks: Incorporating group dynamics into models of population spread and growth. *Proceedings of the Royal Society B: Biological Sciences*, 275(1638), 1101–1109. <https://doi.org/10.1098/rspb.2007.1688>
- Heikkinen, R. K., Pöyry, J., Virkkala, R., Bocedi, G., Kuussaari, M., Schweiger, O., ... Travis, J. M. J. (2015). Modelling potential success of conservation translocations of a specialist grassland butterfly. *Biological Conservation*, 192, 200–206. <https://doi.org/10.1016/j.biocon.2015.09.028>
- Hinderer, R. K., Litt, A. R., & McCaffery, M. (2017). Movement of imperiled Chiricahua leopard frogs during summer monsoons. *Journal of Herpetology*, 51(4), 497–503. <https://doi.org/10.1670/16-093>
- Holloway, P., Miller, J. A., & Gillings, S. (2016). Incorporating movement in species distribution models: How do simulations of dispersal affect the accuracy and uncertainty of projections? *International Journal of Geographical Information Science*, 30(10), 2050–2074. <https://doi.org/10.1080/13658816.2016.1158823>
- Howell, P. E., Muths, E., Hossack, B. R., Sigafus, B. H., & Chandler, R. B. (2018). Increasing connectivity between metapopulation ecology and landscape ecology. *Ecology*, 99(5), 1119–1128. <https://doi.org/10.1002/ecy.2189>
- IUCN/SSC. (2013). *Guidelines for reintroductions and other conservation translocations*. Version 1.0. Gland, Switzerland: IUCN Species Survival Commission, viiii + 57 pp.

- Jiménez-Valverde, A., Peterson, A. T., Soberón, J., Overton, J. M., Aragón, P., & Lobo, J. M. (2011). Use of niche models in invasive species risk assessments. *Biological Invasions*, 13(12), 2785–2797. <https://doi.org/10.1007/s10530-011-9963-4>
- Keeley, A. T. H., Beier, P., & Gagnon, J. W. (2016). Estimating landscape resistance from habitat suitability: Effects of data source and nonlinearities. *Landscape Ecology*, 31(9), 2151–2162. <https://doi.org/10.1007/s10980-016-0387-5>
- Keeley, A. T. H., Beier, P., Keeley, B. W., & Fagan, M. E. (2017). Habitat suitability is a poor proxy for landscape connectivity during dispersal and mating movements. *Landscape and Urban Planning*, 161, 90–102. <https://doi.org/10.1016/j.landurbplan.2017.01.007>
- Keith, D. A., Akçakaya, H. R., Thuiller, W., Midgley, G. F., Pearson, R. G., Phillips, S. J., ... Rebelo, T. G. (2008). Predicting extinction risks under climate change: Coupling stochastic population models with dynamic bioclimatic habitat models. *Biology Letters*, 4(5), 560–563. <https://doi.org/10.1098/rsbl.2008.0049>
- Keller, D., Van Strien, M. J., & Holderegger, R. (2012). Do landscape barriers affect functional connectivity of populations of an endangered damselfly? *Freshwater Biology*, 57(7), 1373–1384. <https://doi.org/10.1111/j.1365-2427.2012.02797.x>
- Lalas, C., & Bradshaw, C. J. A. (2003). Expectations for population growth at new breeding locations for the vulnerable New Zealand sea lion (*Phocarctos hookeri*) using a simulation model. *Biological Conservation*, 114(1), 67–78. [https://doi.org/10.1016/S0006-3207\(02\)00421-4](https://doi.org/10.1016/S0006-3207(02)00421-4)
- Laperriere, V., Brugger, K., & Rubel, F. (2016). Cross-scale modeling of a vector-borne disease, from the individual to the metapopulation: The seasonal dynamics of sylvatic plague in Kazakhstan. *Ecological Modelling*, 342, 34–48. <https://doi.org/10.1016/j.ecolmodel.2016.09.023>
- Larson, M. A., Thompson, F. R., Millspaugh, J. J., Dijk, W. D., & Shifley, S. R. (2004). Linking population viability, habitat suitability, and landscape simulation models for conservation planning. *Ecological Modelling*, 180, 103–118. <https://doi.org/10.1016/j.ecolmodel.2003.12.054>
- Leathwick, J., Morgan, F., Wilson, G., Rutledge, D., McLeod, M., & Johnston, K. (2002). *Land environments of New Zealand: A technical guide*. Ministry for the Environment, GP Publications. Retrieved from https://www.landcareresearch.co.nz/_data/assets/pdf_file/0020/21773/LENZ_Technical_Guide.pdf
- Lee, D. E., & Bolger, D. T. (2017). Movements and source-sink dynamics of a *Masai giraffe* metapopulation. *Population Ecology*, 59(2), 157–168. <https://doi.org/10.1007/s10144-017-0580-7>
- MacPherson, B., & Gras, R. (2016). Individual-based ecological models: Adjunctive tools or experimental systems? *Ecological Modelling*, 323, 106–114. <https://doi.org/10.1016/j.ecolmodel.2015.12.013>
- Magory Cohen, T., & Dor, R. (2019). The effect of local species composition on the distribution of an avian invader. *Scientific Reports*, 9(1), 1–9. <https://doi.org/10.1038/s41598-019-52256-9>
- Mateo-Sánchez, M. C., Balkenhol, N., Cushman, S., Pérez, T., Domínguez, A., & Saura, S. (2015). Estimating effective landscape distances and movement corridors: Comparison of habitat and genetic data. *Ecosphere*, 6(4), 1–16. <https://doi.org/10.1890/ES14-00387.1>
- McClure, M. L., Hansen, A. J., & Inman, R. M. (2016). Connecting models to movements: Testing connectivity model predictions against empirical migration and dispersal data. *Landscape Ecology*, 31(7), 1419–1432. <https://doi.org/10.1007/s10980-016-0347-0>
- McGarigal, K., Wan, H. Y., Zeller, K. A., Timm, B. C., & Cushman, S. A. (2016). Multi-scale habitat selection modeling: A review and outlook. *Landscape Ecology*, 31(6), 1161–1175. <https://doi.org/10.1007/s10980-016-0374-x>
- Mestre, F., Cánovas, F., Pita, R., Mira, A., & Beja, P. (2016). An R package for simulating metapopulation dynamics and range expansion under environmental change. *Environmental Modelling & Software*, 81, 40–44. <https://doi.org/10.1016/j.envsoft.2016.03.007>
- Mihoub, J. B., Jiguet, F., Lécuyer, P., Eliotout, B., & Sarrazin, F. (2014). Modelling nesting site suitability in a population of reintroduced Eurasian black vultures *Aegypius monachus* in the Grands Causses, France. *Oryx*, 48(1), 116–124. <https://doi.org/10.1017/S0030605312000634>
- Moraes, A. M., Ruiz-Miranda, C. R., Galetti Jr., P. M., Niebuhr, B. B., Alexandre, B. R., Muylaert, R. L., ... Ribeiro, M. C. (2018). Landscape resistance influences effective dispersal of endangered golden lion tamarins within the Atlantic Forest. *Biological Conservation*, 224(May), 178–187. <https://doi.org/10.1016/j.biocon.2018.05.023>
- Nüchel, J., Bøcher, P. K., Xiao, W., Zhu, A. X., & Svenning, J. C. (2018). Snub-nosed monkeys (*Rhinopithecus*): Potential distribution and its implication for conservation. *Biodiversity and Conservation*, 27(6), 1517–1538. <https://doi.org/10.1007/s10531-018-1507-0>
- Ovaskainen, O., Roy, D. B., Fox, R., & Anderson, B. J. (2016). Uncovering hidden spatial structure in species communities with spatially explicit joint species distribution models. *Methods in Ecology and Evolution*, 7(4), 428–436. <https://doi.org/10.1111/2041-210X.12502>
- Ovaskainen, O., Rybicki, J., & Abrego, N. (2019). What can observational data reveal about metacommunity processes? *Ecography*, 42(11), 1877–1886. <https://doi.org/10.1111/ecog.04444>
- Ovenden, T. S., Palmer, S. C. F., Travis, J. M. J., & Healey, J. R. (2019). Improving reintroduction success in large carnivores through individual-based modelling: How to reintroduce Eurasian lynx (*Lynx lynx*) to Scotland. *Biological Conservation*, 234(October 2018), 140–153. <https://doi.org/10.1016/j.biocon.2019.03.035>
- Panfylova, J., Bemelmans, E., Devine, C., Frost, P., & Armstrong, D. (2016). Post-release effects on reintroduced populations of hihi. *Journal of Wildlife Management*, 80(6), 970–977. <https://doi.org/10.1002/jwmg.21090>
- Peters, W., Hebblewhite, M., Cavedon, M., Pedrotti, L., Mustoni, A., Zibordi, F., ... Cagnacci, F. (2015). Resource selection and connectivity reveal conservation challenges for reintroduced brown bears in the Italian Alps. *Biological Conservation*, 186, 123–133. <https://doi.org/10.1016/j.biocon.2015.02.034>
- Peterson, A. T., Papeş, M., & Soberón, J. (2015). Mechanistic and correlative models of ecological niches. *European Journal of Ecology*, 1(2), 28–38. <https://doi.org/10.1515/eje-2015-0014>
- Phillips, S. J., Anderson, R. P., & Schapire, R. E. (2006). Maximum entropy modeling of species geographic distributions. *Ecological Modelling*, 190(3–4), 231–259. <https://doi.org/10.1016/j.ecolmodel.2005.03.026>
- Pollock, L. J., Tingley, R., Morris, W. K., Golding, N., O'Hara, R. B., Parris, K. M., ... McCarthy, M. A. (2014). Understanding co-occurrence by modelling species simultaneously with a Joint Species Distribution Model (JSDM). *Methods in Ecology and Evolution*, 5(5), 397–406. <https://doi.org/10.1111/2041-210X.12180>
- Pulliam, R. (2000). On the relationship between niche and distribution. *Ecology Letters*, 3, 349–361. <https://doi.org/10.1046/j.1461-0248.2000.00143.x>
- Raines, G. L. (2002). Description and comparison of geologic maps with FRAGSTATS – A spatial statistics program. *Computers & Geosciences*, 28, 169–177.
- Rendall, A., Coetsee, A., & Sutherland, D. (2018). Predicting suitable release sites for assisted colonisations: A case study of eastern barred bandicoots. *Endangered Species Research*, 36, 137–148. <https://doi.org/10.3354/esr00893>
- Roy, H. E., Brown, P. M. J., Adriaens, T., Berkvens, N., Borges, I., Clusella-Trullas, S., ... Zhao, Z. (2016). The harlequin ladybird, *Harmonia axyridis*: Global perspectives on invasion history and ecology. *Biological Invasions*, 18(4), 997–1044. <https://doi.org/10.1007/s10530-016-1077-6>
- Schurr, F. M., Pagel, J., Cabral, J. S., Groeneveld, J., Bykova, O., O'Hara, R. B., ... Zimmermann, N. E. (2012). How to understand species'

- niches and range dynamics: A demographic research agenda for biogeography. *Journal of Biogeography*, 39(12), 2146–2162. <https://doi.org/10.1111/j.1365-2699.2012.02737.x>
- Seddon, P. J., Griffiths, C. J., Soorae, P. S., & Armstrong, D. P. (2014). Reversing defaunation: Restoring species in a changing world. *Science*, 354(6195), 406–412.
- Sewell, D., Baker, J. M. R., & Griffiths, R. A. (2015). Population dynamics of grass snakes (*Natrix natrix*) at a site restored for amphibian reintroduction. *Herpetological Journal*, 25, 155–161.
- Sharkey, K. J. (2011). Deterministic epidemic models on contact networks: Correlations and unbiological terms. *Theoretical Population Biology*, 79(4), 115–129. <https://doi.org/10.1016/j.tpb.2011.01.004>
- Simpkins, C. E., Dennis, T. E., Etherington, T. R., & Perry, G. L. W. (2018). Assessing the performance of common landscape connectivity metrics using a virtual ecologist approach. *Ecological Modelling*, 367, 13–23. <https://doi.org/10.1016/j.ecolmodel.2017.11.001>
- Slone, D. H. (2011). Increasing accuracy of dispersal kernels in grid-based population models. *Ecological Modelling*, 222(3), 573–579. <https://doi.org/10.1016/j.ecolmodel.2010.11.023>
- Stadtmann, S., & Seddon, P. J. (2018). Release site selection: Reintroductions and the habitat concept. *Oryx*, 1–9. <https://doi.org/10.1017/S0030605318001199>
- Stone, O. M. L., & Guy, A. J. (2017). Predicting optimal release sites for rehabilitated monkeys: A vervet monkey (*Chlorocebus aethiops*) case study. *International Journal of Primatology*, 38(3), 485–499. <https://doi.org/10.1007/s10764-017-9956-y>
- Stubben, C., & Milligan, B. (2007). Estimating and analyzing demographic models. *Journal of Statistical Software*, 22(11), 1–23. <https://doi.org/10.18637/jss.v022.i11>
- Sun, Y., Wang, T., Skidmore, A. K., Palmer, S. C. F., Ye, X., Ding, C., & Wang, Q. (2016). Predicting and understanding spatio-temporal dynamics of species recovery: Implications for Asian crested ibis *Nipponia nippon* conservation in China. *Diversity and Distributions*, 22(8), 893–904. <https://doi.org/10.1111/ddi.12460>
- Thompson, P. L., Rayfield, B., & Gonzalez, A. (2017). Loss of habitat and connectivity erodes species diversity, ecosystem functioning, and stability in metacommunity networks. *Ecography*, 40(1), 98–108. <https://doi.org/10.1111/ecog.02558>
- Tikhonov, G., Abrego, N., Dunson, D., & Ovaskainen, O. (2017). Using joint species distribution models for evaluating how species-to-species associations depend on the environmental context. *Methods in Ecology and Evolution*, 8(4), 443–452. <https://doi.org/10.1111/2041-210X.12723>
- Viljugrein, H., Lingjærde, O. C., Stenseth, N. C., & Boyce, M. S. (2001). Spatio-temporal patterns of mink and muskrat in Canada during a quarter century. *Journal of Animal Ecology*, 70(4), 671–682. <https://doi.org/10.1046/j.1365-2656.2001.00526.x>
- Walker, L. E., Marzluff, J. M., & Cimprich, D. A. (2016). Source-sink population dynamics driven by a brood parasite: A case study of an endangered songbird, the black-capped vireo. *Biological Conservation*, 203, 108–118. <https://doi.org/10.1016/j.biocon.2016.09.016>
- Xia, J., Lu, J., Wang, Z. X., Hao, B. B., Wang, H. B., & Liu, G. H. (2013). Pollen limitation and allee effect related to population size and sex ratio in the endangered *Ottelia acuminata* (Hydrocharitaceae): Implications for conservation and reintroduction. *Plant Biology*, 15(2), 376–383. <https://doi.org/10.1111/j.1438-8677.2012.00653.x>
- Zanin, M., Tassarolo, G., Machado, N., & Albernaz, A. L. M. (2017). Climatically-mediated landcover change: Impacts on Brazilian territory. *Anais Da Academia Brasileira de Ciências*, 89(2), 939–952. <https://doi.org/10.1590/0001-3765201720160226>
- Zeller, K. A., Jennings, M. K., Vickers, T. W., Ernest, H. B., Cushman, S. A., & Boyce, W. M. (2018). Are all data types and connectivity models created equal? Validating common connectivity approaches with dispersal data. *Diversity and Distributions*, 24(7), 868–879. <https://doi.org/10.1111/ddi.12742>
- Ziółkowska, E., Perzanowski, K., Bleyhl, B., Ostapowicz, K., & Kuemmerle, T. (2016). Understanding unexpected reintroduction outcomes: Why aren't European bison colonizing suitable habitat in the Carpathians? *Biological Conservation*, 195, 106–117. <https://doi.org/10.1016/j.biocon.2015.12.032>
- Zurell, D. (2017). Integrating demography, dispersal and interspecific interactions into bird distribution models. *Journal of Avian Biology*, 48(12), 1505–1516. <https://doi.org/10.1111/jav.01225>

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