A Patchy Approach to Food Web Persistence

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ABSTRACT. Traditionally, community models have focused on density-dependent factors. More recently, though, studies that consider populations interacting on a spatial (as well as temporal) scale have become very popular. These metacommunity models often use the patch-occupancy approach, where the focus is on regional dynamics (patches are classified as simply *occupied* or *vacant*). A few studies have extended this work by modelling local dynamics explicitly, although the food webs involved have been relatively simple. This paper takes the next step and considers a spatially explicit habitat where species interact across three trophic levels. The aim is to investigate how web connectance, patch abundance and dispersal patterns affect a community's ability to recover from the loss of a species. I find that asynchrony among patch dynamics may arise from relatively low rates of migration, and that the inclusion of space significantly reduces the risk of cascading extinctions. It is shown that communities with sparsely connected food webs are the most sensitive to perturbations, but also that they are particularly well stabilised by the introduction of space. In agreement with theoretical studies of non-spatial habitats, species holding the highest trophic rank are the most susceptible to secondary extinctions, although they often take the longest to die out. This is particularly pronounced in spatial habitats, where the top predator appears to be the least well adapted to exploit the stabilising properties of space. Results such as these are discussed in detail, and their implications are set in the context of habitat management.

1. Introduction

It is often instantly apparent that space is fundamental to species' interactions; the positioning of an individual sessile organism, for example, strongly influences with whom it must compete. The literature is rich with empirical studies of such organisms, their immobility making reliable data collection a relatively simple task. When studying communities of highly mobile organisms, however, consideration of spatial processes brings with it both practical and theoretical complications. Some degree of spatial structure is apparent in all natural communities, yet for a long time the general opinion was that the inclusion of space in a theoretical model might obsure more than inform. Instead, the vast majority of ecological modelling during the 20th century concerned itself with density-dependent factors, assuming no spatial element. Such work has been invaluable in providing insights into local community interactions and demographics, and is vital in laying the foundations for a larger scale approach. In recent times, however, it has become increasingly apparent that if we are to make true headway in unravelling nature's processes then the role of space can no longer be ignored, particularly in view of the ever increasing demand for scientific guidance on environmental issues.

Over the past 15 years, the potential of metapopulation models to shed light on ecological processes has been rapidly realised[1], though the idea is not a new one. As early as the 1930s, examples were emerging of how considering space might provide new clues, previously obscured in the haze of panmictic population models. Gause (1935) observed the persistence of certain predator-prey communities in the wild, but could not promote similar stability in the laboratory: wild fluctuations in population densities invariably led to extinctions. Gause suggested that in a natural setting populations might be spread across an ensemble of spatially distinct local communities; so long as dynamics were asynchronous among patches, localised drops in population could perhaps be countered by reinvasion from neighbouring communities, thus promoting long-term coexistence. Experimental studies in the 1950s (Andrewartha and Birch 1954; Huffaker 1958) vindicated Gause's conjectures, although it was not until the works of Levins (1969, 1970) that the metapopulation paradigm was formalised.

Levins's classic patch-occupancy model considers space implicitly, focussing simply on the proportion of occupied patches resulting from a uniform distribution of migrants. Extensions of this work have included metacommunity models (see Leibold *et al.* 2004), and also spatially explicit models, whereby dispersal is localised and the flickering mosaic of occupied sites is followed through time (see Tilman and Kareiva 1997). In this paper, inspiration is taken from such frameworks, although here the number of inhabitable patches is limited to a spatially discrete few (to be varied) positioned randomly across a lattice. The aim is not to question how the spatial distribution or frequency of patches might arise — it is assumed that the metacommunity is already well established — but rather to investigate the robustness of regional persistence.

The populations within each patch are modelled explicitly using a tri-trophic web of interactions. Consequently, more than one species may coexist locally and population densities may vary from patch to patch. This can lead to complicated dynamics (Nee *et al.* 1997), but this does not discourage since cyclic and chaotic solutions may be consistent with natural coexistence (Hastings 1988). In fact, similar models have used cyclic dynamics to great effect. For example, Ranta *et al.* (1997) successfully predicted fluctuations in Canadian lynx populations, the results of their spatially linked population model striking a strong resemblance to the empirical data. The fact that local population densities may fluctuate rather than settling to equilibrium values can often promote coexistence in spatially explicit predator-prey models: spatially shifting refuges serve both to prolong persistence of inferior competitors as well as to provide temporary respite for prey (Jansen 1995; Tilman and Kareiva 1997). Of course, the level of dispersal is an important factor in promoting such coexistence: too little and local populations could not be rescued from

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[1]Using figures from the BIOSIS database, Hanski and Gilpin (1997) graph a dramatic rise in the number citations to the key word "metapopulation" since 1990.

extinction; too much and patch dynamics may be synchronised, allowing a particular species to become extinct simultaneously in all patches (Hollyoak and Lawler 1996).

The idea that asynchrony among patch dynamics prolongs regional coexistence is not, in itself, much of a revelation. What is important is that patchy habitats have been observed in natural settings and thus we must query under what conditions such heterogeneity might arise (de Roos and Sabelis 1995). In an attempt to answer this question, I begin with the null state that all species persist in all patches and that their local dynamics are synchronised. Migration is then introduced using a model that expresses dispersal as a function of both distance and patch abundance. Once the system has settled, the robustness of regional persistence is determined via the forced removal of one species. In particular, the frequency of cascading extinctions is compared for different levels of patch abundance, dispersal and web connectance. Results for a single-patch community are also discussed for comparison.

2. Methodology

2.1. **Local Dynamics.** Each patch is inhabited by six species, coexisting across three trophic levels. The food web is triangular in structure[2], with three basal species (autotrophs requiring no explicit food source for persistence) holding the lowest trophic rank. These are consumed by two intermediate species, which are prey for the one top species. Omnivory is also allowed when web connectance is suitably high.

The interactions within each patch are described by the generalised Lotka-Volterra equations:

$$\frac{dN_i}{dt} = N_i \left(r_i + \sum_{j=1}^{6} \alpha_{i,j} N_j \right) \qquad \text{for species } i = 1, \ldots, 6, \tag{1}$$

where dN_i/dt is the rate of change of density with respect to time, r_i is the intrinsic growth rate and $\alpha_{i,j}$ represents the effect of species j on the per capita rate of increase of species i. For a given web connectance[3], the appropriate number of consumer-resource links are randomly allocated positions in the web, the only proviso being that every consumer must prey on at least one species in the trophic level directly beneath. Research concerning the relative strengths of species interactions is still in its infancy. However, empirical evidence to date strongly suggests that generalist consumers tend to favour just a few of their many possible prey species (see McCann 2000 for a review, or Wootton 1997 for an example). In an attempt to mimic this skewed distribution of interaction strengths, each predator is randomly assigned one strong feeding link, whilst the other links are assumed to be weak. Figure 1 shows three possible web configurations: the first has the lowest possible connectance; the second has a medium level of connectance and the third shows an example where all links are present.

2.2. **Regional Dynamics.** Each patch is continually subject to migration events: per time unit, a fixed proportion, m, of each species' population migrates from its current patch and disperses among the neighbouring communities. For a habitat of s patches, the number of individuals migrating from patch q to patch p, per unit time, is given by (Hanski and Woiwod 1993)

$$M_{i,p,q} = m N_{i,q} \frac{e^{-d_{p,q}/c}}{\sum_{l,l \neq q}^{s} e^{-d_{l,q}/c}} \qquad \text{for } i = 1, \ldots, 6, \tag{2}$$

where $N_{i,q}$ is the density of species i in patch q, the distance between the two patches is $d_{p,q}$, and c is a parameter. Thus the flow of migrants is greatest between patches a relatively small distance apart (the strength of this bias is determined by c: lower values correspond to more localised

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[2]Triangular communities are often found in real food webs, see for example Cohen *et al.*'s recent survey of a lake ecosystem (2002).

[3]Defined to be the number of consumer-resource links divided by the square of the number of species.
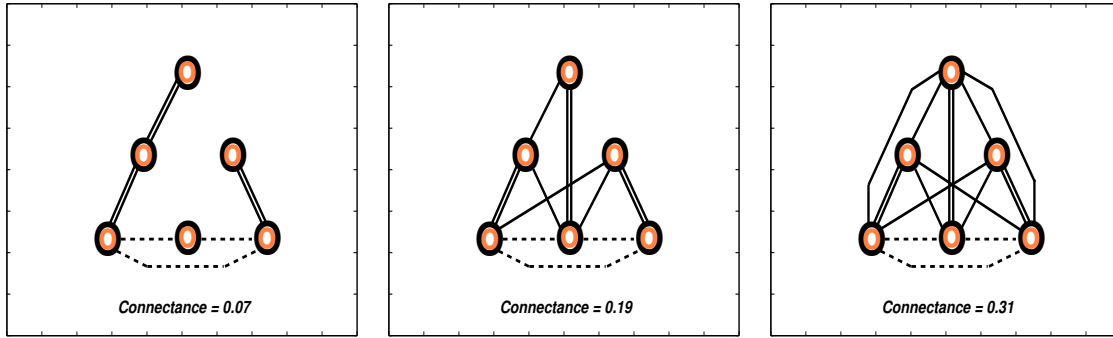
FIGURE 1. Web diagrams show three viable configurations for between-species local interactions. The dashed lines connecting the three basal species represent direct interspecific competition (present in all webs), whilst the solid lines represent consumer-resource links: single for a weak link; double for a strong link. The first diagram illustrates that the lowest connectance does not permit multiple resource links, and hence all predator-prey interactions are strong. The second shows an example of a configuration for an intermediate connectance and the third an example where all possible interactions are present.

dispersal). The change then, per unit time, in patch p densities as a result of migration is given by

$$\widetilde{N}_{i,p} = \underbrace{\sum_{\substack{q \\ q \neq p}}^{s} M_{i,p,q}}_{\text{Flux in}} - \underbrace{m N_{i,p}}_{\text{Flux out}} \qquad \text{for } i = 1, \ldots, 6. \tag{3}$$

The $q \neq p$ condition on the summation term means that no migrant may return to the patch it has just vacated. Migration events are instantaneous and, as such, all individuals are continually subject to the competitive interactions described by Equation (1):

$$\frac{dN_{i,p}}{dt} = (N_{i,p} + \widetilde{N}_{i,p}) \left(r_i + \sum_{j=1}^{6} \alpha_{i,j} (N_{j,p} + \widetilde{N}_{j,p}) \right) \qquad \text{for } i = 1, \ldots, 6. \tag{4}$$

The dispersal rule used here ensures that all migrants are successful in reaching another patch. It is plausible, however, that migration might pose some kind of risk to the individual, and that this risk should increase with the distance travelled. This possibility was tested by multiplying Equation (2) by the term $(1 - \tau d_{p,q})$, where $0 < \tau < 1$ quantifies the risk. However, for realistically small values of τ, the results are qualitatively similar to the original model and are therefore not described here.

2.3. **Parameters.** All migration and growth rates are defined per day and hence the time variable relating to Equations (1) through to (4) should be interpreted similarly. The parameters to be varied are: patch abundance ($s = 1$ to $s = 17$); the migration coefficients ($m = 0.001$ to $m = 0.1$; $c = 0.1$ to $c = 1$) and web connectance ($C = 0.07$ to $C = 0.31$). Intrinsic growth rates are fixed at 1, -0.01 and -0.001 for the basal, intermediate and top species respectively. To give meaning to these values, an example of estimated generation times is given[4]: one day for basal species; 26 days for intermediate species and 318 days for the top species. If no interaction exists between two species then $\alpha_{i,j}$ is set to zero; otherwise, the strength of the link is drawn at random from a continuous uniform distribution, the limits of which are outlined below.

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[4]Generation times are estimated from allometric relations between mortality rates and body size (Roff 1992), and between body size and maturation times (Blueweiss *et al.* 1978).

Predation Coefficients. If a consumer has only one prey then the feeding link is assumed to be strong, its value being drawn from the interval -(0, 0.5]. Otherwise, the one randomly selected strong link is assigned a value from the interval -(0, 0.4], whilst all weak links are assigned values from -(0, 0.1]/(number of prey - 1). Hence the average link strength is negatively correlated with the number of prey species (McCann *et al.* 1998).

Prey Coefficients. The effects that prey have on their predators are given by $\alpha_{j,i} = -e\alpha_{i,j}$, where e is the conversion efficiency (0.02 for omnivorous links, 0.2 otherwise). Thus predator-prey interactions are strictly asymmetric and no mutualistic relations exist within the system.

Direct Interspecific Competition. Basal species compete with one another for the implicit resource that fuels their growth. The strength of these links are drawn from the interval -(0, 0.5]. There is no direct interspecific competition within higher trophic levels, although indirect competition exists implicitly between consumers that share a common resource.

Intraspecific Competition. All individuals are subject to within species competition, the self-limitation terms, $\alpha_{i,i}$, being drawn from the interval -(0, 1].

The competitive interaction strengths defined here are based on those used by Ebenman *et al.* in their study of how single-patch communities respond to species loss (2004).

2.4. **Generating Starting Communities.** The global habitat is a 25 cell by 25 cell grid, in which the patches are allocated their positions at random from a continuous uniform distribution. Initially, the conditions for each distinct local community are identical: a permanent single-patch starting community is found (see Appendix A for details) and replicated s times. Migration is then introduced and the system, starting from equilibrium values, is integrated over 20,000 time units (this equates to approximately 55 years). This gives the opportunity for spatial heterogeneity to emerge and the system time to settle. Since I am interested in the deterministic behaviour of the system, no restrictions are made on how large a population might become (competition for space is not considered). However, a lower bound is imposed, below which a species' patch density is considered too small to avoid stochastic extinction. This threshold is set at

$$0.05 \ \times \ \min \left\{ N_{i,p}\big|_{t=0} : \ i = 1 \ldots 6; \ p = 1 \ldots s \right\}, \tag{5}$$

that is, five percent of the smallest starting density. During integration, local densities are checked to see whether they have fallen below this threshold and, if so, they are set to zero. Only if no local extinctions have occurred after 20,000 time units are the final densities accepted as a viable starting community; otherwise, new interaction coefficients and patch layout are generated and the process is repeated until a persistent community is found.

In the majority of cases, the system settles well within the allotted time. Occasionally though, the inclusion of the non-linear migration terms give rise to heteroclinic cycles, where three or more species' densities oscillate with increasing amplitude over time. The ultimate extinction of at least one of the species is inevitable, although since the period of the oscillations increases over time it sometimes takes a while before the extinction threshold is breached. It is for this reason that the system is integrated over such a long time period: it is the asymptotic state of the system that is of interest and therefore all destabilising transients must be lost before the integration is halted.

2.5. **Species Removal.** In order to investigate how dispersal and patch abundance affect meta-community stability, the system is perturbed by a forced extinction event: species i is removed from the starting community in all patches. That is, the species' global density is set to zero, leaving no means by which it might recover. The model is then integrated over 20,000 time units and the final densities are recorded. This procedure is repeated 150 times for each species, $i = 1$ to $i = 6$, allowing comparisons to be made between the effects of disruptions at the different trophic

levels. For each new run performed, a new starting community is constructed, as outlined above.

The removal of a species is a convenient means by which to assess the robustness of coexistence in spatial habitats. More than this, though, species extinctions are a very real occurrence and so it is hoped that this approach provides some insight into how real ecosystems might respond to species loss. To add realism to the model, *if all resources on which a consumer usually feeds are lost then the consumer forages for any available source of prey.* In terms of the simulations, this means that the consumer is allocated one weak (non-cannibalistic) feeding link at random (the 'foraging link'). Thus, whilst its chances of survival are still low, global extinction is not a certainty. Although this adaptability of endangered species has not been included in earlier (theoretical) work regarding species loss, Kondoh (2003) finds that a consumer's adaptive food choice is key to the long-term stability of complex communities.

3. Results and Discussion

3.1. **The Introduction of Space.** Before looking at how well the communities fared when perturbed by species removal, it is appropriate to draw attention to a couple of interesting results from the community assembly process. In general, the introducion of migration has only a slight effect on local dynamics and the densities soon settle to equilibrium values. There are, however, two exceptions that warrant further discussion. The first arises when the permanent local communities contain a stable limit cycle: migration causes the phase space trajectories to spiral away from the interior fixed point and toward the limit cycle. Consequently, all species' densities exhibit self-sustained oscillations in all patches. Figure 2 gives an example of this phenomenon in an eight-patch habitat with a migration rate of one percent per day. Despite the identical initial conditions, the effect of localised migration is to desynchronise oscillations from patch to patch. Thus, Figure 2 gives a clear example of how spatially shifting refuges for prey can arise, even when the rate of migration is very low.

The second example of migration having a dramatic effect on local dynamics is rather more curious. For the majority of parameter values investigated, the introduction of migration proves to be destabilising in less than one percent of cases. The exception to this otherwise ubiquitous result occurs when an intermediate web connectance ($C = 0.19$) is combined with the highest migration rate (ten percent per day). In this case, at least one species becomes extinct in over two percent of cases and, for high patch abundances (≥ 11), stability is too frequently disrupted to generate an adequate number of starting communities. At first glance, the fact that the middle connectance is found to be the most sensitive to migration is perhaps surprising: increasing the frequency of interactions is often found to enhance stability (see McCann 2000 and references therein). However, closer inspection of the frequency and position of consumer-resource links reveals a subset of web configurations that are impossible for the two extreme connectances, but are common for the intermediate connectance. The critical feature of such configurations is that the top species has one strong omnivorous link and just one weak non-omnivorous link (see Figure 1 for an example). As this is the only feature of note that is unique to the intermediate connectance, it is reasonable to suppose it is this which makes these webs particularly sensitive. I suggest a possible explanation to be that the efficiency with which prey biomass is converted into predator biomass is ten times lower for omnivorous links than for non-omnivorous links ($e = 0.02$ versus $e = 0.2$). Thus, if the one 'strong' interaction happens to be omnivorous then the consumer's equilibrium density will be considerably lower. In the case described above, the top species has only one alternative prey item and therefore its density is likely to lie dangerously close to the extinction threshold. In such cases, the highest migration rate could well cause the top species to become extinct in at least one patch, and therefore the starting community would not be deemed viable. Consistent with this reasoning is the fact that the top species is invariably the first to become locally extinct for the connectance in question.
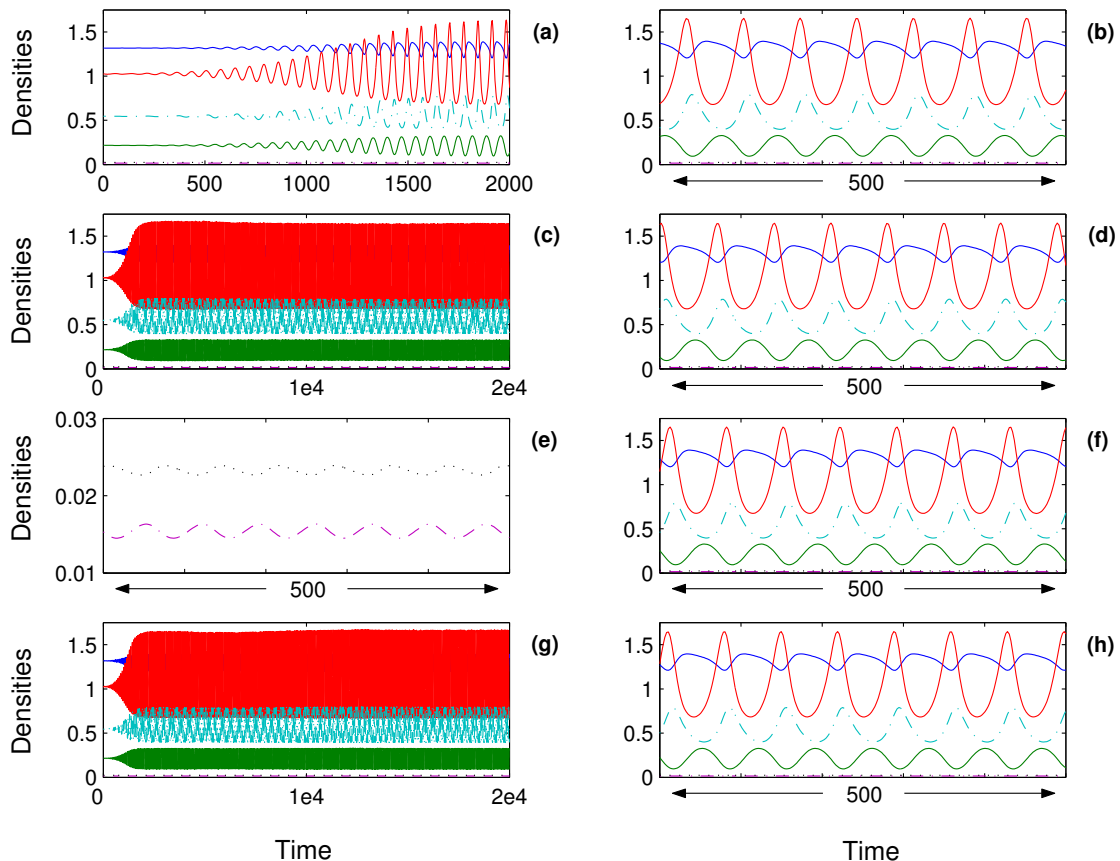
FIGURE 2. Following the introduction of migration between eight identical patches, population densities are followed over a period of 20,000 time units. The solid lines track the basal species' densities; the dashed track the intermediate, whilst the dotted line tracks the top species. For clarity, six of the patches show zoomed perspectives of their dynamics: patch (a) focuses on the first 2,000 time units; patches (b), (d), (e), (f) and (h) all focus on the last 500, by which time the system has settled to reveal stable asynchronous oscillations. The web connectance is 0.19 and the migration coefficients are $m = 0.01$ and $c = 0.4$.

3.2. **The Risk of Cascading Extinctions.** In Figure 3, the probability that a primary extinction event leads to the global loss of at least one further species is compared for different patch abundances. Results for the single-patch habitat are consistent with those found by Eklöf and Ebenman (unpublished manuscript). Since their food web structure and interaction strengths are similar to those used here, the similarity with their results indicates that the foraging ability of an endangered species (described in Section 2.5) rarely prevents its extinction in this case. Single-patch results also match closely with those found by Lundberg *et al.* (2000) and Frodin *et al.* (2002). This is more surprising because both these studies investigate a highly connected linear web. Thus, the similarity in extinction probabilities suggests that separating the six species into a vertical hierarchy of interactions has surprisingly little effect on their ability to coexist. It is noteworthy, though, that this is only true when web connectance remains high and that a decrease in the frequency of vertical interactions significantly increases the risk of secondary extinctions.

For a migration rate of one percent per day and a dispersal ability of $c = 0.4$, the introduction of space enhances the system's ability to cope with the loss of a species (Figure 3; Table 1). This

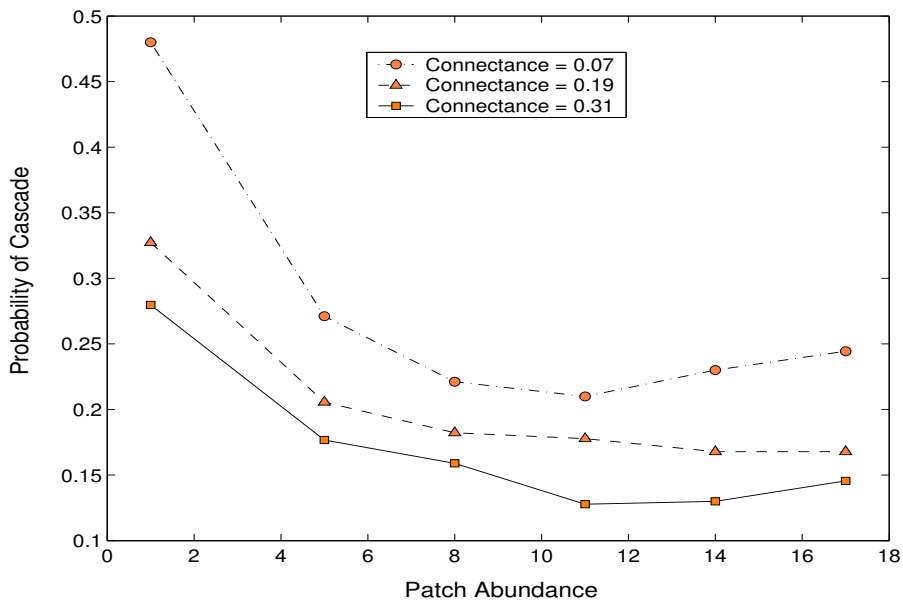
Connectance = 0.07
Connectance = 0.19
Connectance = 0.31
Probability of Cascade
Patch Abundance
0.1
0.15
0.2
0.25
0.3
0.35
0.4
0.45
0.5
0
2
4
6
8
10
12
14
16
18

FIGURE 3. How does the risk of cascading extinctions vary with patch abundance? The results shown are for migration coefficients of $m = 0.01$ and $c = 0.4$.

TABLE 1. Chi-square tests show highly significant differences between the single-patch and five-patch habitats ($m = 0.01; c = 0.4$). Frequencies are the number of cascading extinction events following species removal in 900 runs.

Connectance	**1-Patch**	**5-Patch**	χ^2 **Result**	**p-value (1 d.f.)**
0.07	419	244	72.2931	< 0.0001
0.19	295	185	33.7528	< 0.0001
0.31	259	159	30.5393	< 0.0001

stabilising effect is most pronounced in the transition from one to five patches, although the extinction probabilities continue to decrease for the eight and 11-patch habitats. The robustness of this result is amplified by the fact that community assembly is deliberately biased *against* the emergence of spatial heterogeneity: the (identical) permanent local communities are resilient to disruption by migration which, compared with other models using a similar dispersal rule (Hanski *et al.* 1993; Ranta *et al.* 1995, 1997), is set very low. Whilst, in general, the differences in pre-extinction patch densities are indeed only slight, it is clear that they significantly increase the system's ability to recover from a major perturbation.

Figure 3 hints that higher patch abundances could prove to be destabilising, although tests with a 30-patch habitat reveal no such collapse (Table 2). This indicates that the higher extinction probabilities found in habitats with 14 and 17 patches may well be insignificant. In contrast, Frodin *et al.*'s study of a single-trophic metacommunity (2002) reveals an abrupt return to single-patch extinction probabilities when patch abundance is increased beyond a critical level (somewhere between 13 and 16 patches). Whilst it is reasonable that a habitat in which local communities are too densely packed could exhibit dynamics akin to a non-spatial model, I question whether such an abrupt transition is realistic. The explanation offered in the paper is that increasing patch abundance increases the number of generations required for migration to link all local communities. It is argued that there may therefore come a point where any struggling local population would no longer be open to rescue efforts. However, even if this were so (and it is far from clear), it does not explain the suddenness of the suggested 'isolation'. Frodin *et al.*'s study

TABLE 2. Chi-square tests do not show significant differences between the 11-patch and 30-patch habitats ($m = 0.01; c = 0.4$). Frequencies are the number of cascading extinction events following species removal in 900 runs.

Connectance	11-Patch	30-Patch	χ^2 Result	p-value (1 d.f.)
0.07	189	179	0.2767	0.5989
0.19	160	151	0.2488	0.6180
0.31	115	117	0.0049	0.9440

is particularly intriguing because the dispersal rule they use is similar to Equation (2). One explanation for the differences in our results could be the foraging link included here. However, it is hard to see how this alone could negate a sudden reduction in stability for high patch abundance, especially considering Frodin *et al.* use a higher web connectance than two of the examples in Figure 3. A more plausible reason why the tri-trophic system proves more stable is that, although migration rates *per day* are equal for all trophic levels, the proportion of individuals migrating *per generation* can differ (due to the different life expectancies). Therefore, species at different trophic levels can be considered to experience their worlds at different spatial, as well as temporal, scales. As shown by Chesson and Huntly (1997), coexistence can be promoted by populations' disparate exploitation of spatio-temporal heterogeneity.

In all cases, the risk of cascading extinctions is higher in habitats with a lower web connectance. It is thought that, unless their effects are dampened by weak interactions, strong consumer-resource links have an adverse effect on community level stability (see McCann 2000). For the lowest connectance used here, all consumer-resource links are assumed to be strong (see Figure 1). As connectance increases, so too does the frequency of weak links to alternative prey items, causing an overall reduction in the mean interaction strength. It is therefore not surprising that systems with a higher web connectance are found to be less prone to collapse. The possible instabilities in habitats with an intermediate web connectance (discussed in Section 3.1) are not exposed for the low migration rate used here and, in any case, such configurations would be weeded out in the selection of starting communities. Although the number of interactions is linearly related to connectance, the differences between extinction probabilities attenuate with increasing connectance. Thus, the relationship between connectance and the ability of weak interactions to stabilise the system appears to be non-linear in this model. Whether or not this is a general result is not clear: the existence of skewed interaction strengths is a relatively recent finding and its effects have yet to be fully understood.

3.3. **Dispersal Patterns.** Any asynchrony among local dynamics is a direct consequence of localised dispersal. Thus the degree to which migrants are inclined to settle in nearby patches is clearly central to promoting, or inhibiting, regional coexistence. To investigate just how sensitive the model is to different patterns of dispersal, c is varied between sufficiently large bounds to expose all significant variation in the frequency of cascading extinctions. There is no doubt that dispersal abilities can vary enormously from species to species, and therefore this also serves to encompass a wider variety of natural communities into the scope of the model.

The effect of varying migrants' dispersal ability in a five-patch habitat is shown in Figure 4. Results for habitats with higher patch abundances are qualitatively similar (see Appendix B) and therefore the discussion here can be considered general. It is clear that higher dispersal distances result in communities that are more susceptible to cascading extinctions. This is a consequence of the less pronounced spatial heterogeneity that inevitably results from more uniformed dispersal. The highest parameter graphed is $c = 1$, although inspection of the migration kernel reveals that higher values would continue the trend and, in the limit, extinction probabilities would equal those for the single patch habitat: individuals would be equally dispersed among all patches and
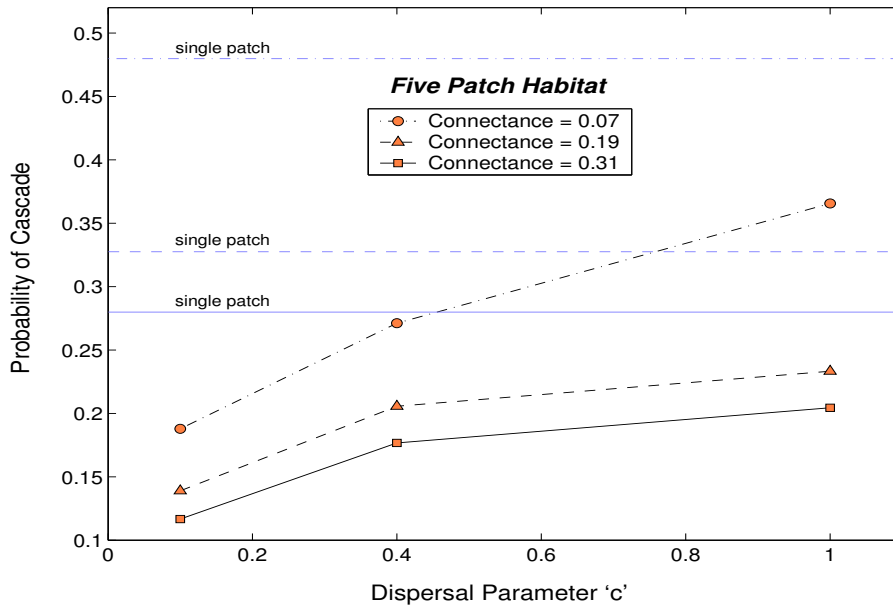
FIGURE 4. Shows how increasing the dispersal distance of migrants affects the risk of cascading extinctions following the loss of a species. The horizontal lines mark the probabilities from the single-patch model. The results shown are for a five-patch habitat ($m = 0.01$); refer to Appendix B for more detailed results and higher patch abundances.

therefore the system would be deterministically identical to the non-spatial model.

3.4. **The Rate of Migration.** Figure 5 shows the risk of cascading extinctions for three different migration rates in a five-patch habitat. As for the dispersal patterns, results for higher patch abundances can be found in the Appendices, although they are qualitatively similar to those described here. For the lowest rate investigated (0.1 percent per day), the extinction probabilities are similar to those for the single-patch model. This is true for all levels of connectance and patch abundance (see Appendix C). The dramatic decrease in extinction probabilities when the rate is increased to one percent suggests a threshold between $m = 0.001$ and $m = 0.01$ where migrants become numerous enough to create differences in patch dynamics. Another reason for this large drop in the risk of cascading extinctions is the nature of the extinction threshold, described by Equation (5); any efforts by migrants to recolonise a patch where a species has become locally extinct will be unsuccessful, unless the propagule size (the density of the 'rescue party') is greater than the extinction threshold.

For a migration rate of 10 percent per day, the vast majority of starting communities are extremely resilient to the loss of a species (Figure 5): secondary extinctions are observed in less than three percent of runs, even for the lowest possible web connectance. A look back at Figure 1 shows that, for a connectance of 0.07, there is a relatively high probability that the primary extinction event will remove a consumer's only source of prey. Recall that in such cases the consumer is given one last chance for survival by the foraging link. Thus Figure 5 shows that, in a spatial habitat with a high rate of migration, consumers are considerably more likely to survive with only this weak interaction than they are in a single-patch habitat. This finding is as unprecedented as it is remarkable, and thus it is important to question its validity. I therefore draw attention to three potential flaws that should be considered. Firstly, the ability of an otherwise doomed population to forage for an alterative food source clearly depends on the adaptive capabilities of the species in question. Since this feature has not been included in theoretical studies of species loss before, it
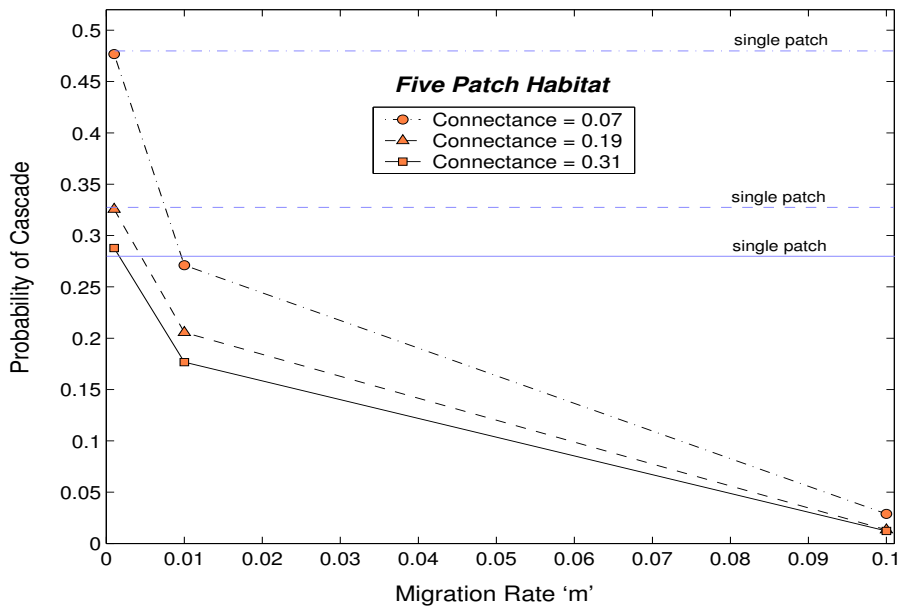
FIGURE 5. Shows how increasing the rate of migration affects the risk of cascading extinctions following the loss of a species. The horizontal lines mark the probabilities from the single-patch model. The results shown are for a five-patch habitat ($c = 0.4$); refer to Appendix C for more detailed results and higher patch abundances.

is hard to make comparisons with previous work. However, Kondoh (2003) models fluctuations in link selection and predicts patterns of interaction consistent with empirical observations. Secondly, consumers surviving with the foraging link are likely to have particularly low densities. Although this model focuses on the deterministic behaviour of the system, it must not be forgotten that populations persisting at lower densities are more prone to extinction in the presence of demographic stochasticity (Engen 1998; Ebenman *et al.* 2004). Finally, a migration rate as high as ten percent can, in some cases, make the generation of stable starting communities very difficult, as explained in Section 3.1. This calls in to question how realistic such a high migration rate is for the kind of metacommunities described in this paper.

3.5. **Trophic Position.** The above discussion has generalised extinction events in two distinct ways. Firstly, in any particular run, the robustness of community persistence has been defined by the presence or absence of a cascade, rather than the frequency of secondary extinction events. Secondly, the trophic position of neither the removed species nor the species becoming subsequently extinct has been considered explicitly. To address this, a closer look is now taken at the nature of secondary extinctions.

Since the frequency of secondary extinctions is non-normally distributed — there is a strong skew toward the lower end of the scale — it is appropriate to use a non-parametric measure to compare results. There is no difference between the median number of secondary extinctions for the different types of spatial habitat (all medians equal one). When considering extinctions caused by removal at different trophic levels, the medians for spatial models (all equal to one) do differ from the single-patch case, where they often equal two; Table 3 shows that the introduction of space decreases the median size of cascades that result from the removal of the top species (and basal species for $C = 0.07$).

TABLE 3. Given that a cascading extinction has occurred, how many species are likely to be lost? This table shows the median number of secondary extinctions for the single-patch habitat. Median values for the spatial habitats are equal to one for all parameter values discussed.

Primary Extinction	$C = 0.07$	$C = 0.19$	$C = 0.31$
Basal Species	2	1	1
Intermediate Species	1	1	1
Top Species	2	2	2

In any multi-tophic model, the basal species provide the foundations on which all other interactions are built. Thus, the removal of a basal species is likely to have particularly severe ramifications, as can be seen in Figure 6. For the lowest connectance, over half of the cascading extinction events recorded result from the loss of a basal species. For the two higher connectances, this proportion is larger still. This is because higher connectances allow omnivory and so both the top consumer and the primary consumers may rely on the basal species directly. This has a particularly large impact on the proportions in Figure 6 because the top species is the most prone to secondary extinction (see Figure 7). Despite the effects of ominivory, the median size of cascades caused by the removal of a basal species is smaller for higher connectances (Table 3), due to consumers relying on more than just one prey species.

The removal of an intermediate species frequently leads to secondary extinctions, either directly (when the top species loses its focal prey) or indirectly (when the competitive interactions beneath are disrupted). The latter is an example of when predator-mediated coexistence previously held prey densities in check, although this behaviour is found to be much less common. Similarly, it is rare that the loss of the top species causes extinctions lower down the food-chain (Figure 6), although when it does the consequences are often severe (Table 3): the absence of top-down regulation releases intermediate species from predation, allowing them to over-exploit the resources on which they depend. In such cases, it is not uncommon for all but one or two species to be lost in the resulting cascade. Empirical evidence for such communitiy collapses is well known (Estes and Palmisano 1974, for example), although it has proved an elusive phenomenon to model. A patch-occupancy study by Caswell (1978) shows that predator-mediated coexistence may be considerably more probable in an open system. I find the introduction of space to have little effect on the proportions shown in Figure 6, although this is a consequence of the local dynamics — it has been known for some time that predator-mediated coexistence in closed Lotka-Volterra systems requires a delicate balance of interaction strengths (Cramer and May 1971).

The risk of a species being caught in the wave of secondary extinctions increases with its trophic rank, as shown in Figure 7. The introduction of space exaggerates this pattern to the point where, for the highest migration rate, no secondary basal extinctions are recorded at all. Thus it appears that the higher in the food-chain a species is positioned, the less well adapted it is to exploit the stabilising properties of space. Patch-occupancy models concerned with the effects of habitat loss find a correlation between trophic rank and the level of habitat destruction at which extinctions occur, whereby predators are lost before their prey (Bascompte and Sole 1998; Holt *et al.* 1999; Melián and Bascompte 2002). One must be careful when comparing patch-occupancy models with those that consider local dynamics explicitly. For example, in this paper a five-patch habitat does *not* represent a depleted eight-patch habitat, as both are necessarily stable, settled systems at time zero; the different patch abundances investigated here are intended to represent distinct forms of spatial structure present in different habitats. However, a common finding of both approaches is that higher order species are particularly sensitive to perturbations in their environment, and that their inferior capacity to exploit spatial heterogeneity renders them more susceptible to extinction events.
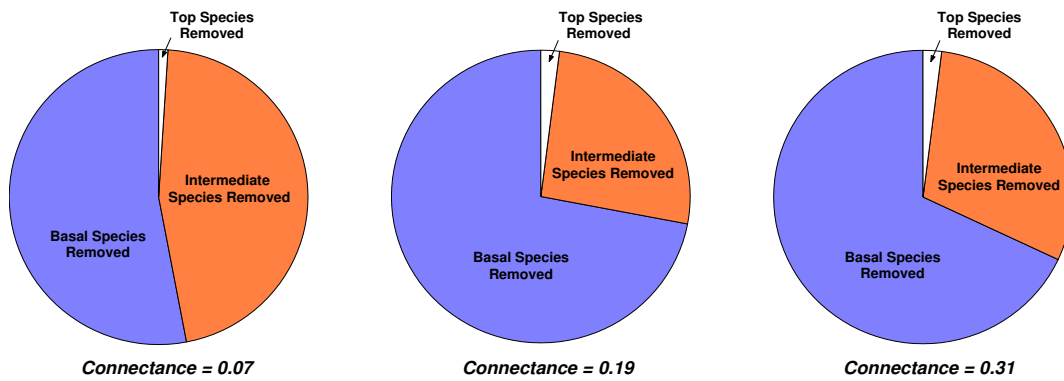
FIGURE 6. Pie diagrams show the proportions of cascades caused by the removal of a species at the different trophic levels. More runs were performed where a basal species was deleted, but this bias has been corrected in the calculation of these fractions. The results shown are for a single-patch community, although these proportions do not vary significantly with the introduction of space.

Whilst the top species is ultimately the most likely to be lost, its population invariably takes the longest of all species to fall below the extinction threshold. This result has important consequences for conservation efforts, because a top predator observed to have a stable population may actually be caught in a long, ultimately terminal, transient. In a system where the predator plays an important role in mediating competition beneath it, its unnoticed decline to extinction is likely to be followed by a relatively quick succession of extinctions among lower trophic ranks. This danger is even more apparent in spatial habitats, where asynchrony in local dynamics lengthens relaxation times still further and where the top predator is even more at risk (in comparison to lower order species — Figure 7).
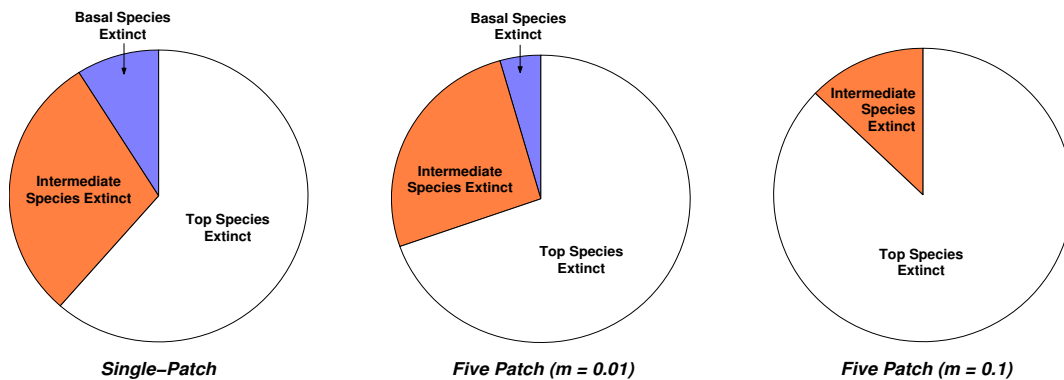

FIGURE 7. Pie diagrams show the proportions of secondary extinction events occurring at the different trophic levels. The bias towards extinctions at lower levels (caused by the triangular food web structure) has been corrected in the calculation of these fractions. The results shown are for a connectance of 0.31 and, for the latter two charts, a five-patch habitat with $c = 0.4$. Charts for lower connectances reveal a similar pattern, and are therefore not included here.

4. CONCLUDING REMARKS

The rate at which populations are being driven to extinction is now thought to exceed that of any mass extinction in the Earth's history (Myers and Worm 2003; C. D. Thomas *et al.* 2004;

J. A. Thomas *et al.* 2004). The depletion of terrestrial and marine habitats has received much attention in recent times, but it is becoming increasingly apparent that freshwater systems are also at great risk; a study of North American freshwaters (Riciardi and Rasmussen 2000) predicts that, unless the hundreds of endangered species can be saved, future extinction rates could equal those of tropical forests. As a species, humans have a unique capacity to manipulate their environment for short-term gains. If we are not wise then this ability to disrupt and exploit will undoubtedly end in irreparable damage and ultimately our own extinction. Untold damage has already occurred and we must now, more than ever, use our intelligence to gain understanding of ecological processes and help guide conservation efforts and habitat management.

Theoretical models such as this serve merely as metaphors for the awe-inspiring complexity that underpins natural processes. Nonetheless, when combined with empirical and experimental data, they are invaluable tools in highlighting possible consequences of disrupting previous stable ecosystems. Key to successful modelling is an awareness of how the simplifications introduced are likely to affect the system's behaviour. It is remarkable, then, that until recently the role of space in ecological models has been so frequently omitted. This paper builds on the foundations laid by both non-spatial and simple patch-occupancy models. However, the explicit modelling of both local and regional dynamics has not been without some important assumptions.

Firstly, so as not to cloud the effects of migration, the starting communities are assembled by linking identical local communities by migration. In a natural setting, however, the structure of any local food web grows out of successive colonisation and extinction events (MacArthur and Wilson 1967; Holt 2002). Whilst modelling community assembly in a realistic manner would be difficult at best, it must be kept in mind that the chosen approach is likely to influence what conclusions are drawn from the model. Secondly, this paper does not attempt to model stochastic processes, and yet they clearly play an important role in any natural community. The short-term fluctuations in populations caused by births and death could perhaps be modelled by adding 'noise' to the local dynamics, although to be truely realistic the interaction strengths must also be subject to spatio-temporal variability. Such an extension of this model would certainly be interesting, although would itself require many new assumptions. Finally, the local dynamics are modelled using the generalised Lotka-Volterra equations. There are, however, a multitude of other ways to model competitive interactions and there is certainly no definitive guide to which might be most appropriate and when. A recent study by Lewis (2004) investigates the post-extinction communities in closed systems for different types of functional response. An interesting result is that a Holling Type III response is less likely to allow the successful reinvasion of an extinct species than the Type I response employed here. This has obvious implications for spatial models, where local extinctions and subsequent (successful) reinvasions are common occurrences.

5. Acknowledgements

APPENDIX A: THE PERMANENCE CRITERION

For a long time, ecologists have attacked the problem of assembling realistic community models by seeking those that yield an asymptotically stable fixed point. However, since its introduction by Schuster *et al.* in 1979, the concept of permanence (in the sense defined below) has given ecologists a new, more appropriate, means of defining stability. By way of justifying its application to the model used here, I offer this brief introduction to the subject (see also: Jansen 1987; Law and Blackford 1992; Law and Morton 1993; Chen and Cohen 2001 for useful discussion on permanence).

Intuitively, permanence simply requires that all species present at time zero persist indefinitely (or so long as the system remains unperturbed). More formally, a system of ordinary differential equations of the form $\dot{\boldsymbol{x}} = \{\dot{x}_i, \ldots, \dot{x}_k\}$ is defined to be permanent if and only if there exist $\delta_u > \delta_l > 0$ such that

$$x_i(0) > 0 \quad \forall i \quad \implies \quad \delta_l < \liminf_{t \to \infty^+} x_i(t) < \limsup_{t \to \infty^+} x_i(t) < \delta_u \quad \forall i.$$

In other words, any trajectory that starts in the positive region of phase space is repelled by all phase space boundaries. Defining stability in this global sense means that the interior fixed point(s) need not necessarily be locally stable. This makes sense in an ecological context, since there is no reason to assume that the densities of coexisting species are always drawn toward some perfect balance. In fact, there are well known examples in nature where such an assumption is known to be false. Consider, for example, the oscillating densities of a lynx-hare community; such dynamics are perfectly acceptable under the permanence criteria, but would not be allowed under the conditions set by local stability analysis because the trajectories spiral *away* from the fixed point. In the case of Lotka-Volterra systems containing omnivory — similar to the within- patch dynamics used here — it has been shown that the presence of an interior fixed point is considerably more likely to imply permanence than local stability (Law and Blackford 1992). Thus, permanence is preferred to local stability for two reasons: so as not to exclude configurations that may represent phenomena present in real food webs; because permanent communities are more robust to perturbations, such as the introduction of migration.

Generally, proving that a system is permanent is not easy. However, for dissipative Lotka-Volterra systems with k species and exactly one interior fixed point, a sufficient condition exists in the form of the following linear program (Jansen 1987). Minimize z subject to $\Omega + 1$ linear constraints:

$$\sum_{i=1}^{k} h_i \left(r_i + \sum_{j=1}^{k} \alpha_{i,j} \hat{N}_j^{(\omega)} \right) + z \quad \geq \quad 0 \qquad \text{for } \omega = 1, \ldots, \Omega \; ;$$

$$h_i \quad > \quad 0 \qquad \text{for all } i.$$

Here, $\hat{N}_j^{(\omega)}$ is the density of species j at the ωth boundary equilibrium and the h_i and the z are variables in the linear programming problem. If the solution, $z_{\min}$, is strictly negative then there exists an average Lyapunov function and therefore the system must be permanent. This is the method used in the generation of starting communities, as described in Section 2.4. The prerequisite that all trajectories in the system must remain finite is always satisfied here because of the nature of the interaction coeffecients: ultimately, all consumers rely on the self-limiting basal species for energy.

Ideally, each time the system is perturbed by species removal, it would be checked for permanence. Unfortunately, the non-linear terms in the migration kernel (Eqaution (2)) mean that the sufficient condition described above no longer holds. Instead, the long-term behaviour of the system is determined using numerical integration, performed by MATLAB's *ode15s* routine[5].

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[5]This is a 'stiff' solver, which means that the step-size is varied depending on the nature of the dynamics. This allows for faster integration during stiff periods (where the step-size can be safely increased), without loss of accuracy during periods of rapid change (where the step-size can be kept very short).

Appendix B: Varying Dispersal Ability

The following figures show how increasing patch abundance affects the risk of cascading extinctions. Each plot compares the results yielded by different values of c. Dispersal abilities of 0.1, 0.4 and 1.0 represent, respectively, extremely strong, strong and moderate tendencies for migrants to settle in the closest of patches. The migration rate is fixed at one percent per day in all cases.
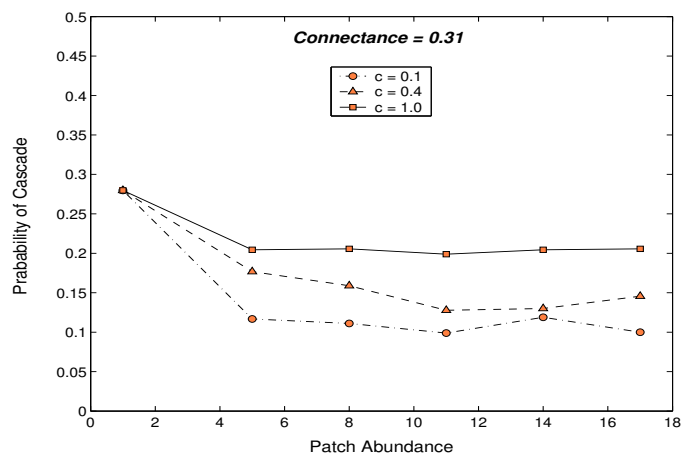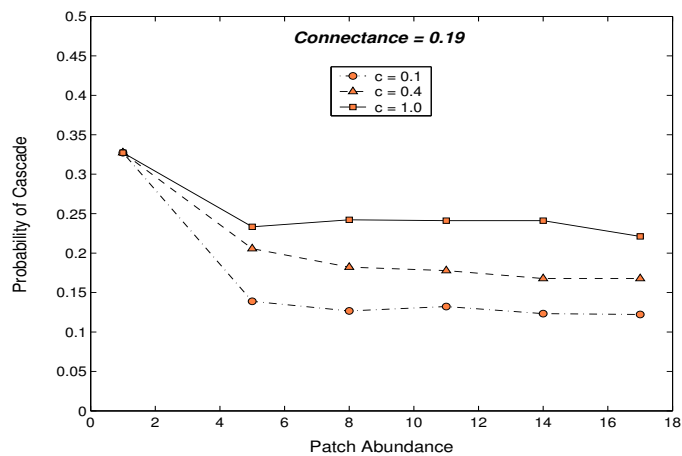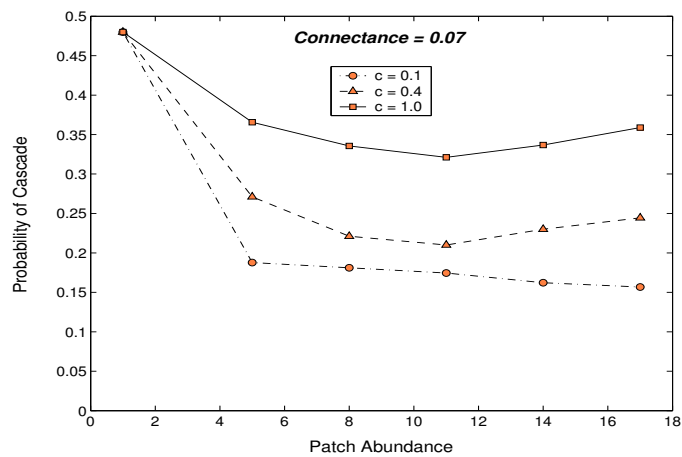
Appendix C: Varying the Migration Rate

The following figures show how increasing patch abundance affects the risk of cascading extinctions. Each plot compares the results yielded by different rates of migration. The dispersal parameter, c, is fixed at 0.4 in all cases.
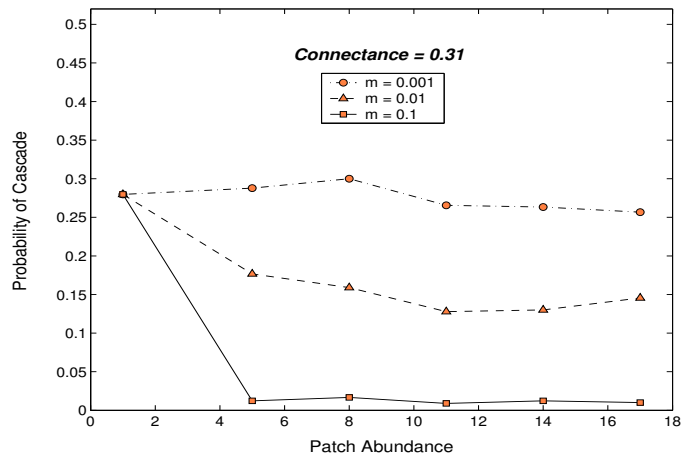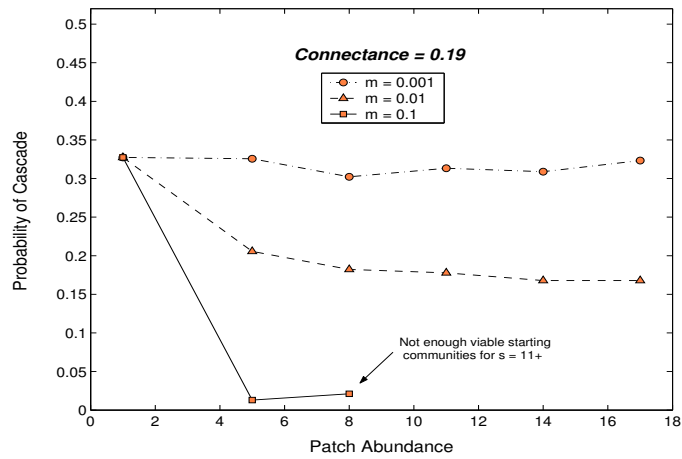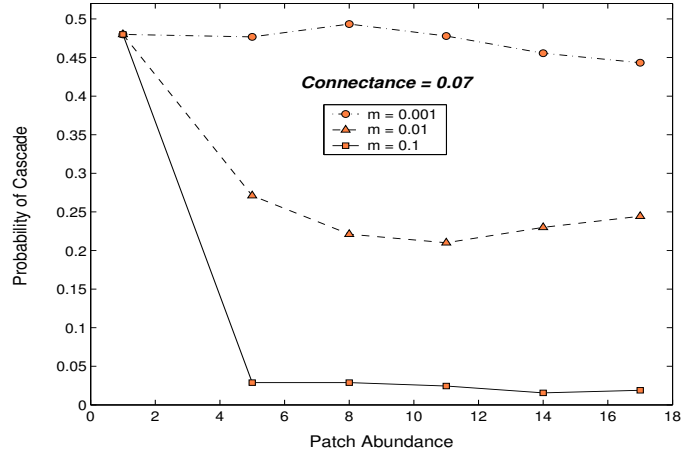
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