Landscape Ecol (2015) 30:763–770
DOI 10.1007/s10980-015-0181-9

EDITORIAL

Model explorations of ecological network performance under conditions of global change

Martha M. Bakker · Paul F. M. Opdam · Rob H. G. Jongman · Adri Van den Brink

Received: 17 February 2015 / Accepted: 18 February 2015 / Published online: 10 March 2015

Abstract Ecological networks facilitate the mobility and vitality of species populations by providing a network of habitat patches that are embedded in a traversable landscape matrix. Climate change and land-use change pose threats to biodiversity, which can potentially be overcome by ecological networks. Yet, systematic assessments of ecological network performance under conditions of climate change and land-use change are rare. In this special issue we explore and evaluate approaches to assess the functionality of ecological networks under scenarios of global change. Hereby we distinguish three research fields: dynamics in the spatial configuration of networks; changes in the abiotic conditions within networks; and population viability and mobility of species within the networks. We present novel approaches for each of these themes, as well as approaches that aim to combine them within one modelling framework. Whilst the contributions featured all show promising developments towards the goal of ecological network performance under conditions of global change, we also see challenges for future research: the need to achieve (i) better integration between the three research fields; (ii) better empirical grounding of theoretical models; and (iii) better design of scientific models in order to assist policymaking.

Keywords Climate change · Biodiversity · Ecosystem restoration · Landscape permeability · Land-use change

Counteracting fragmentation and stimulating the development of ecological networks and corridors are key actions to halt the loss of biodiversity (Convention on Biological Diversity 2006; GEO BON 2011). In light of the threats that climate change and land-use change pose to biodiversity, ecological networks that connect patches of habitat can help species cope with these threats (Jongman et al. 2004; Vos et al. 2008). Ecological networks can either refer to deliberately restored and connected habitats, or to unintentional spatial configurations of land cover types that happen to serve as habitats we find worth protecting (Bennett and Mulongoy 2006). In case of the former, considerable budgets are generally involved, making it sensible to assess the network's (potential) performance at various stages of development (Van Teeffelen et al. 2015); in case of the latter, awareness of the societal role and ecological function of such networks

M. M. Bakker (✉) · P. F. M. Opdam · A. Van den Brink
Land Use Planning Group, Wageningen University,
Wageningen, The Netherlands
e-mail: martha.bakker@wur.nl

P. F. M. Opdam · R. H. G. Jongman
Nature and Society Team, Alterra Wageningen UR,
Wageningen, The Netherlands

A. Van den Brink
Landscape Architecture Group, Wageningen University,
Wageningen, The Netherlands

needs to be enhanced so that we can manage them wisely (Piquer-Rodríguez et al. 2015).

Model experiments allow assessing the performance of ecological networks. They are not confined to the small spatial scales and point-measurements that are typical for field experiments, and therefore allow linking processes occurring at different temporal and spatial scales. Modelling the response of species to specific network configurations and external triggers allows us to improve our understanding of key processes. Moreover, unlike field experiments or monitoring exercises, models can be applied in the preparatory stage to evaluate contexts that do not yet exist. For the design or protection of ecological networks, such ex-ante evaluations are particularly important, as the (re-)establishment of a habitat can take many years. Therefore, in order for networks to be robust against future climate and land-use change, actions have to be taken far in advance. Once models are considered to represent relevant processes adequately, they can be used to conduct experiments that allow us to evaluate effectiveness and pertinence of such precautionary actions.

This special issue brings together model-based approaches that evaluate the performance of ecological networks under conditions of global change. Each paper makes progress towards the goal of increasing our understanding of key network processes by meeting methodological challenges of modelling ecological networks in novel and insightful ways. We showcase their findings in three areas: dynamics in the spatial configuration of networks; changes in the abiotic conditions within networks; and population viability and mobility of species within the networks. We begin by discussing developments within each research area separately, and we then proceed to focus on integration among these research areas. We end with an inventory of topics where more research is required.

Dynamics in the spatial configuration of networks

Ecological networks generally consist of patches of habitat and in-between areas that can be traversed by species, possibly with the help of corridors or stepping stones. Most land-based habitats are composed of natural vegetation or extensively-used agricultural areas. In-between areas are often used for food, timber, or energy production, which may limit the possibilities for traversing. Freshwater habitats, on the other hand, are composed of lakes, rivers, and streams while connectivity is determined by the network of waterways and the presence of anthropogenic obstructions such as dams. Because human activities determine the placement and size of habitat patches, as well as the possibility to cross the in-between area, it is critically important to predict the spatial configuration of human activities, i.e. land use and management, for estimating future performance of ecological networks.

Models for understanding and predicting land use and management have been developed since the 1990s, starting as coarse-resolution, static, bio-economic models, either driven by optimization algorithms (Van Ittersum et al. 2008) or aiming at empirical pattern reproduction (Verburg et al. 2002). More recently, agent-based models (ABMs) gained popularity as they allow for a better incorporation of land user heterogeneity, feedbacks between processes happening at different scales, and social–psychological aspects of land-use decision-making (Filatova et al. 2013; Parker et al. 2003). Moreover, approaches based on ABM acknowledge that land-use decisions are made by autonomous land owners, and in this special issue it is demonstrated how relevant this can be for conservation planning. Several contributions show how top-down-imposed schemes often run afoul of local land owners behaving in ways that do not comply with the goals of policy makers. Bakker et al. (2015), for example, show that the establishment of stepping stones and enlargement of habitats is strongly hindered by farmers that hold on to the agricultural function of the land, of which they are generally the legal owners. Kros et al. (2015) demonstrate that at least in the Netherlands livestock farmers will probably expand at the expense of arable farmers, leading to an increase in nitrate emissions, which is at odds with the policy ambitions for reconstruction of mesotrophic habitats. Gimona et al. (2015) demonstrate that climate change will probably result in further intensification of land use, having detrimental effects on the permeability of the landscape, but their ABM explorations also suggest that many farmers would be sensitive to financial triggers to prevent intensification and implement stepping stones.

ABMs have more advantages from the point of view of ecological modelling. First, they allow for explorations at relatively fine spatial scales (i.e. a landscape in which individual fields and farms can be distinguished), which is often crucial to simulate the dispersal of species. Secondly, they allow simulation of more subtle management changes, such as intensification of input use and the implementation of agri-environment schemes (Valbuena et al. 2010). Such management changes are important determinants of both (agricultural) habitat quality and permeability of areas between habitats.

Although these advantages are essential elements for simulating land use for the sake of ecological network evaluation, they also reveal potential shortcomings. The fact that ABMs run at a fine scale, also implies they are generally limited to areas of several hundreds of square kilometres, which may not be large enough for capturing (connectivity between) habitats of larger species or migration routes of migratory species. Furthermore, current ABM applications are mostly used for subtle changes in land management only, and hardly ever for categorical land-use change that involves land changing from one type of owner to another (e.g. from a farmer to a conservation organization). Two papers featured in this special issue deal with these challenges. Bakker et al. (2015) simulated the land exchange between farmers and nature organizations as driven by the Dutch ecological network program, therewith being one of the very few ABM approaches able to simulate categorical land-use change as the result of land exchange. Gimona et al. (2015) extrapolated ABM-derived land-use mechanisms to a much larger area than for which the ABM was run, so that principles of autonomously operating land users could be applied to scales at which long-term migration of species becomes manifest.

Changes in abiotic conditions within the network

While the size, location, and accessibility of (semi) natural land cover patches are generally determined by surrounding land use activities, the degree to which these patches can actually serve as habitat for to-be-protected species is affected by global change as well. As for climate change, patches of natural land cover lose quality at the trailing edge of a habitat range, while patches—if present—gain quality at the leading edge. Both edges run a risk of distorted trophic networks, as loss and gain in habitat quality vary per ecological trait. Literature on such temperature-driven shifts in habitat ranges is abundant [see review by Lenoir and Svenning (2014)]. In this issue Leito et al. (2015) show how climate change can have a positive influence on habitats of Eurasian Crane (*Grus grus*) as lakes that remain unfrozen during winter become more widespread. Less attention has been paid to climate-change effects occurring at finer scales, which are often driven by local hydrological processes. In this issue, Witte et al. (2015) demonstrate how climate change may lead to wetland desiccation, although effects show considerable spatial variability. By including spatial groundwater models, both Van der Knaap et al. (2015) and Witte et al. (2015) demonstrate that new spatial patterns of wet and dry areas may appear, which requires an adjustment of local designation plans that aim for wetland restoration.

A scientific challenge in the modelling of climate-change driven habitat suitability is that most models that have been developed to simulate e.g. vegetation response to precipitation or temperature change (Anderson et al. 2009) tend to rely heavily on statistical relationships derived from (limited) observational data, the climate envelopes, rather than on the underlying mechanisms (Harfoot et al. 2014; Witte et al. 2015). More mechanistic models are probably safer to use for projections in which climate conditions exceed the calibration range of most empirical models. In this issue Witte et al. (2015) demonstrate such a model by applying a spatially-explicit hydrological model to derive hydrological stress variables to which plants respond mechanistically. By including such mechanisms, the probabilities in spatial patterns of future vegetation assemblages could be predicted.

Next to direct impacts of climate change (i.e. temperature, CO_2, and water availability), indirect impacts may occur if surrounding land users respond to climate change, but this has received much less attention in literature. In this issue, Kros et al. (2015) show that the intensification of land use that is triggered by climate change is likely to result in increased nitrate flows via groundwater and atmospheric deposition to adjacent nature reserves. Van Dijk et al. (2015) demonstrate that climate-induced land management change is likely to result in a deterioration of habitat quality. Both papers suggest that such effects are generally strong, and in many cases possibly stronger than the direct effects of climate change. This suggests that studies of adaptation to climate change should not focus on ecological processes alone, but have to include adaptation strategies by surrounding land users as well.

A final challenge for modellers simulating abiotic conditions in habitat patches is to incorporate mechanisms that allow the evaluation of policy measures. Often, a policy measure concerns a specific action that falls within the mandate of the policy maker. Sometimes these entail physical alterations (e.g. changing drainage leverages) but more often they rely on legislative (e.g. issue a regulation) or economic (e.g. provide a financial trigger to farmers) mechanisms. The degree to which such measures result in the desired conditions is often unclear, and therefore models should be designed so that policy measures can be evaluated, as demonstrated in this issue by Van der Knaap et al. (2015). Some water-management related policy measures can have a strong impact on habitat suitability, to the extent that effects of climate change can be entirely compensated, as shown by Van der Knaap et al. (2015) and Van Dijk et al. (2015) in this issue. Kros et al. (2015), on the other hand, show that policies targeting nutrient loadings in the Netherlands may turn out to be less efficient. This is partly related to the generally long distance between locations where nutrients are emitted and where they are deposited, and partly to the fact that policy measures targeting nutrient application are economic and legislative rather than physical, leaving the actual decision of whether or not to comply with the policy makers' goals with the land users. For the exploration of the effects of policy measures that are economic or legislative rather than physical, such as the provision of incentives for lower use of agricultural inputs, sophisticated ABM models that aim at simulating human decision-making are probably more useful.

Population viability and mobility of species within the networks

Various model approaches analyse the dynamics of species populations living in ecological networks, of which most are represented in this issue. Such dynamics are determined by (a) the number of individuals that on average live in the network (carrying capacity), which is a function of habitat quality and network area, and (b) the spatial spread of dispersing individuals across the network (connectivity), which is a function of the network density and the permeability of the landscape matrix in which the network is embedded (Opdam et al. 2003). Graph theoretical models provide an analytical approach to characterize connectivity, whereby the dispersive capacity of the species of interest defines the threshold beyond which two patches are no longer considered to be connected (Piquer-Rodríguez et al. 2015). Graph models treat dispersal as a deterministic process, which is generally considered a limitation. Metapopulation models, on the other hand, simulate population dynamics as the interplay between local extinction and recolonization of local populations, with dispersal playing a key role in both processes. A specific class of metapopulation models approach the dynamics of local populations by a numerical simulation based on probabilities that individuals disperse, reproduce, or die (Van Teeffelen et al. 2015). Another category is the individual-based models (IBM), which are analogue to the ABMs described earlier, but which take plants or animals as the agents rather than people (DeAngelis and Grimm 2014). Although metapopulation and IBM are more sophisticated and realistic than graph-theory models, they are data hungry, require much computation time, and their results are less transparent than those of analytical models.

For improving connectivity within ecological networks, the role of stepping stones has often been emphasized (Saura et al. 2014; Vos et al. 2008), and this is once more corroborated in this issue by Piquer-Rodríguez et al. (2015), who demonstrate that safeguarding stepping stones in the Argentinian Chaco will probably prevent strongest biodiversity degradation in scenarios where deforestation continues to happen at varying rates. Other papers featured in this special issue discuss limitations to the effectiveness of stepping stones in facilitating species responses to climate change. For example, Van Teeffelen et al. (2015) demonstrates that stepping stones are only functional if their abiotic conditions are favourable for the targeted species. They show that randomly placed stepping stones (patterns that emerge when farmers are paid to create small habitat patches) are often not helpful, as they are surrounded by areas that cannot be traversed by the targeted species. Gimona et al. (2015) demonstrate that efforts to create stepping stones are no panacea for slow dispersers in case of climate rapid climate change, and that dispersal speed shows no linear response to the quantity of stepping stones.

When it comes to invasive species, there is a need to identify at which level of connectivity the spread of species across ecological networks gets inhibited.

Melles et al. (2015) show how dams may prevent the northward migration of invasive aquatic species in the Great Lakes (Canada), while Cowley et al. (2015) show which stepping stones require intensive monitoring in order to prevent a further spread of oak processionary moth in London. Because invasive species are generally not yet established in an area, a metapopulation model would be difficult to parameterize. Therefore, such simulations often make use of electric circuit models (McRae et al. 2008), which combine principles of graph theory and metapopulation theory. Such models apply circuit theory to movement ecology via random-walk theory, and appear to be particularly useful for simulating the initial spread of (invasive) species into a landscape from source populations, before a viable population has been established. Of course, application of such results in practice always requires a trade-off analysis between the effect of decreasing connectivity on the spread of invasive species and the implications of loss of spatial cohesion to existing biodiversity.

Integrating the three research areas

While several of the papers featured in this issue concentrate primarily on one of the three research areas we showcase, other papers invested more in the integration of elements from two or three of these fields. In Fig. 1 we present a framework that illustrates how the three areas discussed so far are complementary and may be integrated to build a more comprehensive analytical tool. Several papers in this issue achieve a certain degree of this integration already. For example, Melles et al. (2015) primarily focussed on species mobility simulated by a circuit model, but they included effects of temperature change on habitat suitability within the habitat patches (lakes and streams in their case), and evaluated how proposed dams affected the spatial configuration of the network. Gimona et al. (2015) studied the dispersion of deciduous forest species in Scotland, but they also simulated how land-use change affected the spatial configuration of habitat patches. This land-use change was the combined result of climate change and human response to economic opportunities. Van Dijk et al. (2015) simulated how effects of climate change influences the habitat quality of meadow birds and how responses by land managers to climate change further affect the spatial pattern of habitat patches. Kros et al. (2015) combined outputs of the land-use ABM by Bakker et al. (2014) with models that simulate how nutrient loadings reduce the quality of adjacent habitat patches. Van Teeffelen et al. (2015) simulated the dispersal of crested newt through small patches of habitats within an intensively used agricultural area, whereby they used the PROBE model by Witte et al. (2015) to simulate how changes in hydrological conditions would affect the utility of stepping stones distributed according to various scenarios.

The importance of a more integrated approach is illustrated by several of the contributions, revealing insights that otherwise would not have been gained. For example, studying effects of climate change and land-use change in concert reveals that the combination can sometimes alleviate pressures for species (Van Dijk et al. 2015), although there are also cases where land use change effects aggravate pressures arising from climate change (Bakker et al. 2015; Gimona et al. 2015; Kros et al. 2015). Gimona et al. (2015) simulated species dispersal in concert with land-use change, and their results suggest that a turnover of stepping stones (i.e. removal of stepping stones and reappearance elsewhere) in the course of time is an important factor in simulating species dispersal. Van Teeffelen et al. (2015) simulated the effects of various land use patterns on species dispersal under varying scenarios of climate change, and showed that landscape configurations that provide adequate dispersal possibilities under current conditions, will no longer do so when anticipated climate change leads to lower groundwater tables. Melles et al. (2015) demonstrated that dams, which are generally considered detrimental for ecological vitality, may safeguard endogenous fish populations from competition by invasive species under conditions of global warming.

Challenges

Based on the findings reported in this special issue, together with our overall view on the scientific domain of ecological networks, we identify three challenges: the need for further integration between the here-presented research fields; a better empirical grounding of theoretical models; and the need to pay more

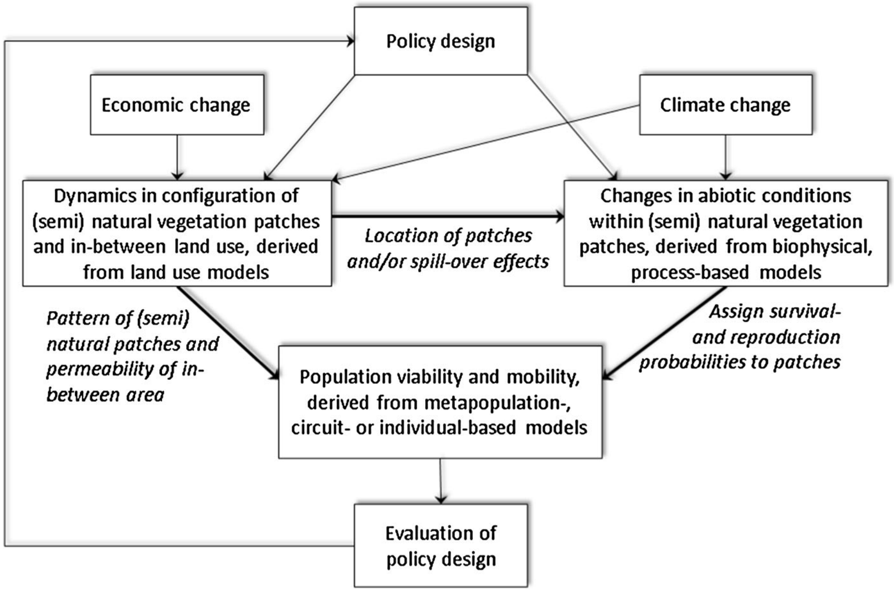

Fig. 1 An overarching framework for exploring the performance of ecological networks under conditions of global change. The three larger blocks in the centre of the figure depict the three areas of research described above. Dynamics in configuration of (semi) natural vegetation patches and in-between land use evolve from (partly planned, partly autonomous) human actions, which are influenced by policy design, climate change, and economic change. These models produce input for biophysical, process-based models that can evaluate how suitable the (semi) natural land cover patches are for to-be-protected species under conditions of global change, including not only climate change but spill-over effects of surrounding land use as well. Together, the land-use configuration and the habitat quality of the (semi) natural land cover patches form input to the models that simulate dynamics in species population, be they metapopulation models, circuit models, or individual-based models. The predicted population dynamics allow evaluation against the initially-stated policy objectives, which, in case of unsatisfactory outcomes, require a policy change, which needs to be evaluated by repeating the modelling procedure

attention to how scientific models can be used for policy design. Below we discuss these in more detail.

Further integration between research fields

While many here-featured contributions integrated two of the three fields displayed in Fig. 1, none of them achieved a full and balanced integration. Although in the real world the three fields are strongly entwined, this is not the case for the scientific communities that study these fields. Often, eco-hydrologists know little of metapopulation dynamics, population biologists know little about fluxes of water and nutrients, while both groups know very little about factors driving land use. It requires intensive collaboration between scholars from the various fields to achieve more comprehensive insights in how ecological networks will perform in the future. Particularly the integration of land use science in ecological studies is called upon by how most ecological networks are managed. For example, in Europe the habitat patches are protected by European law, but structures to enhance connectivity between habitat patches are the responsibility of the individual countries. In-between land is often owned by farmers, who not always show to be receptive to incentives to improve landscape permeability (Burton et al. 2008). Integration of land use and ecological models should be feasible, especially between metapopulation models or IBMs and ABMs, as they are conceptually similar: dynamic, stochastic, and taking a bottom-up approach to the simulation of complex phenomena. More generally stated there is a need to model effects of multiple environmental and man-induced stressors on ecological networks and to evaluate their efficacy (in terms of maintaining key processes) by looking at network configuration, habitat quality, and species composition: a landscape ecological approach.

Better empirical grounding of theoretical models

The use of models as tools to explore future performance of ecological networks will increase in credibility if model parameters are based on empirical measurements. As models become more complex (as a result from incorporation of cascading processes and the inclusion of human behaviour) they tend to accumulate uncertainties. These uncertainties potentially undermine the credibility and usefulness of models to policymakers. Yet, in many scientific fields the notion of *big data* is emerging, describing the exponential growth and availability of data. Also in ecology, data sources become more abundant, time series grow longer, and monitoring devices become more sophisticated, generating an ever-increasing body of information that modellers should make use of. This involves particular challenges, for example when model parameters determining the probability on rare events, such as long distance dispersal have to be estimated—obviously from the infrequent occurrence of rare events. Moreover, using current observations to predict future responses, assumes some degree of stationarity of processes, which involves a potential fallacy [as argued by Witte et al. (2015) in this issue]. Probably, a method in which models continually 'learn' from the ever-increasing amount of observations, by adjusting parameters to better match observed data (e.g. via evolutionary algorithms) could be a promising way forward.

More attention to how scientific models can be used for policy design

Models can and should be used to evaluate policies; consequently they may contribute to developing more effective policies. Evaluations can be done against economic targets (Gaaff and Reinhard 2012) or against ecological targets (Verboom et al. 2001). In a new policy cycle, following an evaluation, a comparison of alternative policy options can be helpful, but it requires that models are designed in such a way that their input variables represent and capture the actual policy actions. Currently, policymakers often have to work with models that were not designed for their use, and while such models are generally well capable of simulating the response of a certain ecological variable to e.g. climate change or economic change, they generally are weak in simulating responses to those factors that can be influenced by policy makers, especially when these concern legislative or economic mechanisms. Once this is achieved, the integrated models designed according to e.g. Fig. 1, can be used as a virtual laboratory in which policy experiments are conducted. An important challenge will be to develop models in such a way that they generate not only scientifically credible output, but also provide information that is salient and legitimate to policy makers and land managers. This calls for developing and applying such models as a cooperative endeavour of scholars, policy makers, and other stakeholders, i.e. a transdisciplinary modelling approach.

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