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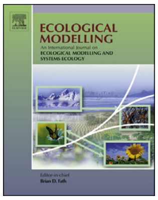

How is habitat connectivity affected by settlement and road network configurations? Results from simulating coupled habitat and human networks

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ABSTRACT

Habitat connectivity is important for species' survival and can be maintained in landscapes with well-connected habitat networks. The integrity of these habitat networks, however, is often threatened by "human networks" consisting of settlements connected by roads with traffic. Both settlement and road network changes can decrease habitat connectivity, either directly or indirectly through changes in traffic flows. Due to these complex interactions, it remains unclear how habitat connectivity in habitat networks is affected by settlement or road network configurations in human networks. To address this issue we develop a new spatially explicit simulation model coupling habitat and human networks. In binary landscape rasters, consisting of settlement patches surrounded by a continuous matrix through which animals could move, we varied the number, the size and the proportion of settlements. Settlements were connected with either dense or sparse road networks. On all roads connecting settlements, we estimated traffic volume based on settlement sizes and topology. Traffic volumes were then used to parameterize landscape resistance networks that quantify the probability of movement for animals throughout the landscape. From these resistance networks, we calculated average habitat connectivity for several animal species (i.e. tree frog, hedgehog and badger). In this innovative model setup, habitat connectivity was thus influenced by a combination of settlement patterns and traffic volumes. For all species, we found a negative correlation between habitat connectivity and the number of settlement patches. Furthermore, in landscapes with a high proportion of settlement, highest habitat connectivity was found when most settlement cells were concentrated in large patches. Surprisingly, in some cases, we found higher habitat connectivity for dense road networks than for sparse road networks. Results from this study can increase our understanding of habitat connectivity in heterogeneous landscapes and lead to recommendations for conservation planning. With this study we demonstrate the importance of considering interactions between spatial networks in ecological analyses.

1. Introduction

Mobility is essential for the survival of animal species; it is necessary to reach food and water sources, find mating partners or move to new habitats (Crooks and Sanjayan, 2006). Moreover, the mobility of animal species ensures seed or pollen dispersal for many natural and cultivated plant species (Hadley and Betts, 2012). The degree to which the landscape facilitates or impedes animal movement among habitats is referred to as habitat connectivity (Taylor et al., 1993). Habitats between which there is (potential) movement of species form intricate spatial networks (i.e. habitat networks; Galpern et al., 2011; Rayfield et al., 2011). There is ample evidence that a network of well-connected habitats, in which the mobility of animals is not impeded, is needed to maintain or increase biodiversity (Bailey et al., 2010; Martensen et al., 2008). However, the integrity of these habitat networks is often threatened by human activities and constructions, such as settlements, roads and transportation. Analogous to habitat networks, settlements connected by roads and traffic form complex spatial networks (e.g. Ren et al., 2014; Simini et al., 2012), which we here term "human networks". The expansion of settlements and associated land-use changes reduce habitat suitability for certain species or reduce the move-

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ment of species between habitats (Pickett et al., 2011; Salafsky et al., 2008; Van Strien et al., 2014). Also roads and traffic can be detrimental to both habitat suitability and habitat connectivity (Charry and Jones, 2009; Forman et al., 2003; Salafsky et al., 2008; Seiler, 2003). Due to the interactions between spatially coinciding human and habitat networks, these networks can be regarded as coupled spatial networks.

In recent years, there has been an increasing focus on coupled spatial networks (also refered to as network of networks or multilayered, multiplex or interdependent networks; Gao et al., 2014), as such networks appear to be more vulnerable to node removal than non-spatial coupled networks (e.g. Bashan et al., 2013; Buldyrev et al., 2010). Whereas the dependency between these coupled networks is often between nodes (Bashan et al., 2013; Buldyrev et al., 2010; Gao et al., 2014), in habitat and human networks this dependency is characterised by two spatial interactions. First, the nodes in both networks are usually mutually exclusive, because settlements and (semi)natural habitats tend to be spatially separated and because the growth of settlements mostly leads to a decrease in size or suitability of animal habitats or, albeit less frequent, vice versa (Radeloff et al., 2005). Second, oftentimes the edges (i.e. roads/traffic and animal movement) in the networks are intersecting and negatively influencing each other, meaning that the more traffic there is on a road, the less animal movement can be expected across that road (provided there are no measures in place that mitigate the negative effect of traffic on habitat connectivity; Coffin, 2007; Van Langevelde et al., 2009; Van Langevelde and Jaarsma, 2009). This two-fold interaction between habitat and human networks makes it especially difficult to determine the consequences of changes in either network.

Several authors have argued that the whole habitat and human networks in a region should be considered when studying the effects of changes in the human network on habitat connectivity (Coffin, 2007; Seiler, 2003; Van der Ree et al., 2011; Van Langevelde et al., 2007). Seiler (2003) stated that “the overall fragmentation impact on the landscape due to the combined road network may thus not be predictable from data on individual roads and railways. When evaluating primary (ecological) effects of a planned transport infrastructure project it is essential to consider both the local and landscape scales, and fundamentally, the cumulative impact of the link when it becomes part of the surrounding road network”. Van Langevelde et al. (2007) support this statement and mentioned that “as soon as interventions [to prevent habitat fragmentation by infrastructure] are implemented on one road section in a road network, unexpected effects can occur elsewhere. This applies to animals (alterations in movement patterns) and humans (alterations of traffic flows).” Yet, very few studies have experimented with coupled habitat and human networks to study the interactions and feedbacks within and between these networks. Considering the whole human and habitat networks in a region is necessary to address several important issues in nature conservation theory, two of which are described below.

A first pressing question in conservation theory is “what spatial pattern of human settlement (e.g., clustered vs. dispersed) has the least impact on biodiversity” (Sutherland et al., 2009). This question cannot be answered without accounting for the effect that different patterns of human settlement have on traffic flows and on the distribution of habitats, which are both factors that will determine habitat connectivity (i.e. an important driver of biodiversity; e.g. Brudvig et al., 2009; Ribeiro et al., 2011). A long-standing debate in nature conservation science is whether biodiversity can best be protected in a single large or several small habitats (e.g. Diamond, 1975; McCarthy et al., 2011). Given the interconnectedness of human and habitat networks, one could similarly wonder whether certain configurations of human settlements are more beneficial for biodiversity conservation than others. Such information would aid landscape planners in developing sustainable landscapes.

A second unresolved issue in conservation theory is uncertainty regarding “the effect of human infrastructure installation (transportation) on ecosystem [or habitat] connectivity” (Braunisch et al., 2012). In order to mitigate the negative effects of roads on species movement, wildlife over- and underpasses are a frequently used and studied mitigation measure (Van der Ree et al., 2007). However, wildlife over- and underpasses are often too costly to be applied to minor roads (Huijser et al., 2009). Yet the vast majority of roads are minor roads (Van Langevelde et al., 2009) and it is especially these minor roads that contribute most to the increasing habitat fragmentation in Europe (Jaeger et al., 2011). For these reasons, more research should focus on finding road network configurations that have least impact on habitat connectivity (Rhodes et al., 2014). Both the road network configuration and the distribution of traffic on the roads are strongly influenced by the configuration of settlements (Hawbaker et al., 2005; Ren et al., 2014; Simini et al., 2012). Therefore, ideally the combined effects of settlement and road network configuration on habitat connectivity are assessed simultaneously. However, to our knowledge, no studies have experimented in this direction.

In the current study we aim to shed light on the above two conservation issues by assessing the effect of settlement and road network configurations on habitat connectivity. In order to capture the main interactions and feedbacks in coupled human and habitat networks, we specifically focus on large landscapes at a regional scale. Our focus is also on rural or forested landscapes outside of city centres where there is considerable non-built land use. We performed a simulation study in which we created road and habitat networks in computer-generated landscapes. Results were obtained by simulating habitat connectivity under a range of settlement and road network configurations. Since species can differ in the likelihood of being killed by traffic (Gunson et al., 2011), species characteristics (e.g. movement speed and body size) were included in the input settings of the simulation model. This allowed us to perform our analysis for three animal species: European tree frog (*Hyla arborea*), European hedgehog (*Erinaceus europaeus*) and Eurasian badger (*Meles meles*). For the tree frog, both roads and settlements have been identified as barriers to dispersal (Pellet et al., 2004). Traffic has also been identified as one of the major causes of fatalities in the badger (Clarke et al., 1998) and the hedgehog (Huijser and Bergers, 2000).

2. Methods

2.1. Model overview

In order to couple human and habitat networks and capture the two types of spatial interactions between these networks (i.e. mutually exclusive nodes and intersecting and interacting edges), both networks had to be constructed and overlaid in the same landscape and subsequently coupled by exchanging information between the networks. To achieve this, we developed a simulation model that determined habitat connectivity in landscapes of which we could vary the configuration of settlements as well as the configuration of the road network. The model consists of four modules (Fig. 1). First, we generated binary landscape rasters with settlements embedded in a matrix through which animals could move (Figs. 1A & 2). Second, using proximity graphs (Adamatzky et al., 2012; Galin et al., 2011) the road networks were constructed by linking neighbouring raster cells that were classified as settlement (Fig. 1B). In this way, several road network configurations were constructed. Traffic volumes were then calculated on all roads connecting settlements, making use of recently developed