
Modelling the impact of a keystone species on community diversity and stability

Jon I Hamley

A thesis submitted in partial fulfilment of the requirements for the degree of Master of Science of Imperial College London and Diploma of Imperial College London

September 2012

Abstract

Despite receiving frequent theoretical attention, the impact of a keystone species on community diversity and stability has not been widely investigated outside of the context of food webs. I developed a framework for layering a neutral model with a stochastic Levins model of a keystone species, in which local community size is dependent on the occupancy status of patches in the Levins model. At each time step, if a new patch becomes occupied it is assigned to a local community which then increases in size. The layered models predict higher species richness but lower temporal stability for all communities, when compared to a neutral model alone. High colonisation rates and low extinction rates in the layered models produced higher temporal stability and species richness. In addition, increasing migration rates, local community sizes and total number of communities resulted in communities with greater levels of stability and species richness. I compare patterns of model outputs and discuss the implications of using a measure of stability for a neutral approach to community ecology. Potential parameterisation methods are suggested for using a bird's nest tree fern (*Asplenium* spp.) – invertebrate system, in which rainforest canopy diversity estimates can almost double when bird's nest ferns are present. This project presents a novel way of modelling keystone species in cases where they support high diversity through habitat creation.

Key words: Neutral Theory, keystone species, Levins model, temporal stability, bird's nest tree fern

Contents

I. Abstract.....	1
II. Contents.....	2
III. Introduction.....	3
IV. Methods.....	6
Models.....	6
Model parameters and simulation.....	10
Model outputs.....	11
V. Results.....	12
VI. Discussion.....	19
VII. Appendices.....	25
VIII. Acknowledgements.....	29
IX. References.....	29

Introduction

The role of keystone species in determining species richness and abundance is widely accepted (Mills *et al.*, 1993; Bond, 1994; Menge *et al.*, 1994; Power & Mills, 1995), and its impact can be understood empirically by comparing spatial areas where its abundance varies. Theoretical approaches applying the keystone species concept to understanding community ecology have so far focused on species interaction networks or identifying keystone species in food web models (Jordan *et al.*, 1999; Brose *et al.*, 2005; Ferenc *et al.*, 2009; Black and McKane, 2012). These models generally generate predictions concerning changes in the number of individuals per species rather than the number of species in the community. Furthermore, they tend to focus on interactions between different trophic levels and changes in species biomass. These frameworks can predict changes in the number of individuals due to keystone species dynamics, but are mostly implemented using ordinary differential equations. Therefore, they rely on setting a threshold for the abundance of particular species at which it is not considered in the model, rather than the number of individuals of that species reaching zero. As each species must be explicitly accounted for, there is a restricted number of species which can be included in food web models, and parameterisation can be difficult, particularly for higher species richness. Here I consider keystone species as those “who’s impact is disproportionate relative to its abundance” (Power *et al.*, 1996). A well-studied example of this concept can be found in rainforest canopies; here bird’s nest tree ferns (*Asplenium* spp.) can almost double invertebrate biomass estimates (Ellwood *et al.*, 2002; Ellwood & Foster, 2004) and alter the local microclimate (Turner & Foster, 2006). I use this system to guide my approach to understanding the long term trends in community composition and stability when a keystone species may be present. Here, stability refers to the measure of “temporal stability” outlined by Tilman (1999), in which stability of a species is given by the mean abundance of a species divided by the standard deviation, this can be extended to give stabilities of multiple species and local communities (Lehman & Tilman, 2000). With this measure of temporal stability, increased stability is achieved by having more normalized fluctuations. This measure is preferable over eigenvalue

stability analysis as it measures nonlinear dynamics rather than using linear approximations, furthermore it does not depend on choice of units (it is “scale invariant”) (Lehman & Tilman, 2000). The output of this measure of stability increases as stability increases; this is beneficial over using the coefficient of variation in which the measure moves towards zero as communities become more stable (as used by Tilman 1996; Doak *et al.*, 1998; Ives and Hughes, 2002). Tilman *et al.* (2006) present empirical evidence from a ten year long grassland experiment showing that species richness increases temporal stability of a system. Steiner *et al.* (2005) demonstrate that the temporal stability of aquatic food webs increase with diversity, and also highlight the importance of considering the scale of biological organization. However, May (1972), argues that species diversity may actually decrease stability of a community.

Black and McKane (2012) have described the benefits of using individual based models (IBM) for modelling community dynamics, highlighting the removal of the need to include a ‘combinatoric factor’ which is concerned with selecting specific individuals to interact in agent based models. Ecological neutral models are examples of IBMs and have stimulated much debate during the past ten years (Alonso *et al.*, 2006; McGill *et al.*, 2006; Ricklefs, 2006; Clark, 2009; Clark, 2012; Rosindell *et al.*, 2012). In neutral models, drift, dispersal limitation and speciation are responsible for structuring communities, not niches and selection. Births and deaths occur randomly at every time step and community structure is determined by a Markovian process. Neutral models can produce species abundance distributions and species area relationships which fit closely with empirical data (see Rosindell *et al.*, 2011 for a review).

A neutral approach to modelling community ecology has been applied to understanding the effects of habitat fragmentation on species diversity (Chave and Norden, 2007); it is yet to be used to investigate the impact of a keystone species on stability and species richness. In a neutral community, local communities can be easily changed in size during simulations; therefore the presence of a keystone species can be modelled by increasing the size of a local community when there is a keystone species in the same area as the local community. Hubbell (2001), developed a spatially

implicit neutral model in which individuals belong to either the metacommunity or the local community. Spatially explicit neutral models have been widely developed and although they are more realistic than implicit ones, they are more difficult to construct and implement (Chave & Leigh, 2001, Rosindell & Cornell, 2007). Etienne (2007) has presented a spatially implicit neutral model in which numerous local communities are connected to the metacommunity.

In the bird's nest tree fern – invertebrate system, trees can be thought of as patches for local communities of invertebrates, when a tree is occupied by a fern, this increases the size of the local invertebrate community (and hence is expected to increase its richness). Rather than integrating a keystone species into a neutral model, a metapopulation model of keystone species dynamics can be simulated alongside a neutral model, with a patch in the metapopulation corresponding (but not fixed) to a local community in the neutral model. Both spatially implicit and explicit metapopulation models have become well developed. In the spatially explicit Incidence Function Model, which gives the probability of a patch being occupied, patch size and isolation determine colonisation and extinction (Hanski, 1994; Hanski & Ovaskainen, 2003). This model not only contains more parameters than a spatially implicit one, but in the biological system we consider for model construction, it is not clear at what scale the environment becomes 'patchy' for the ferns. In the classic Levins model (Levins, 1969); the proportion of patches occupied is considered implicitly, without including details on patch isolation or size. This model is more easily parameterised and is more suitable for situations where patch definition is unclear.

I develop a framework which provides a flexible approach to quantifying the impact of a keystone species on biodiversity using the bird nest tree fern – invertebrate system to guide decisions in model construction. Here both keystone species dynamics and community dynamics are considered in a spatially implicit environment. I develop a stochastic Levins model and produce a framework for layering it with a neutral model composed of multiple local communities (to produce 'layered models'). I then compare the outputs of the layered models with a neutral model which is not altered by the dynamics of a keystone species (herein, 'neutral model' refers only to the

neutral model simulated without the Levins model). I consider species richness alongside temporal stability and discuss these findings in relation to the possible determinants of stability outlined by (Tilman *et al.* 1998), and the implications involved in using it to understand dynamics in neutral communities. In addition, I suggest possible ways to parameterise the framework developed.

Methods

The models are simulated and constructed with two scenarios in mind. Firstly, a neutral model is simulated and the temporal stability of all local communities and species richness of local communities is calculated. Secondly, a neutral model is simulated with a stochastic Levins model of the keystone species (to produce a layered model); in this simulation the size of each local community at each time step is determined by patch occupancy as predicted by the Levins model.

Models

A spatially implicit neutral model is used to simulate community composition. This IBM involves per capita ecological equivalence and communities are entirely saturated; the community follows zero sum dynamics (as soon as an individual dies, it is replaced). Random birth and death processes structure communities. The metacommunity contains J_M individuals which are sampled to reproduce and disperse offspring to the J_N local communities which each contain J individuals. This is similar to the implicit model explored in The Unified Neutral Theory of Biodiversity and Biogeography (Hubbell, 2001) but with multiple local communities. The metacommunity is generated using a coalescence method outlined by Rosindell *et al.* (2008) (see appendix a). This method involves point mutation speciation, as described by Hubbell (2001) and the number of species in the metacommunity is dependent on Hubbell's Fundamental Biodiversity Number ($\theta = (J_m * \nu) / (1 - \nu)$, where ν is the speciation rate). Once the metacommunity is generated it remains unchanged because it is considered large enough to remain stable on the timescales in which the much smaller local

communities change. Similarly, the size of the metacommunity means that the majority of immigration comes from the metacommunity, so immigration from local communities to other local communities or back to the metacommunity is ignored. We assume no speciation occurs in the local communities because they are so small.

A discrete time Levins metapopulation model (1.a) is used to produce the basic framework predicting metapopulation dynamics of the keystone species:

$$N_{t+1} = cN_t(1 - N_t) - eN_t + N_t \quad (1.a)$$

With the rate of change in proportion of occupied patches given by:

$$\frac{dN}{dt} = cN(1 - N) - eN \quad (1.b)$$

and the equilibrium proportion of patches occupied given by:

$$N_{eq} = 1 - e/c \quad (2)$$

Where N_t is the proportion of patches occupied at time t , and N_{t+1} is the proportion of patches occupied at time $t+1$, c is the colonisation parameter, and e is the extinction parameter. The initial value of N_t is the equilibrium value given the model parameters, therefore O_p (the number of occupied patches) at the first time step is given by:

$$O_p = P_N * N_t \quad (3)$$

Where $P_N = J_N$, the total number of patches.

Furthermore:

$$O_p \rightarrow O_p + 1 \quad \text{at rate } cN_t(1 - N_t)$$

$$O_p \rightarrow O_p - 1 \quad \text{at rate } eN_t$$

The Levins model is simulated forwards every time step with the neutral model. Since J steps of the neutral model correspond to a single generation of the invertebrate community, and since ferns are likely to have a longer life span than invertebrates, the rates depicted above are divided by J so they progress in real time at a constant rate. The colonisation and extinction parameters occur between 0 and 1. The rates are considered as probabilities; to incorporate stochasticity into the Levins model, a random number between 0 and 1 for each probability is generated every time step. If this is less than the probability, a patch becomes occupied or unoccupied depending on the rate of change being considered (see appendix d for a complete algorithm). This model is spatially implicit; when there is a colonisation or extinction event all unoccupied or occupied patches respectively are sampled with equal probability to select a patch to change in occupancy status. In order to simulate the model across parameter ranges and avoid the metapopulation reaching an absorbing state (due to the allee effect when the number of occupied patches is low), an immigration parameter (I) (for individuals coming from outside the metacommunity) can be introduced into the simulations, therefore:

$$O_p \rightarrow O_p + 1 \quad \text{at rate } I(1 - N_t)$$

Where N_t is updated after any colonization events within the metacommunity have occurred, thus ensuring the proportion of occupied patches cannot exceed one. Here immigration is determined in the same way as colonisation and extinction.

As the model is simulated forwards one time step, an individual dies in each local community, a new individual is then produced from within the local community with probability $(1 - m)$, or is dispersed from the metacommunity with probability m . In the same time step, the stochastic Levins model is simulated forwards one step as described above. When a patch becomes occupied, a local community which did not have the keystone species present at the previous time step is sampled to increase by $K * J$ (K is the proportional increase in J provided by the keystone species), conversely, when a patch becomes unoccupied, a local community which had the keystone species present during the previous time step is sampled to decrease by $K * J$ (see figure 1) $.K$

remains unchanged throughout the entire simulation and all local communities are reduced or increased in size by the same value of K . The framework is kept entirely implicit; patches and local communities are randomly sampled to change in occupancy status respectively; there is no assignment of specific patches to specific local communities for the entire simulation. Specific assignment of patches to local communities would require use of a spatial neutral model (e.g Rosindell and Cornell 2007) and a spatial metapopulation model (such as Hanski 1994), which would consider dispersal kernels and connectivity between patches respectively.

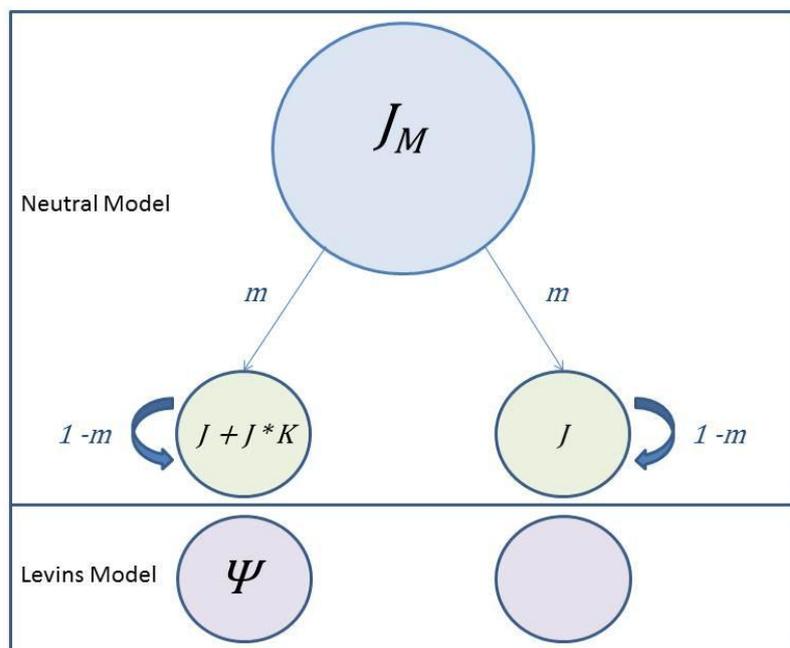


Figure 1: The local communities, which are produced by sampling the metacommunity J times before the simulation, receive new births from the metacommunity ($1 - m$) or from within the local community (m) each time step. At the time step depicted, a patch in the Levins model (lower box, left) is occupied by the keystone species (Ψ) and has been assigned to a local community in the neutral model (upper box, left). Consequently, this local community is size $J + J * K$. This is a simplified example with only two local communities. For most simulations, 30 local communities are produced by the neutral model.

Model parameters and simulation

Simulations of the neutral model are run for ranges of m . Simulations of the layered models were run for ranges of m and combinations of e and c , and J_N and J (see table 1 for values). A metacommunity of 700000 individuals is generated with $\theta = 50$ to produce the local communities in the simulations and provide immigrants. I present an exploration of some of the parameter space of the models and twenty repeats per parameter range or combination are simulated. Species richness and temporal stability calculations are made after an initial burn in period for the system to reach equilibrium, and the simulation is carried out for a total of 60000 time steps. For the most part, m in the neutral models is fixed at 0.3. This enables the species richness in the local communities to reach equilibrium faster than with lower migration rates, thus requiring less simulation time to reach equilibrium. I present simulations plotted over time with $m = 0.01$ and $J = 300$, $J_N = 30$ to confirm burn in time is sufficient for an equilibrium state to be reached. For all the layered model simulations K is set at 1, meaning that the presence of the keystone species doubles the local community size, this is the impact bird's nest tree ferns have on invertebrate diversity estimates in tropic rainforest canopies (Ellwood and Foster, 2004). During the parameter combination and range simulations, the parameters not of direct interest are fixed at intermediate values ($J = 300$, $J_N = 30$, $c = 0.3$, $e = 0.3$, $m = 0.3$, $I = 0.3$). Comparison of the layered models and neutral model species richness and temporal stabilities are made over a range of m values. Species abundance distributions are plotted by pooling local communities at equilibrium for the neutral model and layered models. Possible approaches to parameterisation with the fern invertebrate system in mind are presented in the future directions section. The models were coded and simulated using R version 2.15.1 (<http://www.r-project.org>) and run using the Imperial College London High Performance Computing Service (<http://www.imperial.ac.uk/ict/services/teachingandresearchservices/highperformanc computing>).

Table 1: Parameter values for simulations of the layered models and neutral model

Model	Parameter(s)	Parameter values
Layered Models	J, J_N	$J = 100, 300, 1000; J_N = 10, 30, 100$
Layered Models	e, c	$e = 0.01, 0.1, 0.3, 0.6; c = 0.01, 0.1, 0.3, 0.6$
Layered Models	m	$m = 0.01, 0.1, 0.3, 0.6$
Neutral model	m	$m = 0.01, 0.1, 0.3, 0.6$

Model outputs

The neutral model and layered model are compared by both their predictions of species richness in local communities and temporal stabilities, which are calculated by using the measure outlined by Lehman & Tilman (2000):

$$S_T(n) = E \left\{ \frac{\sum_i \bar{B}_i(n)}{\sqrt{\sum_i \text{Var} [B_i(n)] + \sum_{i \neq j} \text{Cov}[B_i(n), B_j(n)]}} \right\} \quad (4)$$

Where $S_T(n)$ is the temporal stability of the communities, B_i is the abundance of species i in a local community during a time interval, \bar{B}_i is the mean abundance and the expected value (E) is calculated over local communities. The mean is then calculated for all repeats (x20) of the parameter ranges. In the original construction of the measure, B_i was intended as the biomass of a species; here it is used to describe the number of species in the local community. Lehman & Tilman (2000) argue that mean stability over total communities eliminates bias resulting from certain species combinations; here it is used as an opportunity to increase the reliability of the simulations. The species richness outputs of the layered models and neutral model are compared, and considered with the temporal stabilities.

Results

In all parameter simulations the layered models produced local communities with increased species richness but reduced temporal stability compared to the neutral model. Temporal stability varied for combinations of colonisation and extinction rates in the layered models. Local community size and number of local communities was predicted to influence temporal stability also. Although species richness changed for different combinations of colonisation and extinction, only the size of local communities appeared to alter species richness and not the number of local communities. Migration rate in both the layered models and neutral model impacted on temporal stability and species richness.

The layered models reached equilibrium by around 30000 time steps whilst the neutral model reached equilibrium at around 15000 time steps. There appears to be a difference in the fluctuations in equilibrium species richness between the two modelling frameworks, with the layered models producing less stable species richness predictions (see figures 2 & 3).

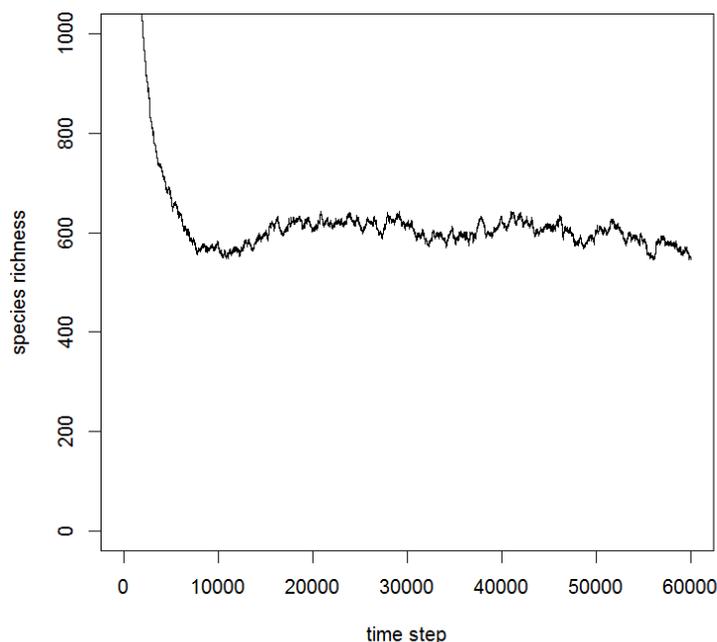


Figure 2: Simulating local communities to equilibrium in the neutral model layered with the Levins model. Species richness was calculated by taking the mean of all local communities. Parameter values: $J = 300$, $J_N = 30$, $m = 0.01$, $c = 0.3$, $e = 0.3$, $I = 0.3$.

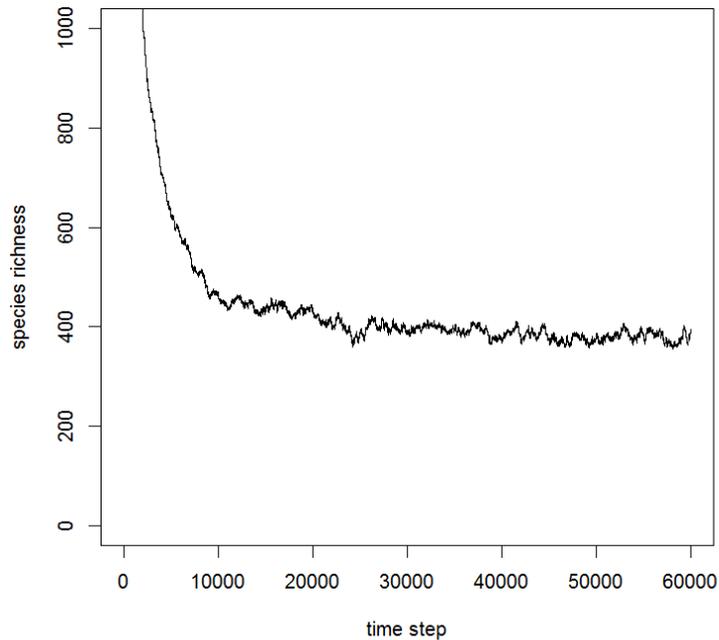


Figure 3: Simulating local communities to equilibrium in the neutral model only. Species richness was calculated by taking the mean of all local communities. Parameter values: $J = 300$, $J_N = 30$, $m = 0.01$

In the layered models and neutral model, a higher migration rate was conducive to higher temporal stability and increased species richness across local communities. The layered models produced communities with higher species richness than the neutral model, but had lower temporal stability (figures 4 & 5). Differences in temporal stability and species richness between the two frameworks appear to increase with migration rate, with the maximum difference at the highest rate tested (0.6) and a more marked difference in temporal stability compared to species richness.

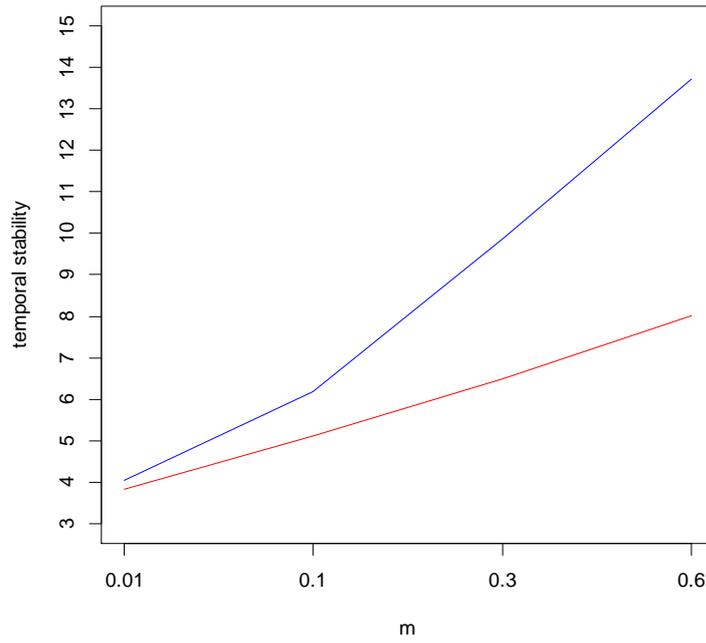


Figure 4: Temporal stability calculated for the layered models (red line) and the neutral model only (blue line). Parameter values: $J = 300$, $J_N = 30$, $c = 0.3$, $e = 0.3$, $I = 0.3$.

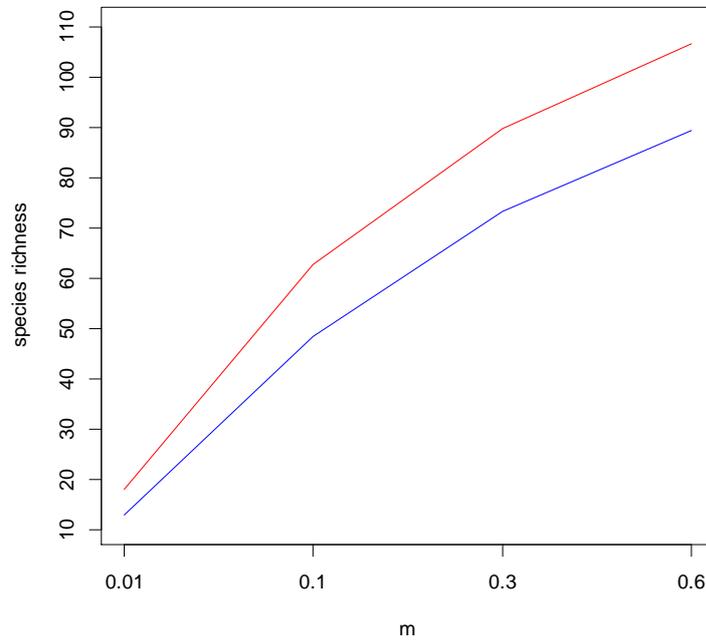


Figure 5: Species richness calculated for the layered models (red line) and the neutral model only (blue line). Parameter values: $J = 300$, $J_N = 30$, $c = 0.3$, $e = 0.3$, $I = 0.3$.

In the layered models, both the highest species richness and highest temporal stabilities were found at a colonisation rate of 0.6 and an extinction rate of 0.01 (see figures 6 and 7). As extinction rate was increased, increasing the colonisation rate provided smaller increases in temporal stability and species richness. Consequently a combination of the highest rates of colonisation and lowest rates of extinction produced higher species richness and temporal stability than a combination of the maximum values. The transition of temporal stabilities and species richness over parameter space followed a gradual gradient although the highest levels of species richness appeared to persist for higher levels of extinction compared to the highest levels of temporal stability.

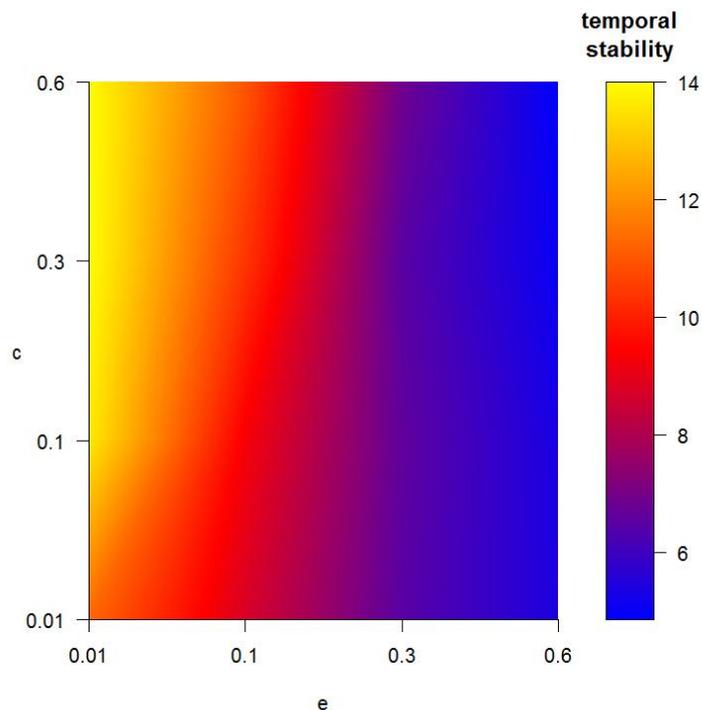


Figure 6: Temporal stability calculated for combinations of e and c for the layered models. Parameter values: $J = 300$, $J_N = 30$, $m = 0.3$, $I = 0.3$. Note the different legend for each colour plot.

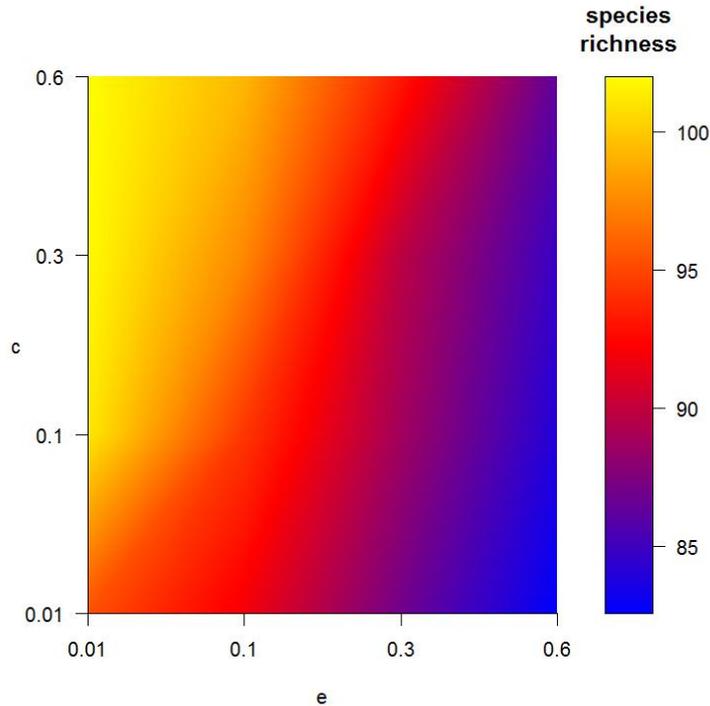


Figure 7: Species richness calculated for combinations of e and c for the layered models (calculated by taking means of local communities). Parameter values: $J = 300$, $J_N = 30$, $m = 0.3$, $I = 0.3$. Note the different legend for each colour plot.

The highest values simulated for local community size and number of local communities gave the highest temporal stability in the layered models, whilst the lowest temporal stabilities were found with low community sizes when there were few local communities (see figure 8). Increasing local community size of 10 local communities did not achieve the same increase as increasing local community size of 100 local communities, although local community size did appear to be the more important factor in influencing temporal stability than the number of local communities in this simulation. Species richness in the layered model increased as a result of higher community size but the number of local communities had little to no impact on species richness (see figure 9).

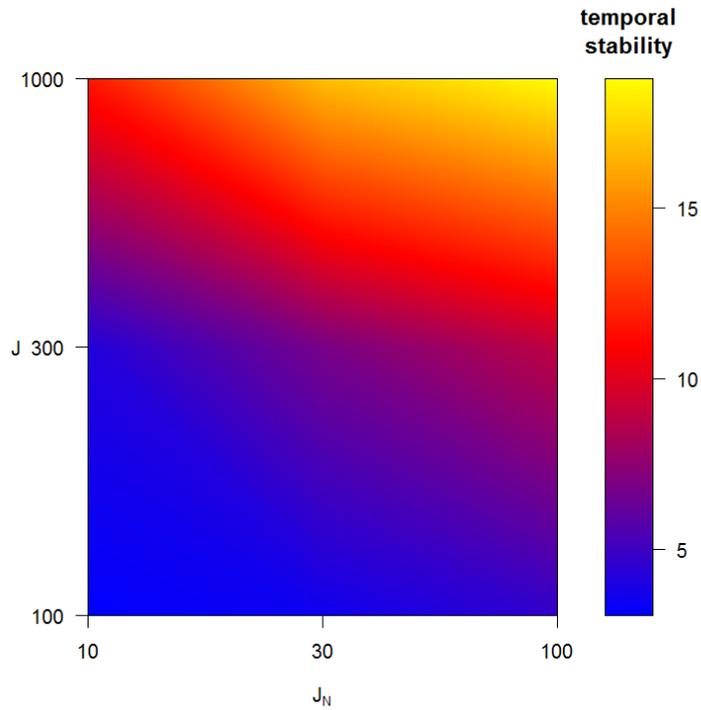


Figure 8: Temporal stability calculated for combinations of local community size and number of local communities. Parameter values: $m = 0.3$, $c = 0.3$, $e = 0.3$, $I = 0.3$. Note the different legend for each colour plot.

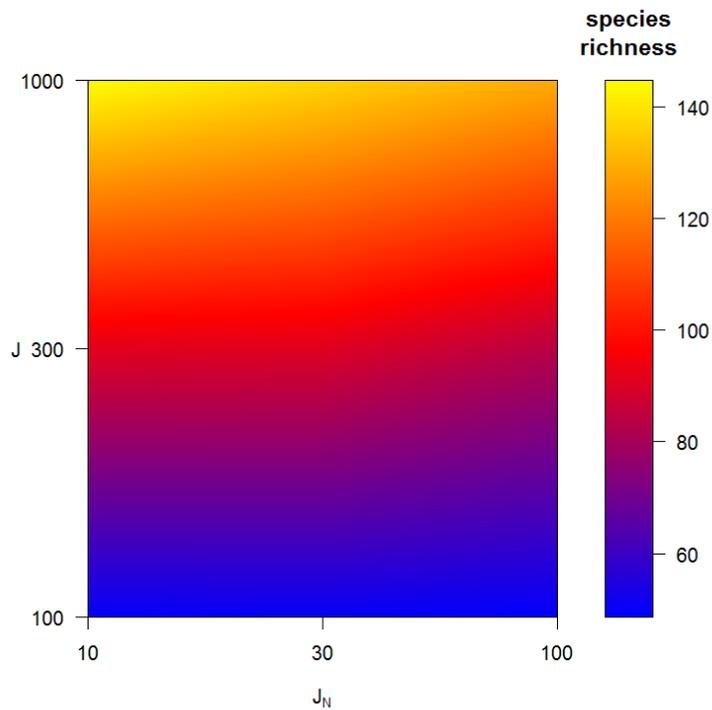


Figure 9: Species richness for combinations of local community size and number of local communities (calculated by taking means of local communities). Parameter values: $m = 0.3$, $c = 0.3$, $e = 0.3$, $I = 0.3$. Note the different legend for each colour plot.

The patterns of species richness observed from the outputs of the layered models and neutral model over migration values appear to behave in a way expected by the species abundance distributions (SAD) of pooled local communities at equilibrium species richness (see figures 10 and 11). The higher frequency of lower abundance classes is common between the SADs for the layered models and neutral model. However, the SAD for the neutral model is characterised by having a lower number of species per abundance class and fewer abundance classes. This implies not only that there are more individuals in the communities produced by the layered models but that these communities are also more diverse. The SAD for the neutral model follows a slightly smoother transition from low to high abundance classes. The SAD for the layered models is marked by more severe fluctuations in the number of species as abundances classes reach around 150.

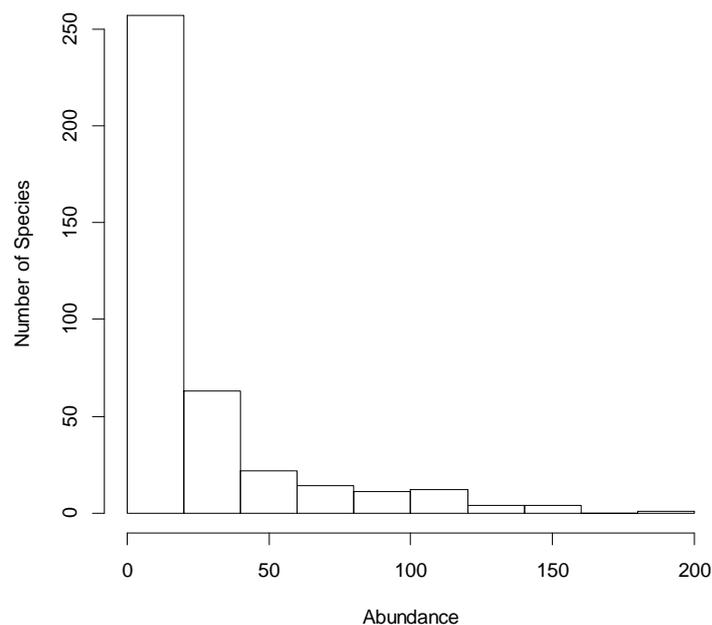


Figure 10: Species abundance distribution for pooled local communities from the neutral model at equilibrium. Parameter values: $m = 0.01$, $J = 300$, $J_N = 30$.

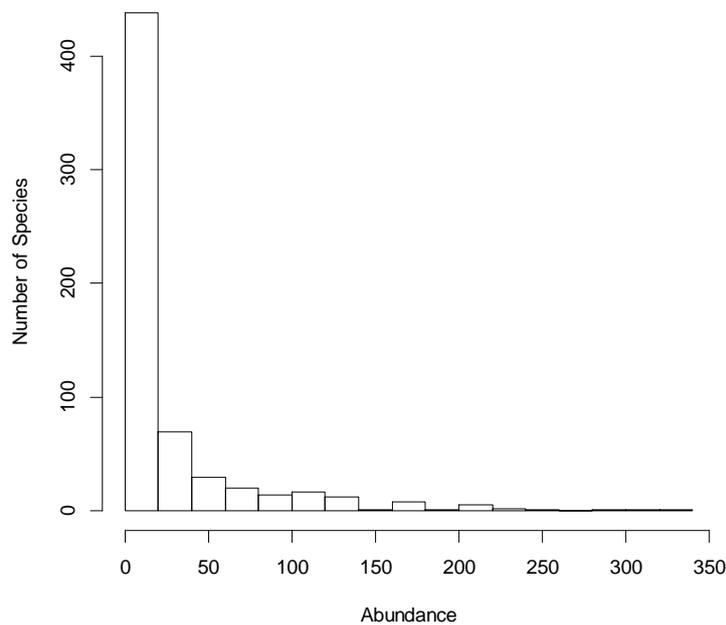


Figure 11: Species abundance distribution for pooled local communities from the layered models at equilibrium. Parameter values: $m = 0.01$, $c = 0.3$, $e = 0.3$, $I = 0.3$, $J = 300$, $J_N = 30$.

Discussion

The layered models predicted higher species richness than the neutral model, which conforms to previous empirical predications (Bond, 1994; Ellwood & Foster, 2004; Power *et al.*, 1996), and lower temporal stability. Furthermore, the patterns of increased species richness produced by the layered models and neutral model by increasing migration rate correspond with the predictions made by Hubbell (2001). Generally, stability varied depending on colonisation and extinction rates in the Levins model, and depending on both the number of local communities and the size of local communities.

There may be two potential reasons for the highest temporal stabilities being found at the maximum colonisation rate and the minimum extinction rate. Firstly, when a community is suddenly reduced in size a large proportion of species are removed, this is understood in terms of the SAD distributions (figures 10 & 11), which show high

numbers of species, with low numbers of individuals per species. Consequently, if extinction rate of the keystone species is high and local communities are frequently reduced in size, the number of species will show increased variation over time (in an individual community). Here it is important to note that the immigration rate from outside the metapopulation will aid in increasing patch occupancy when colonisation rate is low. Secondly, when colonisation rate is high and extinction rate is low, and there are few reductions in the size of local communities, species richness should show lower variation over time. Here, the number of local communities increased by the keystone species is higher, and when there is a newly occupied patch, the local community chosen to receive it will change in species richness more slowly over time compared to when a patch suddenly becomes unoccupied. It does not appear that at high rates of extinction in the layered models that an increased colonisation rate provides any benefit to the temporal stability of communities, indeed a colonisation rate of 0.6 shows little difference to a colonisation rate of 0.01. In this instance the frequent reduction of local community sizes may cause such large fluctuations in species richness than the gradual increases in species richness provided by the increased colonisation parameter has little influence.

For all simulations, immigration of individuals from outside the metapopulation was set at 0.3. A suitable next step for the research would be to do more extensive simulations of combinations of extinction, colonisation and immigration. If extinction rate was high, and immigration and colonisation rate were low, there may be a more sustained number of unoccupied patches. In this instance, there would be less species but also lower variations in community size over time. This may provide further insights on the relationship between species richness and temporal stability.

My argument concerning extinction and colonisation rates isn't completely consistent with the stability and diversity outputs from ranges of migration rate in both the layered models and neutral model. As migration rate is increased there is a pattern of increase in both species richness and temporal stability. Increasing migration allows species richness in the local communities to increase more quickly after a change in the distribution of the keystone species, and thus indicates that maintaining a higher

number of species in the local communities may be more important for increasing temporal stability than reducing the time over which species richness changes take place.

The patterns of species richness from the layered models for combinations of c and e conform reasonable well to the temporal stability predictions; however temporal stability appears to drop off prior to a reduction in species richness as extinction increases. Although species richness may have been high over communities, there may be increased variation within local communities which reduced the temporal stability of the system. Tilman *et al.* (1998) and Lehman and Tilman (2000) outline and discuss three main factors which may influence the stability level of a system. “The Covariance Effect” does not necessarily apply to outputs of stability for a neutral model as it refers to an increase in the summed covariances (i.e positive or negative species interactions). In real communities where species diversity is determined by interactions between species, summed covariances may decrease with diversity thus increasing temporal stability (see equation 4). “The Portfolio Effect” occurs due to the decrease in the number of individuals per species as diversity increases, when this occurs there is a decrease in the summed variances that is not proportional to the reduction in abundance. This may produce a gradient over which at high levels of species richness, temporal stability increases; this is speculative however and would require the explicit consideration of the variation of species abundances. Temporal stability may also increase by “over yielding”, although this concerns the relationship between community diversity and biomass.

The predictions of the layered models concerning species richness over increasing local community sizes are consistent with the findings of Hubbell (2001), in that species richness increases with local community size. However, due to the way birth and death processes occur and that sampling to create the local communities is done without replacement, there appears to be no reason why the number of local communities should influence model predictions in a neutral model only. Indeed, this was the case for species richness predictions from the layered models; however, the layered models predicted that temporal stability should increase with the number of local

communities. This has important implications for the patterns observed for combinations of colonisation and extinction rates because it indicates that species richness alone may not determine temporal stability predictions from the models. The Levins model is layered with a neutral model in a way that ensures turnover for keystone species is slower than turnover of individuals in the neutral model, however as the number of local communities increases the probability of a patch changing in occupancy status decreases. For the colonisation and extinction rates set to produce figure 9, species richness over all communities is maintained at higher community sizes but it is likely that there are less frequent changes in single local communities when the total number of communities is increased and hence they are more stable (figure 8). Considering a different approach to modelling keystone species dynamics which takes number of patches into account may change the influence of community number on temporal stability. In reality, as the distribution of occupied or unoccupied patches in a metapopulation changes, the colonisation and extinction rates of individual patches should change. Consideration of this would lead to a spatially explicit model (Hanski, 1994; Hanski & Ovaskainen, 2003). To apply this to a biological system, it would be required that patch definition is known and time series data is available or can be collected for patch colonisation and extinction.

Caution is required when interpreting the temporal stability outputs; this is a measure originally developed with real communities in mind (i.e ones with interactions between species). Therefore, recognition of the components involved in calculating temporal stability is an important next step in applying this measure to neutral communities. Doak *et al.* (1998) argue that stability increasing with species richness is a “statistical inevitability” due to statistical averaging, however this is relevant when species biomass is used to calculate stability rather than species number. Future work should aim to understand the changes in variance and covariance of species over time in the local communities in relation to species richness, as this may shed light on the mixed results concerning species richness and temporal stability.

At this stage, this modelling framework cannot make specific predictions about the bird’s nest tree fern – invertebrate system it was motivated by. Parameterisation of

the Levins part of the layered models presents the biggest challenge. Freiberg and Turton (2007) investigate the importance of drought on bird's nest tree fern distribution and reconstruct establishment estimates of ferns from 1984 to 2000. This paper may provide possible estimates for the colonisation rate in the Levins part of the layered models. Fayle *et al.* (2009) presents extensive data on fern distribution in the canopy of dipterocarp forest, sampling 719 ferns in total. Consequently, fern distributions can be plotted in cartesian space, however the number of ferns per tree was not recorded. Yamakura (1986) present data on tree size in Dipterocarp forest; a possible solution to estimating initial equilibrium patch occupancy would be to map tree crowns over plots of fern distributions. Groups of trees could be seen as patches for ferns; as previously suggested, the scale at which ferns are panmictic is unclear, and therefore using one tree as a patch for ferns may be unrealistic. With these estimates of equilibrium proportion of patches occupied and colonisation, using equation (2), an extinction rate could be calculated. As this still leaves an estimate for immigration from outside the metapopulation unaccounted for, a range of parameters could be simulated. An alternative to the stochastic Levins model simulated here could be a stochastic Mainland – Island metapopulation model such as the one suggested by Alonso and McKane (2002).

Data is available for invertebrate abundance in the canopy, ferns and leaf litter (Fayle *et al.*, 2010) which could provide parameter estimates for the neutral model and the neutral model part of the layered models. Rampal Etienne has presented numerous parameterisation methods for neutral models, including a method for samples of different dispersal limitation (Etienne 2009), an “enhanced version of the Ewens sampling formula” (Etienne, 2005) and a sampling formula suitable for when there are numerous local community samples from the same metacommunity (Etienne, 2007). Etienne (2007) appears to be the most suitable of the three but still requires investigation to confirm its relevance to the framework developed here. In addition to this, as an alternative to using the point mutation algorithm presented by Rosindell *et al.* (2008), real data could be used directly to construct a metacommunity distribution. In addition to parameterisation, qualitative comparisons between model outputs and

empirical data (such as in Rosindell and Phillimore, 2011) could be conducted to compare any emergent patterns.

Previous studies have indicated theoretically and empirically, that species richness tends to increase temporal stability (Tilman *et al.*, 2006; Steiner *et al.*, 2006) although theoretical studies have also suggested that diversity can decrease it (May, 1972; Gardner & Ashby, 1970). The predictions presented here, indicate that when using a neutral model, temporal stabilities are generally higher as species richness increases. However there may be artifacts from either unrealistic modelling of metapopulation processes or using a measure of temporal stability intended to work around species biomass rather than number of individuals. This study has provided a flexible framework for quantifying the impact of a keystone species on biodiversity. Some of its predictions may be a truism, although this in itself indicates another application of neutral theory to understanding community ecology. It has generated predictions concerning the influence of community size, and the colonisation and extinction rates of a keystone species on community dynamics. Although the application of temporal stability to neutral communities requires caution, it presents a new approach to understanding the implications for using temporal stability measures and how their predictions relate to species richness. I hope that this framework will provide a basis for the development of more spatially realistic layered models to understand the role keystone species play in community diversity.

Appendices

Below, the algorithms used to produce the simulations are presented. Algorithm (a) is reproduced exactly as it is found in Rosindell *et al.* (2008). Algorithm (b) uses processes outlined by Hubbell (2001) and is then called and altered by algorithms (c) to (d) which are used to produce the predictions described in this paper.

(a) Coalescence algorithm for a point mutation metacommunity sample. Taken directly from the additional materials for Rosindell *et al.* (2008).

1. Inputs: θ and J .
2. Define a vector V of length J with $V_i = 1$ and $i = 1, 2, \dots, J$ and define $q = J$, the number of lineages in the vector.
3. Define an empty vector W which will contain a list of species abundances when the algorithm terminates.
4. Pick a random number $0 \leq r \leq 1$ (to choose if coalescence or speciation will happen).
5. Pick a random entry V_i from the vector V (to choose which lineage this will happen to).
6. If:

$$r \leq \frac{\theta}{\theta + K - 1}$$

Speciation happens: remove V_i from the vector V and append it to vector W (then go to 8.)

7. If:

$$r > \frac{\theta}{\theta + K - 1}$$

8. Set $q = q - 1$; now the vector V should have one less element.

9. Set ($q > 0$), the simulation is not finished, go to 4.

10. If ($q \leq 0$), the algorithm is complete and W contains the abundances of all species.

(b) Algorithm for computing a change in species number in a single local community over one time step

1. Inputs: J_M, J, θ, m .

2. Compute the metacommunity using algorithm (a).

3. Sample the metacommunity J times to produce the local community. The probability of a species being selected depends on its abundance in the metacommunity.

4. Sample the local community to choose an individual to die.

5. Remove this individual from the local community vector.

6. Generate a random number $0 \leq r \leq 1$.

7. If $r \leq m$ sample the metacommunity vector to choose an individual to reproduce and fill the space. m is the probability of migration, the probability of reproduction within the local community is given by $1 - m$. Add this new individual to the local community vector.

8. If $m > r$ sample the local community vector to choose an individual to reproduce and fill the space. Add this new individual to the local community vector.
9. Go to step 4 unless correct number of steps have been taken.

(c) Algorithm for computing a change in species number in more than one local community over one time step

1. Inputs: J_M, J, J_N, θ, m .
2. Compute the metacommunity using algorithm (a).
3. Sample the metacommunity J times for each of the J_N local communities.
4. For each local community follow steps 4 – 8 of algorithm (b) for each local community in turn.
5. Return to step 4 if number of simulations required is not complete.

(d) Algorithm for layering a neutral model with a discrete time stochastic Levins model

1. Inputs for neutral model: J_M, J, J_N, θ, m . Inputs for Levins model: e (extinction parameter), c (colonisation parameter), I (immigration of individuals from outside the metapopulation). Other inputs: the increase in local community size in the neutral model due to presence of an individual from Levins model at the same patch (K).
2. Follow steps 2 -3 of algorithm (c).

3. Calculate the equilibrium proportion of patches occupied for the Levins model from chosen input values.
4. Multiple this proportion by J to give the number of occupied patches and then randomly assign patches to local communities.
5. Increase the local communities associated with occupied patches by $J * K$ individuals.
6. Follow steps 4 -8 of algorithm (b).
7. Generate three random numbers $0 \leq r_i \leq 1$.

8. If:

$$r_1 < \frac{cN_t(1 - N_t)}{J}$$

Select an empty patch at random to become occupied. Update N_t . Follow steps 7-8 of algorithm (b) $K*J$ times for the local community associated with that patch.

9. If:

$$r_2 < \frac{eN}{J}$$

Select an empty patch at random to become unoccupied. Update N_t . Follow steps 4-5 of algorithm (b) $K * J$ times for the local community associated with that patch.

10. If:

$$r_3 < \frac{I(1 - N)}{J}$$

There is an immigration event. Select an empty patch at random to become occupied. Update N_t . Follow steps 7-8 of algorithm (b) K^*J times for the local community associated with that patch.

11. Check if required number of simulations have been completed, if not, go to step 6.

Acknowledgements

I principally thank Rob Ewers and James Rosindell for their continued advice, support and patience throughout the duration of the project. I am grateful to Tom Fayle for his advice on the ecology of bird's nest tree ferns and providing data on them, and Ed Turner who provided data on invertebrate communities. I am very thankful to Will Pearse for his contribution to my understanding of the Imperial College London PC cluster. I acknowledge Sime Darby for their research support as part of the Stability of Altered Forest Ecosystems (SAFE) Project.

References

- Alonso, D. & McKane, A. (2002) Extinction dynamics in mainland-island metapopulations: An N-patch Stochastic model. *Bulletin of Mathematical Biology*. 64 (5), 913-958.
- Alonso, D. & McKane, A. (2004) Sampling Hubbell's neutral theory of biodiversity. *Ecology Letters*. 7 (10), 901-910.
- Alonso, D., Etienne, R. S. & McKane, A. J. (2006) The merits of neutral theory. *Trends in Ecology & Evolution*. 21 (8), 451-457.

Black, A. J. & McKane, A. J. (2012) Stochastic formulation of ecological models and their applications. *Trends in Ecology & Evolution*. 27 (6), 337-345.

Bond, W. J. (1995) Keystone species. In: Schulze, E. - M., H.A. (ed.) *CT: Symposium. CY: October 1-4, 1991, CL: Bayreuth, Germany*. Heidelberger Platz 3, D-1000 Berlin, Germany; 175 Fifth Avenue, New York, New York 10010, USA, Springer-Verlag, Heidelberger Platz 3, D-1000 Berlin, Germany; Springer-Verlag New York, Inc., 175 Fifth Avenue, New York, New York 10010, USA. pp.237-253.

Brose, U., Berlow, E. & Martinez, N. (2005) Scaling up keystone effects from simple to complex ecological networks. *Ecology Letters*. 8 (12), 1317-1325.

Chave, J. & Leigh, E. (2002) A spatially explicit neutral model of beta-diversity in tropical forests. *Theoretical Population Biology*. 62 (2), 153-168.

Chave, J. & Norden, N. (2007) Changes of species diversity in a simulated fragmented neutral landscape. *Ecological Modelling*. 207 (1), 3-10.

Clark, J. S. (2012) The coherence problem with the Unified Neutral Theory of Biodiversity. *Trends in Ecology & Evolution*. 27 (4), 198-202.

Clark, J. S. (2009) Beyond neutral science. *Trends in Ecology & Evolution*. 24 (1), 8-15.

Doak, D., Bigger, D., Harding, E., Marvier, M., O'Malley, R. & Thomson, D. (1998) The statistical inevitability of stability-diversity relationships in community ecology. *American Naturalist*. 151 (3), 264-276.

Ellwood, M. & Foster, W. (2004) Doubling the estimate of invertebrate biomass in a rainforest canopy. *Nature*. 429 (6991), 549-551.

Ellwood, M., Jones, D. & Foster, W. (2002) Canopy ferns in lowland dipterocarp forest support a prolific abundance of ants, termites, and other invertebrates. *Biotropica*. 34 (4), 575-583.

Etienne, R. S. (2009) Maximum likelihood estimation of neutral model parameters for multiple samples with different degrees of dispersal limitation. *Journal of Theoretical Biology*. 257 (3), 510-514.

Etienne, R. S. (2007) A neutral sampling formula for multiple samples and an 'exact' test of neutrality. *Ecology Letters*. 10 (7), 608-618.

Etienne, R. (2005) A new sampling formula for neutral biodiversity. *Ecology Letters*. 8 (3), 253-260.

Fayle, T. M., Chung, A. Y. C., Dumbrell, A. J., Eggleton, P. & Foster, W. A. (2009) The Effect of Rain Forest Canopy Architecture on the Distribution of Epiphytic Ferns (*Asplenium* spp.) in Sabah, Malaysia. *Biotropica*. 41 (6), 676-681.

Fayle, T. M., Turner, E. C., Snaddon, J. L., Chey, V. K., Chung, A. Y. C., Eggleton, P. & Foster, W. A. (2010) Oil palm expansion into rain forest greatly reduces ant biodiversity in canopy, epiphytes and leaf-litter. *Basic and Applied Ecology*. 11 (4), 337-345.

Ferenc Jordan, Liu, W. & Mike, A. (2009) Trophic field overlap: A new approach to quantify keystone species. *Ecological Modelling*. 220 (21), 2899-2907.

Freiberg, M. & Turton, S. M. (2007) Importance of drought on the distribution of the birds nest fern, *Asplenium nidus*, in the canopy of a lowland tropical rainforest in north-eastern Australia. *Austral Ecology*. 32 (1), 70-76.

Gardner, M. & Ashby, W. (1970) Connectance of Large Dynamic (Cybernetic) Systems - Critical Values for Stability. *Nature*. 228 (5273), 784.

Hanski, I. (1994) A Practical Model of Metapopulation Dynamics. *Journal of Animal Ecology*. 63 (1), 151-162.

Hanski, I. & Ovaskainen, O. (2003) Metapopulation theory for fragmented landscapes. *Theoretical Population Biology*. 64 (1), 119-127

Hubbell, S. P. (2001) *The Unified Neutral Theory of Biodiversity and Biogeography*. Princeton University Press. Princeton, NJ.

Ives, A. & Hughes, J. (2002) General relationships between species diversity and stability in competitive systems. *American Naturalist*. 159 (4), 388-395.

Jordan, F., Takacs-Santa, A. & Molnar, I. (1999) A reliability theoretical quest for keystones. *Oikos*. 86 (3), 453-462.

Lehman, C. & Tilman, D. (2000) Biodiversity, stability, and productivity in competitive communities. *American Naturalist*. 156 (5), 534-552.

Levins, R. (1969) Some demographic and genetic consequences of environmental heterogeneity for biological control. *Bulletin of the Entomological Society of America* (15), 237-240.

May, R. (1972) Will a Large Complex System be Stable. *Nature*. 238 (5364), 413-414.

McGill, B., Maurer, B. & Weiser, M. (2006) Empirical evaluation of neutral theory. *Ecology*. 87 (6), 1411-1423.

Menge, B., Berlow, E., Blanchette, C., Navarrete, S. & Yamada, S. (1994) The Keystone Species Concept - Variation in Interaction Strength in a Rocky Intertidal Habitat. *Ecological Monographs*. 64 (3), 249-286.

Mills, L., Soule, M. & Doak, D. (1993) The Keystone-Species Concept in Ecology and Conservation. *Bioscience*. 43 (4), 219-224.

Power, M. & Mills, L. (1995) The Keystone Cops Meet in Hilo. *Trends in Ecology & Evolution*. 10 (5), 182-184.

Power, M., Tilman, D., Estes, J., Menge, B., Bond, W., Mills, L., Daily, G., Castilla, J., Lubchenco, J. & Paine, R. (1996) Challenges in the quest for keystones. *Bioscience*. 46 (8), 609-620.

Ricklefs, R. (2006) The unified neutral theory of biodiversity: Do the numbers add up? *Ecology*. 87 (6), 1424-1431.

Rosindell, J. & Cornell, S. J. (2007) Species-area relationships from a spatially explicit neutral model in an infinite landscape. *Ecology Letters*. 10 (7), 586-595.

Rosindell, J., Wong, Y., Etienne, R. S. (2008) A coalescence approach to spatial neutral ecology. *Ecological Informatics* 3 (2), 259-271

Rosindell, J., Hubbell, S. P. & Etienne, R. S. (2011) The Unified Neutral Theory of Biodiversity and Biogeography at Age Ten. *Trends in Ecology & Evolution*. 26 (7), 340-348.

Rosindell, J., Hubbell, S. P., He, F., Harmon, L. J. & Etienne, R. S. (2012) The case for ecological neutral theory. *Trends in Ecology & Evolution*. 27 (4), 203-208.

Rosindell, J. & Phillimore, A. B. (2011) A unified model of island biogeography sheds light on the zone of radiation. *Ecology Letters*. 14 (6), 552-560.

Steiner, C., Long, Z., Krumins, J. & Morin, P. (2005) Temporal stability of aquatic food webs: partitioning the effects of species diversity, species composition and enrichment. *Ecology Letters*. 8 (8), 819-828.

Steiner, C., Long, Z., Krumins, J. & Morin, P. (2005) Temporal stability of aquatic food webs: partitioning the effects of species diversity, species composition and enrichment. *Ecology Letters*. 8 (8), 819-828.

Tilman, D. (1999) The ecological consequences of changes in biodiversity: A search for general principles. *Ecology*. 80 (5), 1455-1474.

Tilman, D., Lehman, C. & Bristow, C. (1998) Diversity-stability relationships: Statistical inevitability or ecological consequence? *American Naturalist*. 151 (3), 277-282.

Tilman, D., Wedin, D. & Knops, J. (1996) Productivity and sustainability influenced by biodiversity in grassland ecosystems. *Nature*. 379 (6567), 718-720.

Tilman, D., Reich, P. B. & Knops, J. M. H. (2006) Biodiversity and ecosystem stability in a decade-long grassland experiment. *Nature*. 441 (7093), 629-632.

Turner, E. & Foster, W. A. (2006) Assessing the influence of bird's nest ferns (*Asplenium spp.*) on the local microclimate across a range of habitat disturbances in Sabah, Malaysia. *Selbyana*. 27(2), 195-200.

Yamakura, T., Hagihara, A., Sukardjo, S., Ogawa, H. (1986) Tree Size in a Mature Dipterocarp Forest Stand in Sebulu, East Kalimantan, Indonesia. *Southeast Asian Studies*. 23(4), 452-478.