Ecological Complexity 11 (2012) 28–37

Contents lists available at SciVerse ScienceDirect

Ecological Complexity

journal homepage: www.elsevier.com/locate/ecocom

Original Research Article

Assessing the importance of individual habitat patches as irreplaceable connecting elements: An analysis of simulated and real landscape data

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ARTICLE INFO

Article history:
Received 22 June 2011
Received in revised form 8 November 2011
Accepted 17 January 2012
Available online 15 February 2012

Keywords:
Landscape connectivity
Habitat availability metrics
Network analysis
Neutral landscape models
Fragmentation
Stepping stones

ABSTRACT

Habitat loss and fragmentation are considered to be severe threats to biodiversity, and maintaining natural levels of landscape connectivity may be one of the best responses to these issues. Graph-based habitat availability (reachability) metrics have been shown to be an appropriate method for a multifaceted but coherent landscape connectivity assessment. These metrics can be partitioned into three commensurate fractions (intra, flux, connector) that quantify the different ways in which habitat patches contribute to the overall landscape connectivity and habitat availability. In particular, the connector fraction measures the contribution of patches to the connectivity between other habitat areas as irreplaceable connecting elements or stepping stones. Because many conservation efforts and initiatives are focused on conserving or restoring corridors and other linkages between habitat areas, it is critical to understand more thoroughly the conditions under which investing in these connecting elements is an efficient management strategy. For this purpose, we analysed the contribution of the connector fraction in different simulated habitat patterns under different levels of habitat amount and fragmentation and in natural habitats for endangered forest bird species in Catalonia (Spain). We show that a prominent role of individual stepping stone patches as irreplaceable providers of habitat connectivity and availability arises only under a relatively narrow set of conditions, characterised by low habitat amount, high habitat fragmentation and modest to intermediate species dispersal abilities. We suggest that to support connectivity-related investments, it is necessary to focus on those few species or dispersal distance ranges that are likely to be both most dependent on and most benefited by the conservation or restoration of stepping stone patches. We conclude that the total amount of reachable habitat for a particular species is rarely determined by the contribution of individual connectors as the only dominant factor. Therefore, conservationists should be cautious not to overemphasise the importance of connectivity investments and to balance them with other conservation alternatives and strategies to promote species conservation in heterogeneous landscapes.

1. Introduction

Habitat loss and fragmentation are considered to be severe threats to biodiversity (Crooks and Sanjayan, 2006a; Fahrig, 2003; Fischer and Lindenmayer, 2007), and maintaining natural levels of landscape connectivity may be one of the best responses to these issues. Sustaining connectivity may also facilitate the shifts in species distribution caused by climate change and the persistence of species in landscapes modified by human activities (Crooks and Sanjayan, 2006a). Connectivity is defined as the degree to which the landscape facilitates or impedes the movement of species and other ecological flows across the resources in the landscape (modified from Taylor et al., 1993). This definition highlights the interaction between the spatial heterogeneity of the landscape and the response of organisms to that structure (Taylor et al., 2006). Therefore, assessing landscape connectivity requires a species-specific approach because the same landscape can be perceived as either connected or disconnected by two species with different dispersal abilities (Bunn et al., 2000). The importance of integrating landscape connectivity into landscape management and planning purposes is currently widely recognised (Crooks and Sanjayan, 2006b).

Amongst the methods and metrics used to characterise landscape connectivity, it has been suggested that the graph theoretical approach possesses the greatest benefit to effort ratio for conservation problems that require a characterisation of connectivity at relatively large scales (Calabrese and Fagan, 2004). Indeed, graph-based metrics have been applied in a large number of studies regarding landscape network connectivity in recent years (Bodin and Norberg, 2007; Brooks, 2006; Erös et al.,

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doi:10.1016/j.ecocom.2012.01.003

2011; Fall et al., 2007; Galpern et al., 2011; Jordán et al., 2007; Minor and Lookingbill, 2010; Neel, 2008; Pautasso et al., 2010; Pereira et al., 2011; Ribeiro et al., 2011; Saura and Pascual-Hortal, 2007). In such studies, habitat patches are modelled as nodes, and the functional connexions between them are represented as links (Urban and Keitt, 2001). Recently, new graph-based metrics have been developed based on the concept of measuring habitat availability (reachability) at the landscape scale (Pascual-Hortal and Saura, 2006; Saura and Pascual-Hortal, 2007). This concept consists in considering a patch as a space where connectivity exists, integrating in a single measure the connected area within the individual habitat patches (intrapatch connectivity) with the area made available by (reachable through) the connexions with other habitat patches in the landscape (interpatch connectivity) (Saura, 2008). In this way, connectivity is considered as that property of the landscape that determines the amount of the habitat resources that are available to a particular species, regardless of whether such reachable habitat comes from a large continuous patch (intrapatch connectivity), from strong connections among different patches (interpatch connectivity) or, more frequently, from a combination of both. The metrics developed based on this conceptual perspective, i.e., the Integral Index of Connectivity (*IIC*) (Pascual-Hortal and Saura, 2006) and the Probability of Connectivity (*PC*) (Saura and Pascual-Hortal, 2007), have been shown to comply with a set of desirable properties for the effective detection of relevant changes that occur in the landscape and to identify the most critical landscape elements to maintain the overall landscape connectivity, which was not the case for other previously available metrics. The importance of an individual landscape element for the maintenance of the overall habitat network connectivity and availability can be calculated as *dIIC* or *dPC*, which is the relative decrease in *IIC* or *PC*, respectively, after the removal of that element from the landscape network. Saura and Rubio (2010) proposed partitioning the *dIIC* and *dPC* values into three different fractions (intra, flux and connector), each of them quantifying the different ways in which a particular landscape element (patch or link) can contribute to the habitat connectivity and availability in the landscape. These three fractions are measured in the same units and can be directly compared and summed within a unifying framework. The intra fraction represents the contribution of a patch in terms of the habitat area (or some other relevant habitat patch attribute) available within the patch itself (intrapatch connectivity). The flux fraction corresponds to the dispersal flux through the connections of a particular patch with all of the other patches in the landscape, considering that patch as either the starting or ending point of those fluxes. This fraction measures how well a patch is connected to the rest of the habitat in the landscape but does not indicate the importance of that patch to maintain connectivity among other habitat patches, which is quantified by the subsequent fraction. The connector fraction (*dIICconnector*, *dPCconnector*) quantifies the degree to which a particular landscape element serves as an irreplaceable connecting element or stepping stone that upholds the connectivity and ecological fluxes amongst the other elements in the habitat network. This fraction is attracting increased research attention in both network analytical (Baranyi et al., 2011; Bodin and Saura, 2010) and ecological application studies (Gurrutxaga et al., 2011; Rippa et al., 2011; Saura et al., 2011), primarily because (1) it is integrated within a coherent and multifaceted framework for network connectivity analysis but provides unique information that is not redundant with other connectivity metrics (Baranyi et al., 2011), (2) it can be assessed jointly with the same units of measurement for both the habitat patches and links in a network and (3) it is independent from the local characteristics (e.g., habitat area or quality) of the individual landscape elements being evaluated for their contribution to the connectivity (Bodin and Saura, 2010; Saura and Rubio, 2010). However, it remains unclear how and when individual landscape elements can be more valuable as connectivity providers and, therefore, when conservation management efforts should preferably target the maintenance or restoration of these potentially irreplaceable patches. Only a few forest habitats in the province of Lleida (northeast Spain) have been analysed from this perspective (Saura and Rubio, 2010). Therefore, such assessment lacks enough generality to robustly support a solid knowledge of the topological constraints and the effective roles of landscape elements in the functioning of habitat networks or to support management guidelines based on understanding the relative importance of connectivity considerations for different conservation problems. In summary, it is unclear how important connecting elements could be in a wider range of landscape patterns, such as those in different situations and management contexts.

However, at the landscape level, it is difficult to perform experiments involving large landscapes and many replications, and therefore, we must frequently resort to computer simulations to develop and test hypotheses (With and King, 1997). The validity of these landscape models depends on their realism and on their ability to reproduce the values of the landscape metrics that are found in real landscapes (Saura and Martínez-Millán, 2000). With neutral models, which produce an expected pattern in the absence of specific processes (Gardner et al., 1987; With and King, 1997), it is possible to overcome these difficulties. Neutral landscape models have been used in conservation biology for (1) the prediction of critical thresholds in landscape ecology (With and Crist, 1995), which consist of abrupt, nonlinear changes in ecological responses (e.g., functional connectivity or species abundance) as a result of a small variation in a landscape characteristic or species trait (e.g., habitat fragmentation, habitat amount or species dispersal abilities); (2) the determination of landscape connectivity; and (3) the identification of species' perceptions of landscape configuration, among other applications (With, 1997; With and King, 1997).

Among the various types of neutral landscape models (With and King, 1997), those that present some degree of spatial contagion (spatial autocorrelation) allow obtaining more realistic landscape patterns, as is the case of the simulated patterns generated through the modified random clusters (MRC) method (Saura and Martínez-Millán, 2000). Such MRC patterns appear patchy and irregular, similar to real landscapes, and are able to replicate the pattern characteristics (as quantified by selected landscape configuration metrics) found in real landscape settings (Saura and Martínez-Millán, 2000). Moreover, one of the improvements provided by the MRC method is that it allows separating the level of fragmentation and habitat abundance, which can be varied independently.

Our objectives in this study were (1) to assess the degree to which individual habitat patches are able to serve as irreplaceable connecting elements that uphold the habitat connectivity and availability (reachability) in the landscape, as evaluated by the connector fraction of the *IIC* and *PC* metrics; (2) to assess how the connecting role of habitat patches varies with the amount of habitat and its fragmentation and with species dispersal abilities; and (3) to discuss how such an approach can be used to determine in which situations management should concentrate most on the preservation of habitat patches as connecting elements that contribute to maintain connectivity in a wider landscape context. For these purposes, we contrasted a wide range of simulated landscape patterns obtained through the MRC method with empirical data on endangered forest bird species habitat. This approach may allow the identification of those cases and typical landscape settings in which investing in connecting elements per se is an effective conservation strategy and presents a way to