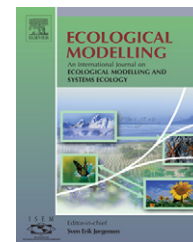


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Using complex network metrics to predict the persistence of metapopulations with asymmetric connectivity patterns

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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.

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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

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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 used 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.

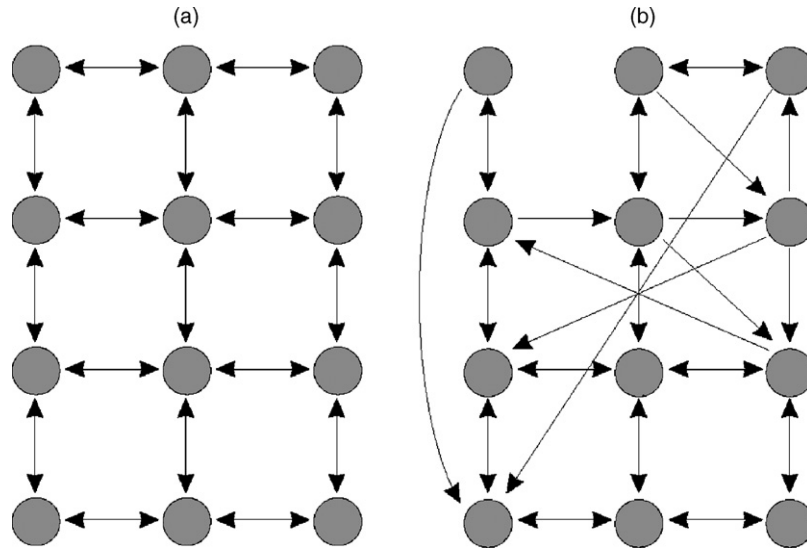


Fig. 1 – The mechanics of the small-world network generation algorithm. We begin with a two-dimensional lattice (a), where each patch is connected to its nearest neighbours. Each connection is then either left unchanged, or is moved with a probability q to connect two other unconnected patches. The magnitude of q determines how asymmetric the resultant connectivity pattern, (b), is. Here, $q = 0.2$.

4. Finally, the predictive ability of the network metrics is tested by comparing them with the exact metapopulation dynamics.

These steps are explained in more detail below. The technique that generates the connectivity patterns in step 1 can result in many possible asymmetric connectivity patterns, and so the steps are repeated a large number of times to ensure that the diversity of possible patterns is adequately captured. The predictive performances of the metrics are also tested over a wide range of parameter values.

2.1. Step 1: Generating asymmetric connectivity patterns

In metapopulation theory, connectivity patterns are stored in a connectivity matrix, which we denote P . Connectivity matrices are $M \times M$ square matrices, where M is the number of patches in the metapopulation. Their elements, p_{ij} , represent the probability at each timestep that the unoccupied patch j will be colonised from patch i , if patch i is occupied.

To construct an asymmetrically connected metapopulation, we begin with a two-dimensional lattice of patches, where each occupied patch can recolonise each of its nearest neighbours with the same probability ($p_{ij} = p$). This is a “regular” network (Fig. 1a), a type of distance-based connectivity pattern. We then move each existing connection with a “rewiring” probability q , to connect another randomly chosen, unconnected pair of patches. If a connection is not moved (with probability $1 - q$), it remains in its original position. The expected asymmetry of a connectivity pattern is thus defined by q . When $q = 0$, no connections are moved and the pattern remains distance-based; as q increases, the resultant network becomes increasingly asymmetric (Fig. 1b). The original definition of small-world networks began with the nodes of the

regular network arranged along the perimeter of a circle (Watts and Strogatz, 1998). The results of our analyses did not change if the original regular network had circular topology.

Some of the resultant asymmetric connectivity patterns may not be “strongly connected”. In a strongly connected metapopulation, it is possible to travel from any patch to any other patch, either directly or through intermediate patches. Mathematically, a connectivity matrix is strongly connected if $P = \sum_{i=1}^M P^i$ is strictly positive. Biologically, in a non-strongly connected metapopulation some patches cannot colonise, or cannot be colonised by other patches. Rather than acting as a single entity, these non-strongly connected metapopulations are actually split into a number of sub-metapopulations that are not connected, or are connected only in a source-sink manner.

The number of patches is a crucial determinant of metapopulation persistence (Etienne, 2004), and so a metapopulation split into two or more unconnected sections will have a much lower viability than a strongly connected metapopulation. Non-strongly connected metapopulations are more likely to occur when connectivity is asymmetric, and this will unfairly bias the assessment of persistence against asymmetric patterns. For example, it is unclear whether the lower persistence of asymmetrically connected metapopulations in Vuilleumier and Possingham (2006) analysis is due to the detrimental effects of asymmetric connectivity, or the increased likelihood of disconnected metapopulations. To avoid this bias, and to more directly focus on the effects of asymmetry, we discard all metapopulations that are not strongly connected.

2.2. Step 2: Calculating the network metrics

1. Asymmetry (Z): We measure the degree of metapopulation asymmetry by the difference between the asymmetric con-

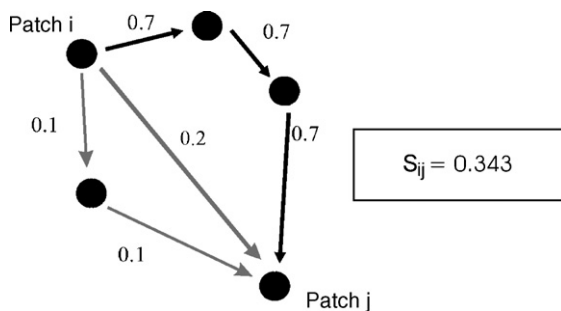


Fig. 2 – Calculation of the strongest connection between patches i and j. The numbers indicate the strengths of each connectivity path. Although the dark path requires the most steps, the magnitude of its connectivities makes it the stronger connection. Its path strength is 0.7^3 , while the strengths of the two grey paths are 0.2 and 0.01.

nectivity pattern and its symmetric equivalent (the mean of the asymmetric connections in both directions). We define an “asymmetry matrix”: $[Z]_{ij} = z_{ij} = |p_{ji} - p_{ij}|/2$, and an “asymmetry metric”: $Z = \sum_{i=1}^M \sum_{j=1}^M z_{ij}$, for the connectivity pattern. When $Z=0$ the matrix is perfectly symmetric; as the asymmetry increases, Z also increases to a maximum value ($Z_{\max} = (M^2 - M)/2$).

2. Average path strength (\bar{S}): The “path strength”, S_{ij} , between two patches in a metapopulation is defined as the path with the maximum associated probability—the strongest connection. Direct connections between patches may not exist, and thus indirect connections must also be considered (Ovaskainen, 2002). When connectivity is asymmetric, it is possible that an indirect path may be the strongest even when a direct path exists (Fig. 2). This phenomenon is not possible when connectivity is distance-based, where the strongest connection is always the path that transverses the fewest edges.

The average path strength, \bar{S} , of an asymmetric connectivity pattern is the average of S_{ij} over all pairs of patches. Biologically, \bar{S} is a measure of how closely connected the entire metapopulation is. As \bar{S} increases, the average unoccupied patch in the metapopulation can be recolonised more rapidly by an occupied patch. We therefore expect metapopulations with a high \bar{S} to be more persistent than similar metapopulations with a lower \bar{S} . To determine the S_{ij} values of a metapopulation connectivity pattern, we implement the “burning algorithm” of Newman (2001), which we have modified to cope with probabilistic, directed networks. This method provides the strongest connection between each pair of edges, and the associated strength of those connections.

3. Centrality (C_i): Centrality can be used to assess the importance of individual patches in the context of connectivity. Urban and Keitt (2001) defined metapopulation patches as either an “end” or a “centre” patch, depending on their position in a minimum spanning tree. Preferential removal of the “end” patches yielded a more persistent metapopulation than removal of the “centre” patches. This method however is limited to symmetric connectivity patterns, and can only categorise patches as either “ends” or “centres”.

The centrality of a patch is related to the end/center designation, but is a quantitative valuation, and is defined for both symmetric and asymmetric networks.

The strongest connection between two patches may be direct, or may pass through a sequence of intermediate patches. The centrality C_i of a patch is the number of strongest connections that pass through patch i , weighted by their strengths (Newman, 2003). Biologically, the centrality of a patch provides a measure of how important it is to the rapid movement of individuals through a metapopulation, and thus how able it is to recolonise temporarily unoccupied patches. Conversely, it also measures how close a patch is to the strongest connectivity paths through a metapopulation, and thus its probability of being recolonised in the event of local extinction.

2.3. Step 3: The Day and Possingham model

To determine whether these three metrics can predict the effect of connectivity patterns on metapopulation dynamics, we will compare them with the results of a model that can explicitly incorporate asymmetric connectivity—the Day and Possingham (DP) model. The DP model is a stochastic metapopulation model that focuses on patch occupancy rather than intra-patch dynamics. There are only two events in the dynamics of a metapopulation: the extinction, and the recolonisation of local patches. These events are modelled as processes that occur with probabilities that are conditional on the occupancy state of the metapopulation. Patch occupancy models assume that local patch dynamics occur at a much faster rate than metapopulation dynamics (Hanski, 1994), and are widely used in metapopulation theory (Day and Possingham, 1994; Ovaskainen, 2002; Vuilleumier and Possingham, 2006).

The extinction of individual patches is a stochastic process, as is recolonisation. As we are particularly interested in the effects of the asymmetric connectivity patterns, we have not included any variation in the extinction probabilities of the different patches. The probability of a patch becoming extinct at each timestep is thus assumed to be the same value, μ , for each of the patches. The dynamics of a particular metapopulation can thus be completely modelled with the connectivity matrix P and the extinction probability, μ . By computing the second-largest eigenvalue of the associated state transition matrix, we can determine the probability of metapopulation extinction in a particular time period. For a thorough explanation of the model, see Day and Possingham (1995).

2.4. Step 4: Testing the complex network metrics

To determine whether complex network metrics can be used to estimate dynamic metapopulation properties, we compare the set of network metrics to the exact predictions of the DP model. The limitations of the DP model will restrict these comparisons to metapopulations with small numbers of patches ($M < 12$). In particular, we will judge the ability of the network metrics to predict the following two dynamical metapopulation properties.

2.4.1. Probability of metapopulation extinction

Many methods exist to assess the health of a particular metapopulation: Ovaskainen and Hanski postulated a number of patch-based measures (Ovaskainen and Hanski, 2003), including the effective number of patches (Ovaskainen, 2002); Frank and Wissel (2002) used the mean lifetime of a metapopulation; Urban and Keitt (2001) measured the sum of the connectivity strengths. We choose to measure metapopulation health by using the probability that a metapopulation that is initially fully occupied will become extinct within a particular time, following a tradition beginning with MacArthur and Wilson (1967). We have arbitrarily chosen this time as 100 years: $P_{ext}(100)$.

It is important that our results are valid for the entire range of possible asymmetric connectivity patterns. The analyses are therefore repeated for one thousand 10-patch metapopulations with different asymmetric connectivity patterns. These connectivity patterns are generated by repeatedly applying rewiring probabilities, q , that range between 0 and 1, to a regular lattice. Because all of the resultant metapopulations begin as the same regular lattice, the total amount of migration in each of the 1000 metapopulations ($\sum_{i=1}^M \sum_{j=1}^M p_{ij}$) is the same, and the different resulting connectivity patterns are the result of the probabilistic variation in the small-world algorithm. The variation in the probability of metapopulation extinction is therefore solely attributable to the different asymmetric connectivity patterns. For each connectivity pattern we calculate the asymmetry and average path strength of the connectivity pattern, and use these as predictor variables for the probability of metapopulation extinction in a non-linear regression. We select the optimal model using the Akaike information criteria (AIC). This fit is not performed to determine a general model of the extinction probability, but to better understand the effects of the different metrics on the persistence of the metapopulation.

2.4.2. Importance of individual patches

We also use the centrality metric to estimate the relative importance of different patches in the metapopulation, and test these estimates using simple sequential patch removal experiments. We propose that if the patches with the lowest centrality are removed first, the resulting decrease in metapopulation viability will be small, relative to other removal strategies.

We examine how patch removal based on lowest centrality compares with all alternative removal methods. First, we generate a metapopulation of 10 patches, connected by an asymmetric connectivity pattern. The patch with the lowest centrality is “destroyed”, and the viability of the remainder of the metapopulation is determined. Additional patches are then removed sequentially. It is important that the C_i values be recomputed after each successive removal, as the loss of patches – which leads to a re-routing of some strongest connections and the elimination of others – alters the dynamics of the metapopulation connectivity. To determine the effectiveness of this centrality method, we compare it to all other removal strategies (there are 10 factorial options, which we search exhaustively), and measure its performance by the number of alternative removal strategies it outperforms. To examine the robustness of the results, we repeated these

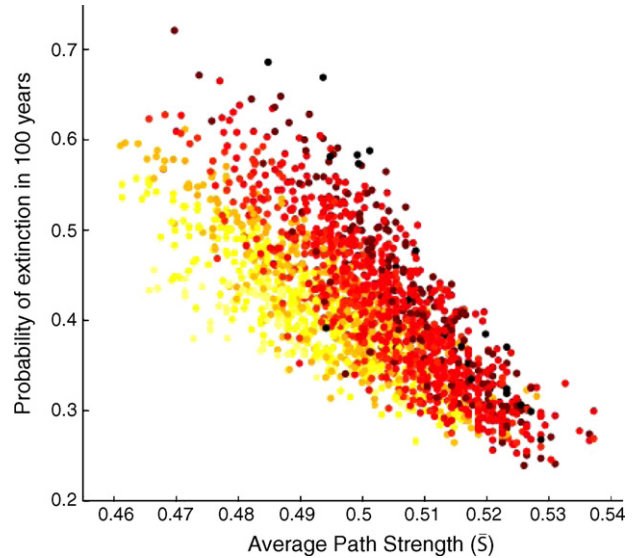


Fig. 3 – The effect of average path strength, \bar{S} , and asymmetry, Z , on the probability of metapopulation extinction. Each point represents a 10-patch metapopulation with the same total connectivity strength. The only difference between metapopulations is the asymmetric connectivity pattern. The average path strength of the particular connectivity pattern is given by the position on the abscissa, and the colour of the points indicates the asymmetry of the connectivity pattern. Darker points are more asymmetric.

patch experiments with many different asymmetric connectivity patterns, generated with different rewiring probabilities (q). We also examined how the method performed when the connectivity strengths (p_{ij}) were not all equal, but varied randomly about a mean value.

3. Results

3.1. Probability of metapopulation extinction

Fig. 3 shows the results of the first experiment, estimating the probability of metapopulation extinction using the asymmetry and average path strength of the asymmetric connectivity patterns. Each point represents the probability of a 10-patch metapopulation becoming extinct in 100 years. Each of the 1000 dots in this figure represents a different, strongly connected asymmetric connectivity pattern. The rewiring probability q has been varied across its entire range ($0 \leq q \leq 1$) to generate these metapopulations, and this results in asymmetric connectivity patterns with very different \bar{S} and Z combinations. In this figure, the extinction probability of each patch is $\mu = 0.4$, and the probability of each connection is $p = 0.75$. Varying these constant values alters the average probability of extinction, but does not have a significant effect on the predictive capabilities of the two metrics.

It is immediately apparent from this figure that connectivity structure has an important effect on the viability of a metapopulation. Although all of these metapopulations have

the same number of patches and the same total amount of migration, the viability of the metapopulations varies greatly, ranging from 20% to 70% probability of extinction within 100 years. The location of each point on the x-axis indicates the average path strength of the connectivity pattern. We can see that, as we predicted, the probability of metapopulation extinction is negatively correlated with \bar{S} . Much of the variation around this trend can be explained by Z , the asymmetry of the connectivity pattern, which is indicated by the colour of the point (lighter dots indicate more symmetric connectivity patterns).

The asymmetry of a connectivity pattern is negatively correlated with the metapopulation's persistence: the more asymmetric a connectivity pattern (darker circles), the higher the probability of metapopulation extinction. Fitting a polynomial regression to the data shown in Fig. 3 reveals that both the average path strength and the asymmetry are important predictor variables. The fit of all subsets of a third degree polynomial model were calculated:

$$P_{\text{ext}} = a_0 + \sum_{i=1}^3 a_i(\bar{S})^i + b_i(Z)^i. \quad (1)$$

Based on the R^2 statistic, AIC chooses the best predictive model as

$$P_{\text{ext}} = a_0 + a_1\bar{S} + a_2(\bar{S})^2 + b_1Z. \quad (2)$$

This model has an R^2 value of about 0.85, indicating that the average path strength and the asymmetry together account for a large proportion of the variation in the probability of metapopulation extinction.

3.2. Importance of individual patches

It seems common sense that if patches must be lost from a metapopulation, we should try to maximise the connectedness of the remaining metapopulation. In Fig. 4, we have used the centrality metric to decide which patch is the least important for metapopulation connectedness. At each step, the patch with the lowest centrality (C_i) is removed. Fig. 4a shows this method applied to a single asymmetric connectivity pattern.

The pattern was generated from a regular lattice with $p = 0.7$ and $\mu = 0.6$. The asymmetry results from a rewiring probability of $q = 0.3$. The triangle on the ordinate axis indicates the probability that the full 10-patch metapopulation will become extinct in 100 years. As we remove more patches, the probability of extinction increases. The small dots indicate the results of all possible patch removal strategies; the open circles indicate the performance of the average removal strategy. The particular strategy suggested by the centrality method is indicated by the closed, dark circles. As more patches are removed from the metapopulation, the probability of extinction increases rapidly under all removal strategies. In terms of extinction probability, the removal method based on centrality is consistently much better than the average strategy, and is very close to the optimal strategy.

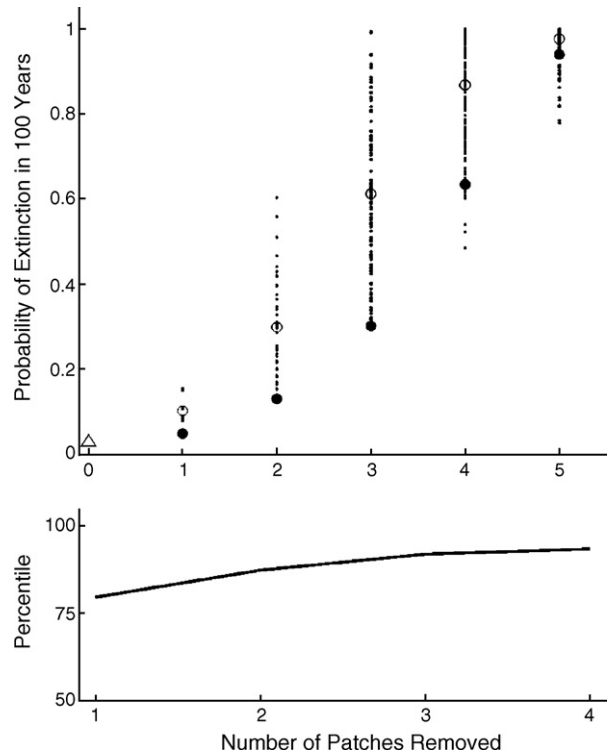


Fig. 4 – (a) We remove five patches sequentially from a 10-patch metapopulation, always removing the patch with the lowest centrality. The probability of metapopulation extinction that result from this method is indicated by the y-position of the large closed black circles (●). Marked with small dots (·) are all of the possible methods for removing patches from the metapopulation. The open circles (○) indicate the average removal strategy. The triangle (Δ) indicates the probability of extinction of the metapopulation with no patches removed. (b) The centrality removal method is repeated on 100 different metapopulations with asymmetric connectivity, and the average performance of the centrality method is recorded when four patches are removed sequentially. The centrality method performed better than a certain percentage of the alternative removal strategies, indicated by the black line.

Fig. 4b records the average results of applying the centrality method to many asymmetric connectivity patterns such as the single example in Fig. 4a. The performance of the method is measured by the percentage of removal strategies that the centrality method performs as well as or better than, in terms of P_{ext} . We investigated the performance of this method under more general conditions, by (1) varying the rewiring probability, q and (2) allowing the values of p_{ij} to vary randomly between 0.6 and 0.8 ($\pm 15\%$). Neither alteration reduced the relative performance of the centrality method, which performed consistently well.

4. Discussion

These results demonstrate that complex network metrics can reflect properties that define the dynamics of stochastic patch

occupancy metapopulations. A complex network perspective complements existing metapopulation analysis techniques as it focuses on statistical properties of the connectivity patterns that have direct intuitive interpretations. Although it is typically quite difficult to quantify dynamic quantities from static interconnection patterns, our results indicate how an understanding of metapopulation dynamics can be advanced using this method.

We used the DP model to predict the probability of a metapopulation becoming extinct, and applied these results to demonstrate the potential of a complex network approach to metapopulation theory. Such stochastic patch occupancy models will not be feasible for metapopulations with more than a small number of patches. Modelling an M -patch metapopulation requires calculating 2^{2M} probabilities. When complexity increases at this rate, even a moderately sized metapopulation is impossible to cope with. Using complex network metrics to directly analyse the same metapopulation requires a relatively manageable M^2 probabilities. Unfortunately, the complexity of the DP model restricted our analyses to small metapopulations ($M < 12$), and it is therefore not possible to guarantee that these network metrics exhibit similar accuracy when applied to larger metapopulations.

The complex network analyses show that the two metrics, asymmetry (Z) and average path strength (\bar{S}), are quantitatively associated with metapopulation persistence. Together, the average path strength and asymmetry of a connectivity pattern explain much of the variation in metapopulation persistence when the probability of patch extinction is uniform. The average path strength can be thought of as a measure of how closely connected the patches are in connectivity space. If the value of \bar{S} is high, any patch in the metapopulation can be rapidly recolonised by another patch, either directly or through a series of intermediate recolonisations. Increasing asymmetry in a connectivity pattern has a negative effect on metapopulation persistence. To help understand this phenomenon, consider an isolated pair of connected patches. If the sum total of colonisation probabilities is constant ($p_{12} + p_{21} = C$) then the probability of metapopulation extinction is minimal when the matrix is perfectly symmetric ($p_{12} = p_{21}$, see Appendix). This analytical result cannot be easily extended to larger metapopulations, however it is feasible that this mechanism, working between all pairs of patches, helps ensure that large metapopulations with symmetric connectivity are the most persistent.

The negative effect of asymmetry on persistence is likely to particularly affect metapopulations in areas with strong landscape gradients. For example, marine metapopulations would be susceptible, as the unidirectional advective effect of currents in marine settings can be pronounced (Largier, 2003), and migrating individuals are frequently in their larval stages, where their ability to counteract these flow-fields is limited (Leis, 2002). Connectivity can also be made more asymmetric by population factors (e.g., individuals leaving overcrowded patches; McIntire et al., 2007).

Patch removal strategies that focus on low centrality ensure that the persistence of the remaining metapopulation is maximised, a result we have demonstrated holds for many different asymmetric metapopulations. Intuition suggests that patches with high centrality are more likely to be frequently

occupied, and thus cannot be easily spared from the metapopulation. Stochastic metapopulation simulations (not shown here) support this assertion, showing increased occupancy on patches with high centrality. The removal method based on centrality is an asymmetric extension of Urban and Keitt (2001) patch removal method, both of which focus on the importance of “core” patches.

We have assumed throughout our analysis that all of the patches have an equal probability of extinction, an unlikely scenario in real metapopulations. This assumption was made to better focus on the effects of connectivity. If this approach is to be directly useful to conservation practitioners, the varying extinction probabilities of the different patches must also be included in the analyses. Both asymmetric connectivity and patch variability could be incorporated using a method similar to that described by Urban and Keitt (2001): an *ex post* inclusion of patch area (frequently considered a surrogate for extinction probability), where the least important patches for connectivity (“end” patches) are removed in order of increasing size. A better method would incorporate both factors into the initial viability analysis, thus acknowledging their interdependence. If complex network approaches to metapopulations are to advance beyond theoretical analyses, this is an important direction for future research.

The connectivity patterns analysed in this paper are all generated by the small-world network model of Watts and Strogatz (1998). Small-world network generation can be summarised in two steps: (1) A regular network is proposed and then (2) edges from this network are rewired with a set probability q to random positions. The underlying spatial nature of metapopulations can be used to rationalise the first decision. As a first assumption we expect that each patch is most strongly connected to its closest neighbours. Small-world connectivity patterns are thus rooted in space, distinguishing them from methods that merely assign connections between patches at random (e.g., Vuilleumier and Possingham, 2006). In a real environment however, some of these close connections are blocked by obstacles or difficult terrains, while other paths are corridors which facilitate long distance connectivity—these mechanisms are simulated in the second-step. The closer q is to one, the greater is the influence of the heterogeneous landscape compared with the distance between the patches. The two extreme cases of the algorithm have been frequently used in metapopulation modelling: randomly connected metapopulations ($q = 1$; e.g., Vuilleumier and Possingham, 2006) and distance-based metapopulations ($q = 0$; e.g., Hubbell, 2001). However, future empirical connectivity analyses may show that real connectivity patterns do not conform to small-world models, despite their plausibility. In addition, the networks used in these analyses may not be of sufficient size to exhibit some of the key features of small-world networks (e.g., drastically increased average path strengths, compared with regular networks).

Analysing metapopulation dynamics by using complex network metrics offers a feasible method for predicting and understanding very large metapopulations with asymmetric connectivity patterns. Deducing system processes from complex network structure is difficult however, and a complete, systematic framework for such analyses does not yet exist (Newman, 2003). Although the systems in these theoretical

analyses are ecologically simplified, we have shown in this paper the considerable potential of easily calculated network metrics for determining dynamic properties of metapopulations.

Appendix A. Effect of asymmetry on a two-patch metapopulation

We assert in this paper that asymmetry in the connectivity pattern of a stochastic patch occupancy metapopulation has a negative effect on its persistence. In this Appendix we show this to be analytically true for a two-patch metapopulation. The fundamental events in the dynamics of stochastic patch occupancy metapopulations are the extinction and recolonisation of patches. Extinction of the population on patch i occurs with a probability μ_i , and recolonisation of a patch i from another occupied patch j occurs with probability p_{ij} . We store all the colonisation probabilities in a metapopulation connectivity matrix P , which for two patches takes the form:

$$P = \begin{bmatrix} 0 & p_{12} \\ p_{21} & 0 \end{bmatrix} \quad (3)$$

The current state of a metapopulation completely defines its future dynamics. For a two-patch metapopulation we label possible states (a,b) , where a and b take the values of 1 or 0, indicating an occupied (1) or unoccupied (0) patch. The value of a indicates the state of the first patch, and b indicates whether the second-patch is occupied. The two-patch metapopulation will therefore be in one of four different states: $(0,0)$, $(0,1)$, $(1,0)$ or $(1,1)$. The state $(0,0)$ corresponds to the extinction of the entire metapopulation. The expected time to metapopulation extinction is inversely proportional to the second-largest eigenvalue (λ_2) of the state transition matrix (Day and Possingham, 1995).

If the connectivity pattern is symmetric (for example, if the connectivity depended on the distances between the patches), then the two connectivity values are equal: $p_{12} = p_{21} = p$. This connectivity matrix has an asymmetry value of $Z=0$. To investigate the effects of asymmetry, we express the colonisation probabilities as deviations from this symmetric connectivity matrix, so that $p_{12} = p + \delta$, and $p_{21} = p - \delta$. The resulting asymmetric connectivity matrix is

$$P(\delta) = \begin{bmatrix} 0 & p + \delta \\ p - \delta & 0 \end{bmatrix}, \quad (4)$$

which has the same total connectivity as the symmetric connectivity pattern, $\sum_{i=1}^2 \sum_{j=1}^2 p_{ij} = 2p$. The degree of asymmetry in the new matrix is $Z(P_2(\delta)) = 2\delta$. The state transition matrix for this metapopulation can be written as

$$T_2 = \begin{bmatrix} 1 & 0 & 0 & 0 \\ \mu & (1-\mu)(1-p-\delta) & 0 & (1-\mu)(p+\delta) \\ \mu & 0 & (1-\mu)(1-p+\delta) & (1-\mu)(p-\delta) \\ \mu^2 & \mu(1-\mu)(1-p-\delta) & \mu(1-\mu)(1-p+\delta) & 2p\mu(1-\mu) + (1-\mu)^2 \end{bmatrix}, \quad (5)$$

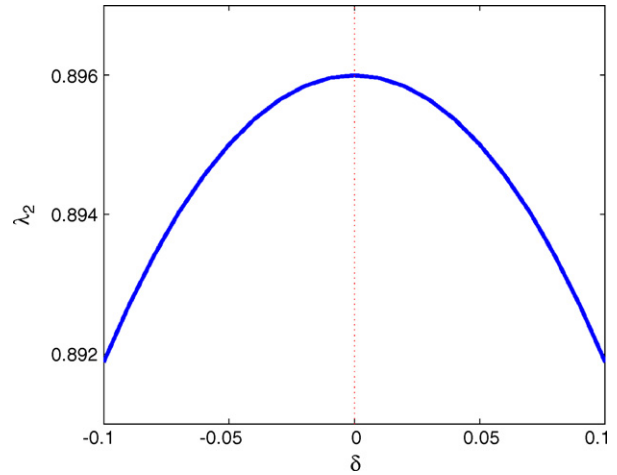


Fig. 5 – The value of λ_2 as a function of δ , the degree of asymmetry in the connectivity pattern. Increasing asymmetry results in a less persistent metapopulation. For this figure, $p = 0.3$ and $\mu = 0.2$.

where the probability of patch extinction at each timestep is assumed to be the same for the two patches. The rate at which this metapopulation becomes extinct can be calculated by using the second-largest eigenvalue, λ_2 , which is the largest eigenvalue of the matrix when the row and column corresponding to metapopulation extinction are removed (Darroch and Seneta, 1965). The characteristic equation of the reduced matrix is a quadratic in δ , and implicit differentiation gives an equation for $(\partial\lambda_2/\partial\delta)$:

$$\frac{\partial\lambda_2}{\partial\delta} = -\delta \frac{(\mu^2 + 2\mu\lambda_2 - 2\mu + 1 - \lambda_2)^2 (\mu - 1)^2}{(\mu - 1 + \lambda_2)(pA + B)}, \quad (6)$$

where $A = (1 - \mu + 2\mu\lambda_2 - \lambda_2)(1 - \mu)^2$, and $B = \mu^3 - \lambda_2^2 - \lambda_2\mu^3 - 5\mu\lambda_2 - 1 - 3\mu^2 + 4\lambda_2\mu^2 + 2\lambda_2 + 3\mu + 2\mu\lambda_2^2$. Eq. (6) seems complicated, but we can immediately see that there is a unique stationary point at $\delta=0$, if $(\mu^2 + 2\mu\lambda_2 - 2\mu + 1 - \lambda_2)^2 \neq 0$. This term is a quadratic in $(1 - \mu)$ that has no real roots. Thus λ_2 has a stationary point only when $\delta=0$.

To show this is a maximum, and that the persistence of the metapopulation is therefore maximised when the connectivity matrix is symmetric, we simply show that $\lambda_2(\delta=0) > \lambda_2(\delta)$ for any $\delta \neq 0$. This is most easily done when $\delta=p$, where $\lambda_2 = (1 - \mu)$. When $\delta=0$,

$$\lambda_2 = \frac{1}{2} \left(2 + 2\mu p - \mu - p + \sqrt{(2\mu p - \mu - p)^2 + 4\mu p} \right) (1 - \mu), \quad (7)$$

and the stationary point is therefore a unique maxima if

$$2\mu p - \mu - p + \sqrt{(2\mu p - \mu - p)^2 + 4\mu p} > 0, \quad (8)$$

which is always true. Thus for two-patch metapopulations, asymmetry has a negative effect on population persistence (e.g., Fig. 5).

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