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Using complex network metrics to predict the persistence of metapopulations with asymmetric connectivity patterns

Michael Bode[a,*], *Kevin Burrage*[b], *Hugh P. Possingham*[b,c]

[a] *Applied Environmental Decision Analysis Group, School of Botany, The University of Melbourne, Parkville, Melbourne 3010, Australia*
[b] *Department of Mathematics, The University of Queensland, St. Lucia 4072, Australia*
[c] *The Ecology Centre, The University of Queensland, St. Lucia 4072, Australia*

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ABSTRACT

Almost all metapopulation modelling assumes that connectivity between patches is only a function of distance, and is therefore symmetric. However, connectivity will not depend only on the distance between the patches, as some paths are easy to traverse, while others are difficult. When colonising organisms interact with the heterogeneous landscape between patches, connectivity patterns will invariably be asymmetric. There have been few attempts to theoretically assess the effects of asymmetric connectivity patterns on the dynamics of metapopulations. In this paper, we use the framework of complex networks to investigate whether metapopulation dynamics can be determined by directly analysing the asymmetric connectivity patterns that link the patches. Our analyses focus on "patch occupancy" metapopulation models, which only consider whether a patch is occupied or not. We propose three easily calculated network metrics: the "asymmetry" and "average path strength" of the connectivity pattern, and the "centrality" of each patch. Together, these metrics can be used to predict the length of time a metapopulation is expected to persist, and the relative contribution of each patch to a metapopulation's viability. Our results clearly demonstrate the negative effect that asymmetry has on metapopulation persistence. Complex network analyses represent a useful new tool for understanding the dynamics of species existing in fragmented landscapes, particularly those existing in large metapopulations.

1. Introduction

Metapopulation theory provides a conceptual framework for predicting and managing the future of species in fragmented habitats. Given the possibility of local patch populations becoming extinct, the ability of species to move across uninhabitable landscapes to recolonise empty patches ("connectivity") is critical to the viability of species that exist in metapopulations. The inter-patch landscape greatly affects the movement of individuals, and thus the connectivity of the metapopulation. Barriers can prevent recolonisation between close patches (e.g., high mountain ranges). Landscapes that hinder connectivity in one direction may help it in the opposite direction (e.g., topographical gradients or consistent wind and water currents).

This interaction between individuals and the landscape will result in inter-patch connectivity patterns that are not simply functions of the distances between patches. If connectivity is modelled solely on this distance, the movement of individuals is implicitly assumed to be isotropic and symmetric. A symmetric connectivity pattern assumes that the probability of an individual travelling from patch i to patch

* *Corresponding author*. Tel.: +61 3 8344 5422; fax: +61 3 9348 1620.
E-mail address: mbode@unimelb.edu.au (M. Bode).
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j (and thus potentially recolonising it) is the same as the probability of patch j recolonising patch i. In a realistic, heterogeneous landscape, such symmetric connectivity will be the exception, rather than the rule (Gustafson and Gardner, 1996). As well as being asymmetric, connectivity strengths (the probability that a particular colonisation occurs) will not only reflect inter-patch distance, but rather a combination of distance, the direction of movement, and landscape type. In general we will call the connectivity patterns that arise from a realistic and complex landscape “asymmetric”. (Note that asymmetric connectivity patterns may contain some symmetric connections).

We acknowledge that the spatial arrangement of patches in a metapopulation will have a very important impact on metapopulation dynamics (Hanski and Gaggiotti, 2004). The recent wealth of metrics that approximate the viability of a metapopulation in a spatially heterogeneous landscape (e.g., Hanski and Ovaskainen, 2000; Vos et al., 2001; Frank and Wissel, 2002; Ovaskainen, 2002, 2003) all focus on metapopulations where connectivity strength depends on distance. However simple, distance-based connectivity overlooks landscape factors that have crucial dynamical consequences. For example, distance-based migration patterns ignore the effects of “patch shadowing” (Hein et al., 2004), and individual behaviour (Gustafson and Gardner, 1996). Assuming that connectivity is symmetric will lead to an underestimation of the number of patches needed for metapopulation persistence (Vuilleumier and Possingham, 2006). Recent work on marine metapopulations shows that advective currents can lead to source-sink behaviour that could not be captured or analysed using distance-based migration (Gaines et al., 2003; Bode et al., 2006). An accurate understanding of many metapopulations will therefore require consideration of asymmetric connectivity.

Connectivity modelling was initially based solely on distance because asymmetric connectivity could not be practically measured (Hanski, 1994), however simulation of the connectivity in real landscapes is now computationally feasible, and is becoming increasingly common. The landscape matrix between patches can be quickly assessed by remote sensing, and individual-based connectivity modelling can then be used to simulate the responses of migrating species to the landscape. These methods have been use to model crickets (Kindvall, 1999), butterflies (Chardon et al., 2003), rodents (Vuilleumier, 2003), grey seals (Austin et al., 2004), and especially marine fish (James et al., 2002; Cowen et al., 2002, 2006). Once these connectivities have been estimated however, making sense of the resulting asymmetric connectivity patterns remains difficult, and very little metapopulation theory has been formulated to address it. Analytic Markov methods that can incorporate asymmetric connectivity (e.g., Day and Possingham, 1995) can only cope with a small number of patches (Ovaskainen, 2002). Urban and Keitt (2001) find the minimum spanning tree of the connectivity “graph”, and value connectivity paths and patches accordingly, however minimum spanning trees are only defined for symmetric connectivity patterns. Much population viability analysis relies on Monte Carlo simulation models (Lacy, 1993; Possingham and Davis, 1995; Ackakaya and Ferson, 1999), which can cope with asymmetric connectivity patterns and large numbers of patches, but drawing generalisable conclusions from the results of such simulations is problematic. Ovaskainen (2003) has devised a metric that can be applied to asymmetric connectivity patterns, however his analyses are performed only on distance-based connectivity patterns. The primary aim of this paper is theoretical: to explore the potential of complex network theory as a framework for quantitatively predicting the dynamics of metapopulations with asymmetric connectivity patterns.

Metapopulations and their connectivity patterns can be modelled as networks (which share many features with graphs, as discussed in Urban and Keitt, 2001), consisting of a number of nodes (metapopulation patches) connected by a set of edges (the connectivity pattern). Complex network theory attempts to understand the dynamical properties of these systems through analyses of their interconnections. Using a complex network framework, we consider the importance of several asymmetric connectivity features to the dynamics of “stochastic patch occupancy” metapopulations (Etienne and Heesterbeek, 2001). In particular, we are interested in the dynamic consequences of increasing asymmetry, as well as the mean strength of direct and indirect connectivity paths between patches in the metapopulation. We define several easily calculated metrics for these attributes, and use them to predict properties of the metapopulation dynamics. We focus on predicting the probability of metapopulation extinction, and on estimating the relative contribution of different patches to metapopulation persistence. While these quantities are of considerable importance to practical applications of metapopulation theory (e.g., ecology and conservation), our analyses focus on simplified representations of these ecological systems, to allow a clearer focus on the influence of the connectivity patterns. A complex network approach has the benefit that it is simple enough to be rapidly applied to metapopulations that contain large numbers of patches. It also focuses on the effects of the connectivity patterns themselves, rather than abstractions such as a Markov state transitions (Day and Possingham, 1995; Ovaskainen, 2002), and thus yields a more intuitive understanding of the system.

2. Methods

We consider three network metrics that characterise asymmetric connectivity patterns, to see if they correlate with particular metapopulation dynamics. The metrics are formulated *a priori*, to quantitatively reflect connectivity features of interest. We then assess the predictive utility of these metrics by using them to estimate the probability of metapopulation extinction. There are four steps in this method.

1. We generate metapopulations with asymmetric connectivity patterns, using a version of the “small-world” network-generating algorithm of Watts and Strogatz (1998).
2. We calculate complex network metrics for the metapopulations.
3. The metapopulation model described by Day and Possingham (1995) is used to determine the exact dynamics of the asymmetric metapopulations.