

Copyright
by
Evan Philip Economo
2009

The Dissertation Committee for Evan Philip Economo
certifies that this is the approved version of the following dissertation:

**The Origins, Maintenance, and Conservation of
Biodiversity in Spatial Networks**

Committee:

Timothy H. Keitt, Supervisor

Daniel Bolnick

Lauren Ancel Meyers

Ulrich Mueller

Sahotra Sarkar

**The Origins, Maintenance, and Conservation of
Biodiversity in Spatial Networks**

by

Evan Philip Economo, B.S.

DISSERTATION

Presented to the Faculty of the Graduate School of

The University of Texas at Austin

in Partial Fulfillment

of the Requirements

for the Degree of

DOCTOR OF PHILOSOPHY

THE UNIVERSITY OF TEXAS AT AUSTIN

August 2009

Dedicated to the memory of my grandfathers,
Evangelos Economo (1914-2006) and Nicholas Damas (1928-2009).

Acknowledgments

I wish to thank my supervisor, Timothy H. Keitt, for collaboration and mentorship. THK is a co-author on the first and second chapters and contributed much to the other chapters. Thank you to my committee, Dan Bolnick, Lauren Meyers, Ulrich Mueller, and Sahotra Sarkar. Thanks to Eli Sarnat for collaboration and friendship, ES was a co-author of the fifth chapter. Thanks to Juanita Choo, Samraat Pawar, Naiara Pinto, Scott Solomon, Sasha Mikheyev, Chris Brooks, Mathew Leibold, Brian J. Enquist, Andrew Kerkhoff, Jesse Lasky, Andrew Noble, Kate Behrman, the HCJC, my cohort in EEB, the IGERT group in phylogenetics, U. Mueller and lab, L.A. Meyers and lab, and the Keittlab for many stimulating discussions about biology and the world. Thanks to Laura Gonzales and Phil Ward for use of lab facilities. Vinaka vakalevu to Dave Olson, Linda Olson, Moala Tokota'a, Akanisi Tokota'a, John Fasi, WCS-Fiji, USP, Linton Winder, Neal Evenhuis, Dan Bickel, Tim Markwell, and the people of Fiji and the Solomon Islands for supporting my work in the south Pacific. Special thanks to Arthur T. Winfree. Thanks to my family, Helena O'Connor, Michael Economo, Kristin Economo, and George Economo. Thank you to UT EEB Stengl Fellowship, UT preemptive fellowship, the Bruton Fellowship, the Marion Elizabeth Eason Scholarship, and especially the NSF IGERT Fellowship in Computational Phylogenetics and NSF Graduate Research Training Fellowships for financial support.

The Origins, Maintenance, and Conservation of Biodiversity in Spatial Networks

Publication No. _____

Evan Philip Economo, Ph.D.
The University of Texas at Austin, 2009

Supervisor: Timothy H. Keitt

Biodiversity is distributed unevenly across geographic space and the tree of life. A key task of biology is to understand the ecological and evolutionary processes that generate these patterns. I investigate how the structure and geometry of a landscape, for example the sizes and arrangements of islands in an archipelago, affects processes contributing to the generation and conservation of biodiversity patterns. In the first chapter, I integrate two disparate bodies of theory, ecological neutral theory and network theory into a powerful new framework for investigating patterns of biodiversity in a complex landscape. I examine the consequences of network structure, such as size, topology, and connectivity, for diversity patterning across the metacommunity. The second chapter focuses on how the position of a node within a network controls local community (node) diversity. Network statistics, such as node centrality, are found to predict diversity patterns with more central nodes accumulating the most diversity. In the third chapter, I use the theory to

evaluate how well fundamental concepts in conservation biology perform when neutral metacommunity processes generate diversity patterns. I find that contemporary diversity patterns are poor predictors of the long-term capacity of a network to support diversity, challenging a host of conservation concepts and applications. In the fourth chapter, I consider biodiversity dynamics in a network with a different model of speciation, where spatial structure is needed for divergence. In this case, speciation hotspots form where the dispersal properties of an organism and the spatial structure of the landscape coincide. In the final chapter I study the biodiversity of a natural structured metacommunity, the ants of the Fijian archipelago. I used a variety of collecting techniques to inventory the ant species occurring across a system of islands in the southwest Pacific. Approximately 50 new species were discovered, and the distributions of the ant species across the islands are firmly established. Radiations are observed in the genera *Pheidole*, *Camponotus*, *Lordomyrma*, *Leptogenys*, *Cerapachys*, *Strumigenys*, *Poecilomyrma*, and *Hypoponera*.

Table of Contents

Acknowledgments	v
Abstract	vi
Chapter 1. Species diversity in neutral metacommunities: a network approach	1
1.1 Abstract	1
1.2 Introduction	2
1.3 Theory: Neutral biodiversity pattern in a network of communities	5
1.3.1 Alpha diversity	10
1.3.2 Gamma diversity	11
1.3.3 Beta diversity	11
1.4 Analyses and Results	13
1.4.1 Migration rate	14
1.4.2 Network topology	17
1.4.3 Speciation rate	19
1.4.4 Metacommunity size N_m	21
1.5 Discussion	22
Chapter 2. Network isolation and local diversity in neutral metacommunities	34
2.1 Abstract	34
2.2 Introduction	35
2.3 Methods	39
2.3.1 A Network Concept of Isolation in a Metacommunity . .	39
2.3.2 Network Construction	41
2.3.3 Neutral Diversity Theory:	42
2.4 Discussion	47
2.4.1 A reverse-time perspective	50
2.4.2 Caveats and future directions	52

Chapter 3. Conservation strategies are ineffective when dispersal drives biodiversity patterns	59
3.1 Abstract	59
3.2 Introduction	60
3.2.1 Diversity Loss in a Metacommunity	63
3.3 Results	64
3.3.1 Single patch removals	64
3.3.2 Persistence in reserve networks	66
3.4 Discussion	66
3.5 Methods	68
 Chapter 4. The role of connectivity in geographic diversification	 73
4.1 Abstract	73
4.2 Introduction	74
4.3 Connectivity and Speciation Rate on Two Islands	77
4.4 Speciation in a Network of Islands	81
4.5 Discussion	85
 Chapter 5. The ants of the Fijian archipelago	 92
5.1 Introduction	92
5.2 Survey/Curation Methods	96
5.3 Inventory Results	97
5.4 Community Patterns	101
5.4.1 Dominance	101
5.4.2 Species Area Curves	102
5.4.3 Elevational patterns	104
5.5 Taxonomic Summary of the Ants of Fiji	105
5.5.1 Amblyoponinae	106
5.5.2 Cerapachyinae	106
5.5.3 Dolichoderinae	108
5.5.4 Ectatomminae	110
5.5.5 Formicinae	111

5.5.6	Myrmicinae	115
5.5.7	Ponerinae	124
5.5.8	Proceratiinae	127
Appendices		133
Appendix A. Chapter 3 Supplemental Information		134
A.1	Supplemental Methods	134
A.2	Supplemental Analyses and Figures	139
Bibliography		148
Vita		165

Chapter 1

Species diversity in neutral metacommunities: a network approach

1.1 Abstract

Biologists seek an understanding of the processes underlying spatial biodiversity patterns. Neutral theory links those patterns to dispersal, speciation, and community drift. Here we advance the spatially explicit neutral model by representing the metacommunity as a network of smaller communities. Analytic theory is presented for a set of equilibrium diversity patterns in networks of communities, facilitating the exploration of parameter space not accessible by simulation. We use this theory to evaluate how the basic properties of a metacommunity- connectivity, size, and speciation rate- determine overall metacommunity gamma diversity, and how that is partitioned into alpha and beta components. We find spatial structure can increase gamma-diversity relative to a well-mixed model, even when θ is held constant. The magnitude of deviations from the well-mixed model and the partitioning into alpha and beta diversity is related to the ratio of migration and speciation rates. Gamma diversity scales linearly with metacommunity size even as alpha and beta diversity scale nonlinearly with size.

1.2 Introduction

Understanding variation in species diversity and community composition is a central problem in biology (Brown, 1995; Rosenzweig, 1995). Neutral ecological theory links biodiversity pattern to an elementary set of ecological and evolutionary processes (Hubbell, 2001). Despite this simplicity, the theory holds promise for generating a set of baseline expectations, and serves as a useful touchstone for building more complex theory (Alonso et al., 2006). Recent work has extended several dimensions of the model including the mechanism of speciation (Hubbell, 2005; Etienne et al., 2007b; Mouillot and Gaston, 2007), the density dependence of population dynamics (Volkov et al., 2005), the zero-sum assumption (Etienne et al., 2007a), among others (Chave, 2004). Here we focus on the model of space underlying the theory, moving beyond simple spatial templates to develop theoretical results for metacommunities with more complex structure.

The neutral perspective views diversity as an outcome of stochastic speciation, migration, and ecological drift due to birth-death dynamics of individuals. This occurs in a spatial context where a local community receives migrants from a metacommunity (Hubbell, 2001). Various implementations of this general idea can be found in the literature, focusing on different aspects of neutral pattern (Chave, 2004; McGill et al., 2006). McGill et al. (2006) classify neutral metacommunity models as either spatially implicit, where the local community draws migrants from a separate pool of individuals, or spatially explicit, where the metacommunity is an actual set of local communities

with connections among them. The degree to which the behavior of a truly spatially explicit metacommunity deviates from the spatially implicit model is an open question. A somewhat different definition for spatially explicit is used in the broader metacommunity literature, for example by Leibold et al. (2004): A model in which the arrangement of patches or distance between patches can influence patterns of movement or interaction. The theoretical approach we present is spatially explicit according to both definitions. Spatially explicit neutral models have been explored with stochastic simulation and with analytic theory (Durrett and Levin, 1996a; Bell, 2000b; Hubbell, 2001; Chave and Leigh, 2002; Chave et al., 2002; Houchmandzadeh and Vallade, 2003; McGill et al., 2005; Rosindell and Cornell, 2007; Zillio et al., 2005). However, little attention has been paid to how the internal structure of spatially explicit metacommunities determines equilibrium spatial patterns under neutrality. As neutral theory emphasizes the role of dispersal limitation, the number and strengths of connections a local community has with other communities will influence patterns of species diversity and similarity. Beyond these primary connections, the position of a community in the broader metacommunity may have a cascading influence on the local community.

Most spatially explicit applications of neutral theory have been focused on two dimensional continuous habitats, some specifically inspired by spatially extended lowland forest communities (Chave et al., 2002). While this is a logical approach for metacommunities extended in continuous space, many real metacommunities are characterized by discontinuous, or patchy internal struc-

ture. Habitats can be distributed unevenly in space from landscape-level scales to the largest scales- their distribution on and among continents. Network theory is a versatile framework for representing these complex structures, where habitat patches, islands, or even continents, are nodes in a graph, and edges represent some rate of individual movement. Network tools are commonly used in landscape ecology (Urban and Keitt, 2001), metapopulation ecology (Hanski, 1999), and a variety of other fields where a set of units has heterogeneous connections among them (Albert and Barabasi, 2002).

The present study examines how the network structure of metacommunities determines patterns of diversity and similarity among individual communities undergoing ecological drift, speciation, and dispersal. Central to the neutral theory are stochastic biological rates interacting with spatial constraints, and while spatial complexity complicates neutral expectations, it also provides an opportunity to make use of spatial pattern to discriminate neutral processes from competing ideas in ecology. Neutral pattern should respond to the structure of island archipelagoes and the shape of domain boundaries, -the geographic structure of the metacommunity.

We develop analytical theory which predicts equilibrium diversity patterns within and among localities in metacommunities with a diverse set of spatial structures. Following previous spatially explicit theory (Chave and Leigh, 2002), we borrow tools from population genetics and derive spatially explicit predictions for a family of diversity indices based on the Simpson concentration (Simpson, 1949). By connecting this approach to network theory,

we facilitate the investigation of a broad set of questions about neutral diversity patterns in structured geographies.

In this paper we focus on a basic question about spatially explicit metacommunities; how the broad scale structure of the network controls patterns of alpha, beta, and gamma diversity. Using a well-mixed metacommunity as a benchmark, we investigate the effects of spatial structure on overall metacommunity gamma diversity. Metacommunity diversity can be partitioned into within (α) and among (β) community components (Whittaker, 1972; Lande, 1996; Magurran, 2003). We investigate how the basic components of the model- connectivity, speciation, and metacommunity size, determine spatial pattern under neutrality.

1.3 Theory: Neutral biodiversity pattern in a network of communities

The resemblance, if not identity, of ecological neutral theory to the more mathematically mature neutral theory of population genetics (Kimura, 1983) allows concepts and quantitative tools from the latter to be adapted by ecologists. Indeed much of the extant ecological neutral theory has been inspired at least in part by population genetics (Hubbell, 2001; Chave, 2004; Hu et al., 2006). Here we follow a mathematical approach used in population genetics and based on the concept of probability of identity to derive novel theory for species diversity in networks of communities.

A common construction of neutral theory assumes point speciation,

with new species arising randomly as one individual, with zero-sum stochastic community dynamics. This model maps on exactly to the infinite alleles model of population genetics (Kimura and Crow, 1964; Hubbell, 2001). A useful concept in population genetics is the probability of identity in state of two alleles chosen from a population. In this model, two alleles are identical in state if -looking backwards in time- their lineages coalesce into a common ancestor before a mutation has occurred in either lineage. This probability depends on both the coalescence time, how far back in time existed most recent common ancestor, and the rate at which mutations accumulate on the lineages. Coalescence times will normally be dependent on population sizes, migration rates, and the spatial separation of the sampled alleles, as the lineages have to move to the same location before coalescing (Hudson, 1990).

Identity probabilities underlie population genetics statistics describing patterns of genetic diversity (Nei, 1987). Interestingly, we can convert these into diversity statistics that are traditionally used by ecologists, a connection that has been made before in the context of neutral theory (Chave and Leigh, 2002; Condit et al., 2002; Etienne, 2005a; He, 2005; Hu et al., 2006). The Simpson concentration, by definition, is the probability that two randomly chosen individuals chosen at random from a set are the same type (Simpson, 1949). In ecology this is applied to individuals chosen from a community (Magurran, 2003) and is usually calculated directly from the set of species frequencies. Therefore to the extent that genetic models map on to ecological models, theory for allelic probabilities of identity in state also mechanistically predict

community diversity. We develop this further and show how a host of metrics describing diversity patterns in metacommunity with network structure can be analytically found using population genetics theory.

Neutral ecological dynamics in a network of communities correspond to migration matrix models (Bodmer and Cavalli-Sforza, 1968) in population genetics. In this representation a network of n local populations is represented by a stochastic backward migration matrix (\mathbf{M}). Each m_{ij} reflects the fraction of individuals in a given subpopulation i that originated from a parent in subpopulation j in the previous generation, and $\sum_j m_{ij} = 1$. Edge weights m_{ij} , and local population sizes N can vary to capture the underlying spatial structure of the metacommunity. In the following derivation, directed networks (matrices where some $m_{ij} \neq m_{ji}$) are permitted but descendants of individuals in each node must be able to eventually reach every other node ($m_{ij} \neq 1$). Speciation rate v takes the place of mutation, and reflects the per generation probability of change in state of a single individual.

The probability of identity in state (f_{ij}) for alleles sampled from communities i and j under the infinite alleles model can be calculated with a recursive equation originally discovered by Malcot (Malécot and Yermanos, 1970; Malécot, 1948) and developed extensively by later authors (Nagylaki, 1980, 1982; Laporte and Charlesworth, 2002). The equation for the probability of identity in state f'_{ij} in the current generation in terms of the set of f_{ij} in the previous generation can be written as a recursion:

$$f'_{ij} = (1 - v)^2 \left[\sum_{k,l} m_{ik} m_{jl} f_{kl} + \sum_k m_{ik} m_{jk} \frac{1}{N_k} (1 - f_{kk}) \right] \quad (1.1)$$

Where k and l index over all n nodes. This converges to an equilibrium (Nagylaki, 1980).

$$\hat{f}_{ij} = (1 - v)^2 \left[\sum_{k,l} m_{ik} m_{jl} \hat{f}_{kl} + \sum_k m_{ik} m_{jk} \frac{1}{N_k} (1 - \hat{f}_{kk}) \right] \quad (1.2)$$

We rearrange this equation to the form:

$$f_{ij} = (1 - v)^2 \left[\sum_{k,l,k \neq l} m_{ik} m_{jl} f_{kl} + \sum_k m_{ik} m_{jk} \left(1 - \frac{1}{N_k} \right) (f_{kk}) + \sum_k m_{ik} m_{jk} \left(\frac{1}{N_k} \right) \right] \quad (1.3)$$

Two sampled individuals are the same type if neither has speciated since the previous generation (the first term), and *i*) they were from parents of the same type from different patches (the first summation) or *ii*) they were from different parents of the same type located in the same patch (second summation), or *iii*) they had the same parent (coalesced) in the previous generation (third summation).

Equation 1.3 is linear and may be further rearranged and written in the form:

$$(1 - v)^{-2} \hat{f}_{ij} - \sum_{k,l} m_{ik} m_{jl} \hat{f}_{kl} + \sum_k m_{ik} m_{jk} \frac{1}{N_k} \hat{f}_{kk} = \sum_k m_{ik} m_{jk} \frac{1}{N_k} \quad (1.4)$$

For a network of n nodes, there are n^2 (i,j) pairs, and thus n^2 linear equations in this form describe the system at equilibrium. Since there are n^2 unknowns in n^2 equations, the system can be solved for the vector \vec{f} of all f_{ij} . For the analyses in this paper, we coded the left side of equation 4 as a $n^2 \times n^2$ matrix \mathbf{X} , and the right side as a vector \vec{q} of length n^2 , where

$$X_{(ij),(kl)} = (1 - v)^{-2} \delta_{(ij),(kl)} - m_{ik}m_{jl} + \delta_{k,l}m_{ik}m_{jk}(\frac{1}{N_k}) \quad (1.5)$$

and

$$q_{(ij)} = \sum_k m_{ik}m_{jk}(\frac{1}{N_k}) \quad (1.6)$$

and where $\delta_{i,j}$ is the Kronecker delta ($\delta_{i,j} = 1$ when $i = j$ and $\delta_{i,j} = 0$ otherwise), and solved the formula $\mathbf{X}\vec{f} = \vec{q}$ for \vec{f} with Matlab. Migration and speciation rates as well as local community sizes can take on any value without loss of computational efficiency. This allows the exploration of large regions of parameter space inaccessible to simulation. The limitations are mainly in the number of nodes n in the network; as the matrix of length n^2 must be computationally tractable. However, if most nodes in the network are connected to a relatively small number of other nodes (likely a common biological situation) large networks can be computed with sparse matrix methods. In this paper, we used sparse matrix routines for networks with more than 30 nodes.

The set of all f_{ij} represent the probability two individuals, randomly chosen from within local patches i and j at any locations in the network, are identical in state. In terms of the neutral ecological model, it is the equilibrium

probability they are the same species. From these values we can calculate a number of diversity metrics of ecological interest for the local and metacommunity.

1.3.1 Alpha diversity

As discussed before, f_{ii} is equivalent to the Simpson concentration λ for a local community i . In population genetics this is also related to the heterozygosity ($1 - f_{ii}$) of a population. This can be written as Simpsons index of diversity α_i .

$$\alpha_i = 1 - f_{ii} \quad (1.7)$$

For many purposes such as diversity partitioning, a raw Simpson's index is undesirable as a measure of alpha diversity as it converges to 1 as diversity increases unbounded, with highly misleading behavior (Jost, 2006). The index can be linearized by converting to an *effective number of species* or Hill number (Hill, 1973), which is the species richness that would produce a given Simpson's index if all species abundances were equal.

$$D(\alpha_i) = \overline{f_{ii}}^{-1} \quad (1.8)$$

The average alpha diversity expressed as Simpsons index and as an effective number of species over the whole metacommunity are,

$$\alpha_M = (1 - \overline{f_{kk}}) \quad (1.9)$$

$$D(\alpha_M) = \overline{f_{kk}}^{-1} \quad (1.10)$$

where both averages are taken over all k .

1.3.2 Gamma diversity

Metacommunity diversity, or gamma diversity, can be calculated with similar averages. Averaging the whole f_{ij} vector gives the Simpson concentration for the metacommunity, which can be used to give the Simpsons index and effective number of species for the whole metacommunity,

$$\gamma = 1 - \overline{f_{ij}} \quad (1.11)$$

$$D(\gamma) = \overline{f_{ij}}^{-1} \quad (1.12)$$

where both are averaged over all (i, j) pairs.

1.3.3 Beta diversity

Beta diversity, broadly speaking the component of diversity reflected in differences among locations or samples, can also be calculated using the Malcot equation. Gamma diversity can be partitioned into independent alpha and beta components with multiplicative(Whittaker, 1972) or additive

(Lande, 1996) methods. Given the scaling problems of using raw Simpson diversity indices, we can partition total metacommunity (gamma) diversity into alpha and beta components in terms of Hill numbers. There is one caveat, problems of concavity arise when calculating metacommunity-wide (but not node specific) figures for alpha, beta, and gamma diversity based on Simpsons index when community weights are unequal (e.g. when local community sizes are variable, see (Jost, 2006) for further discussion). This paper will consider only networks where nodes are the same size.

Multiplicative Partition: An *effective number of communities*, the number of distinct communities with the average alpha diversity needed to account for overall gamma diversity, can be calculated as follows. In panmixia, this is 1, if all communities are distinct, this is n, the number of local communities.

$$C_e = \frac{D(\gamma)}{D(\alpha_M)} = \frac{\overline{f_{ij}}}{\overline{f_{kk}}} \quad (1.13)$$

Additive Partition: Additive partitioning calculates a beta diversity value in the same units as alpha and gamma diversity. The average effective number of species in a local site (alpha) and effective number of species of the meta-community (gamma) can be used to back calculate the beta contribution.

$$D(\beta) = D(\gamma) - D(\alpha) = (\overline{f_{ij}})^{-1} - (\overline{f_{kk}})^{-1} \quad (1.14)$$

Pairwise Similarity: Similarity of two local communities i and j can be described with the Morisita-Horn index of overlap (Horn, 1966).

$$MH_{ij} = \frac{2f_{ij}}{f_{ii} + f_{jj}} \quad (1.15)$$

1.4 Analyses and Results

The theory described in the previous section can be used to investigate equilibrium diversity patterns generated by neutral processes in complex habitat networks much more quickly than simulation methods for large area of parameter space. In the rest of this paper we solve equation 3 under various conditions to explore how the basic dimensions of the model, migration rate, network topology, speciation rate, and network size, drive alpha, beta, and gamma diversity patterns in spatially explicit metacommunities. We focus on spatial structure on the scale of the metacommunity, or more specifically divisions that break the metacommunity into tens or hundreds of units, rather than fine scale patchiness.

Both migration rate and network topology contribute to connectivity, an important driver of dynamics in landscape (Brooks, 2003), metapopulation (Hanski, 1999), and metacommunity ecology (Leibold et al., 2004). The exchange rates among communities can have variable effects on community di-

versity depending on the underlying model of community dynamics (Cadotte, 2006; Mouquet and Loreau, 2002, 2003).

Network connectivity can be a local property reflecting how connected a given node is to other nodes, or a global statistic characterizing the structure of a network. The former corresponds to the biogeographic concept of patch or island isolation while the latter refers to a landscape or metacommunity level property. In this paper we focus on the latter, network-level connectivity, and how it determines diversity patterns as measured by standard alpha, beta, and gamma diversity concepts.

1.4.1 Migration rate

In the spatially implicit model, the diversity of a panmictic metacommunity is controlled by the fundamental biodiversity parameter $\theta = 2vN_m$, while the diversity of a local community is controlled by θ , the local community size, and the migration rate into the local community (Etienne, 2005a). A basic question about the spatially explicit model is how structuring the metacommunity by restricting dispersal affects overall metacommunity gamma diversity. In addition, we seek to establish what determines the partitioning of that gamma diversity into within alpha and between beta community components. For the purposes of this analysis, we use additive partitioning methods (equations 10, 12, 14).

We consider the effect of restricting migration rates (mathematically represented by edge weights -values of the \mathbf{M} matrix) on diversity patterns in

two test networks representing topological extremes: a linear chain of communities (Fig. 1.1a), and a network where every node is connected to every other node. The latter network corresponds to the island model of population genetics, and we refer to it as the island graph (Fig. 1.1b).

Equilibrium diversity levels were calculated for networks of 20 local communities with a local community size of 20,000 individuals and a range of m values (1×10^{-7} – 1×10^{-2}). All edges m_{ij} in the network were set to equal weight. Figure 1.2 plots the results for a range of theta values on the two networks. The diversities are additively partitioned and presented in terms of effective number of species (equations 10,12, 14).

We find gamma diversity always decreases monotonically with increasing migration rate (edge weight). The relative magnitude of the decrease is also a function of the diversity parameter θ , with the spatial effect having a greater relative impact on metacommunities with substantial dispersal limitation (low m_{ij} values). This can be understood straightforwardly by examining the mathematics of diversity in a well-mixed metacommunity. The Simpsons index of a well mixed metacommunity is, to a very good approximation (Kimura, 1983; Hubbell, 2001; He, 2005),

$$\gamma = \frac{\theta}{\theta + 1} \quad (1.16)$$

Which can be converted to an effective number of species,

$$D(\gamma) = \theta + 1 = 2N_m v + 1 \quad (1.17)$$

Now consider if this metacommunity were split into a set of n smaller communities, each with size $\frac{N_m}{n}$ and no migration among them. The effective number of species of such a system would be

$$D(\gamma) = n \left(2 \frac{N_m}{n} v + 1 \right) \quad (1.18)$$

Subtracting equation 17 from equation 18, we find the difference in gamma diversity in the limit of no migration is $n-1$ effective species. As migration is increased and the metacommunity becomes more and more panmictic, this effect reduces to zero.

The implications are that for systems where the total expected effective number of species is much higher than the number of patches ($\theta + 1 \gg n - 1$), the degree of spatial isolation of those patches will have little relative -but a similar absolute- effect on gamma diversity. If the effective number of species in the metacommunity is small compared to the number of patches ($\theta + 1 \ll n - 1$), then spatial division can have a relatively large effect.

Metacommunity gamma diversity can be additively partitioned into within (alpha) and between (beta) community components, as is represented in Figure 1.2. Intuitively, higher migration rates among communities increases alpha diversity at the expense of beta diversity, which can result in a profound increase in local diversity when migration is high. This is consistent with previous results highlighting the role of immigration in local diversity maintenance (MacArthur and Wilson, 1967; Loreau and Mouquet, 1999; Hubbell,

2001). In terms of coalescence, as migration probabilities become larger, the distribution of coalescence times between individuals chosen from different communities becomes more similar to the distribution of times chosen from the same community.

1.4.2 Network topology

Even when the strengths and number of connections are held constant, the geometry of connections can have a significant effect on the distance between nodes and the spread of information on a network (Watts and Strogatz, 2006; Albert and Barabasi, 2002). To investigate this effect on diversity patterns, we hold migration rates and number of links constant while changing the architecture of the network. We consider three graphs with markedly different topologies, a linear chain graph, a randomly assembled graph, and a star graph (Fig. 1.1). The point of interest here is that for different topologies, node pairs are on average more or less isolated from each other, even when the total number and strengths of links are held constant. In other words, more or fewer intermediate nodes/edges must be traversed in order to travel between two randomly chosen nodes. Longer path length between two communities implies longer coalescence times between lineages chosen from those two communities, as lineages must move to the same patch before coalescing.

The chain and star graphs (Fig. 1.1) represent extremes in topological connectivity, in that a chain has relatively long path lengths and a star graph -where nodes are at most two links away no matter the network size- has short

paths. As an intermediate case, we generate random graphs by haphazardly connecting nodes, while constraining the network to have a given number of edges (in this case $n-1$) and every node reachable by some path from every other node. This generates graphs with tree-like structure (Fig. 1.1d).

We considered networks with 100 local communities of 20000 individuals, and 99 edges total. Larger networks are used than in Fig. 1.1, as topological differences of small networks will have little variation in path lengths. In general, we expect the larger the network, the more topological variation will affect have consequences for diversity pattern. Fig. 1.3a demonstrates the effect of different network topologies on diversity patterns in a metacommunity. The plot is structurally similar to those in Fig. 1.2 but represents several networks simultaneously. Alpha diversity (red) is highest for a given migration rate in the networks with shorter path lengths (star, random) and lowest in the chain graph. For higher migration rates, the difference is pronounced. The effect is not as dramatic as the migration parameter itself for networks of this size- but it underscores the importance of metacommunity geometry in diversity patterns, something impossible to capture in a spatially implicit model.

These topological differences can be measured with network statistics such as network diameter, which is variably defined in the literature as either the minimum distance between the furthest nodes, or the average minimum distance between two nodes, averaged over all node pairs (Albert and Barabasi, 2002; Amaral et al., 2000). We used the latter definition and calculated di-

ameter for the networks considered in Fig. 1.3a, and find that networks with longer diameters have a greater allocation of diversity into the beta component (Fig. 1.3b). This appears a promising direction and further work is needed to investigate the quantitative relationship between diameter and other network statistics with diversity patterns across a broader range of network types. An open question is the extent to which such statistics can substitute for direct modeling of neutral dynamics.

1.4.3 Speciation rate

In the spatially implicit metacommunity, gamma diversity (in effective numbers of species) scales approximately linearly with speciation rate due to equation 17. We investigate whether that scaling holds for metacommunities with internal dispersal limitation. Considering a chain graph identical to the one considered in Fig. 1.2, we held migration rates constant and varied speciation rate to examine its scaling with overall gamma diversity. The relationship between speciation rate and gamma diversity is found to deviate from the spatially implicit model (again by as many as $n - 1$ effective species), with a strong interaction effect with migration rate. Note we are using equation 4 and not equation 17, which is an approximation, to generate predictions for the well-mixed model. Considering migration and speciation together in Fig. 1.4a, we find that the deviations vary between zero and $n - 1$ and are related to the ratio of migration to speciation m/v . This result is qualitatively robust to different network structures (island vs. chain, varying network size), but

differ in quantitative details such as the actual values of m/v that lead to a deviation of a certain magnitude.

Aside from the strong effect on gamma diversity, speciation rates have consequences for the allocation of diversity into among (beta) and within (alpha) site components. Intuitively, higher speciation rates can be expected to promote geographic differentiation, with migration as an opposing, homogenizing force. Fig. 1.2 demonstrates the control of migration rates on the tradeoff between alpha and beta diversity, with local diversity making up increasing fraction of the total metacommunity diversity as migration rates are elevated. Comparing panels in Fig. 1.2, it is clear that the transition from beta to alpha diversity occurs at a higher migration rate when speciation rates are higher.

The joint effect of migration and speciation rate on differentiation can be considered on a chain graph ($n = 20$, local population sizes=20000), shown in Fig. 1.4b. The isoclines for a metric geographic differentiation $\log(\alpha/\beta)$, are parallel and with a slope of 1. This implies the ratio m/v is the relevant quantity with respect to the tradeoff between alpha and beta diversity, when network size and topology are held constant. When m/v is large, alpha diversity dominates, and beta when m/v is small. Again, while m/v controls $\log(\alpha/\beta)$ for a given metacommunity structure (link structure and population sizes), different networks with the same m/v may differ in their allocation of diversity into α and β components.

Interestingly, we do not find the product of local population size and migration rate (Nm) being greater or less than one to have a strong effect on

geographic differentiation, per se, after holding m/v constant (Fig. 1.6). This is in contrast to the commonly cited connection between Nm and F_{ST} taken from analysis of the island model, although clearly the relationship is more complex when idealized assumptions are violated (Wilkinson-Herbots, 1998; Whitlock and McCauley, 1999). We do note that one of the assumptions from the Nm result is that speciation (mutation) is weak compared to migration rates. If $Nm < 1$, then Nv must be at least several orders of magnitude below 1. As metacommunity diversity is generally controlled by theta, and $\theta = 2nNv$, n must be in the hundreds or thousands to recover a theta on the order of 1. So for subcommunities that are a significant fraction of the metacommunity (on the order of tens and hundreds), it is unlikely that a metacommunity would support much diversity to differentiate if $Nm < 1$ and $m \gg v$. We limit the scope of our conclusions to the population structures and diversity statistics explored here, and emphasize the need for further examination of the issue.

1.4.4 Metacommunity size N_m

The number of individuals in a metacommunity is expected to directly control equilibrium diversity under neutrality. In the spatially implicit model, this relationship is linear due to the equation 17. As we have demonstrated, diversity in spatially explicit metacommunities has a more complex relationship with migration and speciation rate than in the spatially implicit model. This is apparently not the case for network size. We grow metacommunities both by increasing the number of individuals in each subcommunity, and by

increasing the number of nodes in the network, holding migration and speciation rates constant. Figure 1.5a shows alpha, beta, and gamma diversity in a chain graph of 20 nodes, as local community size is varied between a range of 2000-60000 individuals. Alpha, beta, and gamma diversity all grow linearly with metacommunity size.

Figure 1.5b shows how diversity scales as local communities are added to a network. Interestingly, overall gamma diversity scales linearly while there is a nonlinear tradeoff between alpha and beta diversity. This occurs as the average distance between pairs of nodes in the network is increased.

1.5 Discussion

Our results highlight the importance of spatial structure and the biological parameters of the neutral model in determining species diversity of a local community, among spatially separated communities, and on the scale of the entire metacommunity. As the results presented in the previous section are in terms of a rather abstract parameter space, it is instructive to discuss how they may relate to natural systems. We find spatially structured metacommunities to have elevated gamma diversity compared to a well-mixed metacommunity if connectivity is low (Fig. 1.2,1.3) relative to speciation rate (Fig. 1.4a). The magnitude of this effect is, at most, $n - 1$ effective species in a network of n patches and the relative effect on metacommunity diversity is determined by the relative magnitude of the number of patches to the fundamental diversity number, the latter a function of speciation rate and metacommunity size.

For metacommunities with high diversity relative to the number of patches ($\theta + 1 \gg n - 1$), because speciation rate is high or metacommunity size is large (because, for example, the areas involved are large) or both, metacommunity structure has little effect on overall diversity even if migration is highly restricted. An example of this situation would be a set of large but isolated mountain ranges distributed on a continent. In these cases, α and β diversity, but not γ diversity, would be highly dependent on the connectivity of such patches.

If diversity is low compared to the number of patches ($\theta + 1 \ll n - 1$), the spatial effect can be of consequence to overall diversity. Hypothetical examples of this situation would be an isolated network of many small oceanic islands, or other numerous but isolated habitat types such as caves or mountain peaks. The total size of the metacommunity (Nm) may be unable to support much diversity if it were one well-mixed unit, but the isolation inhibits one or a few species from numerically dominating and thus enables species persistence. In this situation, the connectivity of the system has important consequences for α , β , and γ diversity.

These results demonstrate that under certain conditions, fragmentation promotes gamma diversity as subcommunities maintain uniqueness. It should be noted that the zero-sum assumption implies the indefinite persistence of subcommunities. In highly fragmented metacommunities with many small subcommunities, one might expect occasional extinction of those subcommunities due to environmental stochasticity, which may depress overall

metacommunity diversity. An interesting extension would be to examine neutral community dynamics in a network with dynamic structure.

Topological differences in metacommunity structure reflect different spatial arrangements of habitat. Some communities are arranged in long chains, such as riverine or coastal systems. Other metacommunities may be hierarchically clustered reflecting patchy habitat distributions on multiple scales, or characterized by asymmetric flows due to wind or water currents. Given the diversity of organisms in variables such as body size, life history, and habitat affinities, and the complexity of landscapes and environmental gradients, the structures of real metacommunities can be expected to be highly variable in nature.

The transition from β to α dominated metacommunities as m/v increases highlights the neutral hypothesis for global patterns of provincialism (Hubbell, 2001; Rosenzweig, 1995). When migration is too weak to overcome the differentiating effects of speciation, provinces with distinct biotas form in the subcommunities. When migration is relatively strong, communities embedded in large networks can have similar compositions. We have shown how the geometry of such networks also contributes to this transition. The linear scaling of gamma diversity with metacommunity size is consistent with the linearity of interprovincial species-area curves (Rosenzweig, 1995), although it remains to be seen if species number has the same behavior as the effective richness predicted by our model.

The main strength of the neutral theory is testability. The models

transparent parameters allow for empirical tests, and quantitative tools for fitting the model to data have blossomed (Etienne, 2005b, 2007, 2005a). Aside from several notable exceptions (Condit et al., 2002; Rosindell and Cornell, 2007), these efforts are based on fitting data to the spatially implicit model, some going so far as to use a spatially implicit model to generate predictions for community similarity (Dornelas et al., 2006). Given that spatial structure is a pervasive feature of real metacommunities, and thus migration rates among pairs of communities are often variable, neutral processes in nature could produce more complex diversity and similarity patterns than can be generated with spatially implicit models.

The challenges are formidable: a spatially explicit metacommunity requires more parameters to describe than a spatially implicit version, when one considers the large number of m_{ij} and local community sizes. Increasing the complexity of that structure increases the number of parameters to be fit to data. However, simplifying assumptions can be made about relations of distance with dispersal rates, and area with community size. From this perspective, the model presented here is not significantly more complex than metapopulation models (Hanski, 1999) which are commonly fit to data by making such simplifying assumptions. An exploration of that potential is left for future work.

Our analytic method permits the exploration of regions of parameter space that are inaccessible to simulation due to computational limits. This is because long transients are not an issue and speciation rates and numbers of

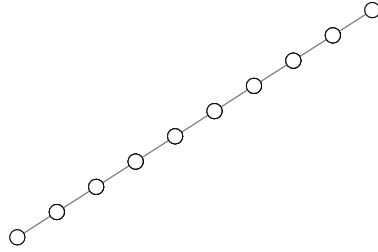
individuals (but not number of subcommunities) can take on any finite values. However, a disadvantage of our method is the focus on diversity indices as opposed to species abundance curves, which contain information on richness and all higher order diversity metrics. We expect this limitation will prove to be temporary, as recursive techniques similar to the Malcot equation can generate more detailed information about the coalescent process than is captured in probabilities of identity (Hudson, 1990; Nagylaki, 2000; Laporte and Charlesworth, 2002; Etienne and Olf, 2004). In addition, our method follows many other neutral models by assuming point speciation, the frequency of which in nature is uncertain. Under allopatric or other speciation mechanisms, it is possible diversity patterns will have a different relationship with spatial structure, and initial steps have been taken in this direction (Mouillot and Gaston, 2007).

The questions addressed here mostly pertain to global properties of the metacommunity, but there are many questions outstanding regarding how the internal network structure of a metacommunity determines neutral pattern. The position of a node in a network has consequences for both local diversity and uniqueness, and similarity with other nodes at a given location in the network (Economo & Keitt, unpublished results). A rich tradition of quantitative methods developed to quantify the local and global structure of networks (Albert and Barabasi, 2002) may prove useful for these ends.

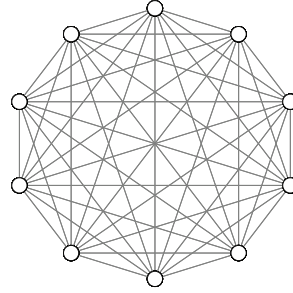
The possibility that relatively simple stochastic ecological and evolutionary processes may underlie biodiversity patterns is an idea that traces back

at least to MacArthur-Wilson island biogeography (MacArthur and Wilson, 1967). Neutral theory shows us again that spatial pattern can arise in the absence of environmental species sorting, niche partitioning, complex interactions, and historical contingencies. As complexity continues to be added to the theory highlighting different biological and geographical realities, we will eventually gain the ability to produce ever more specific and discriminating predictions. The future is promising for a rigorous assessment of the importance of stochastic processes in biodiversity dynamics in space and time, and across the tree of life.

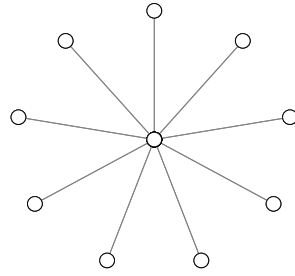
a) Chain



b) Island



c) Star



d) Random

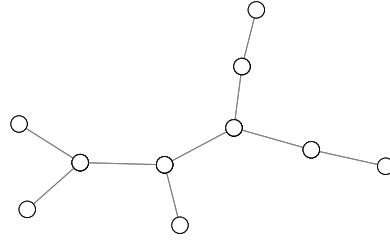


Figure 1.1: Network topologies appearing in this paper, a) chain graph, b) island graph, c) star graph, d) randomly assembled network. The networks used in the analyses have more nodes than those shown here, but have the same basic structure. The random graph is generated by arbitrarily connecting nodes but limiting the number of edges in the network.

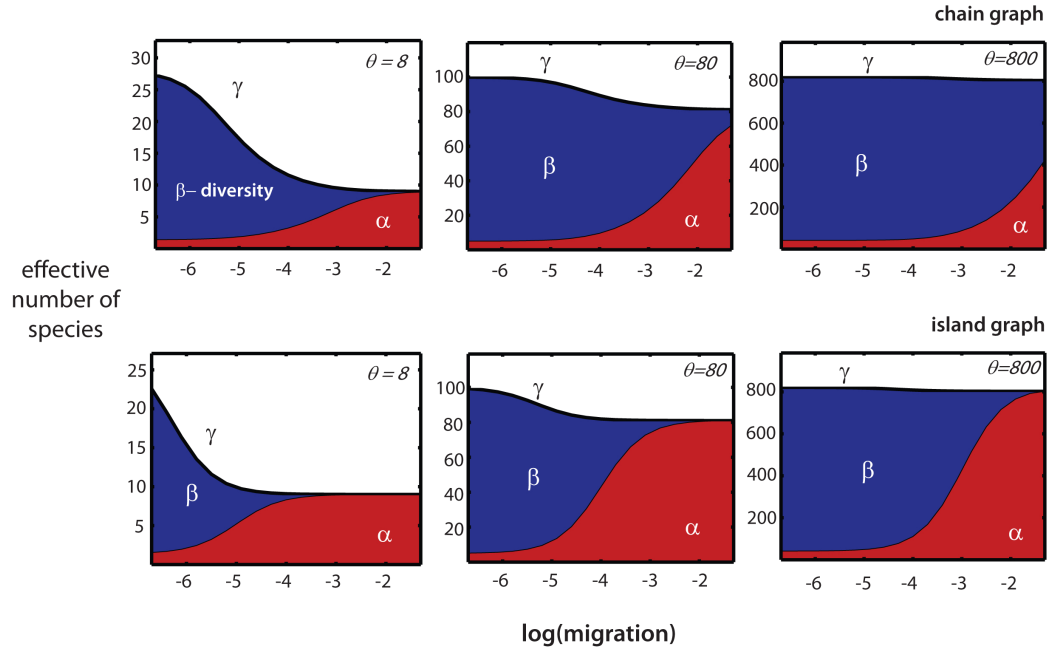


Figure 1.2: γ diversity (black line), partitioned additively into α diversity (red) and β diversity (blue) in a network of 20 nodes plotted as a function of migration rate. The plots represent the equilibrium solution calculated using equations 10,12, and 14, over a range of migration values ($2 \times 10^{-7} - 5 \times 10^{-2}$) and theta (8, 80, 800). Individual node sizes were set to 20000 individuals and not varied, theta was tuned by varying speciation rate (v). Notice gamma diversity converges to $\theta + 1$ as migration increases. Each edge in the network was set to the same migration value for a given calculation. The top row is for a network with chain structure, and the bottom row island structure (see Fig. 1).

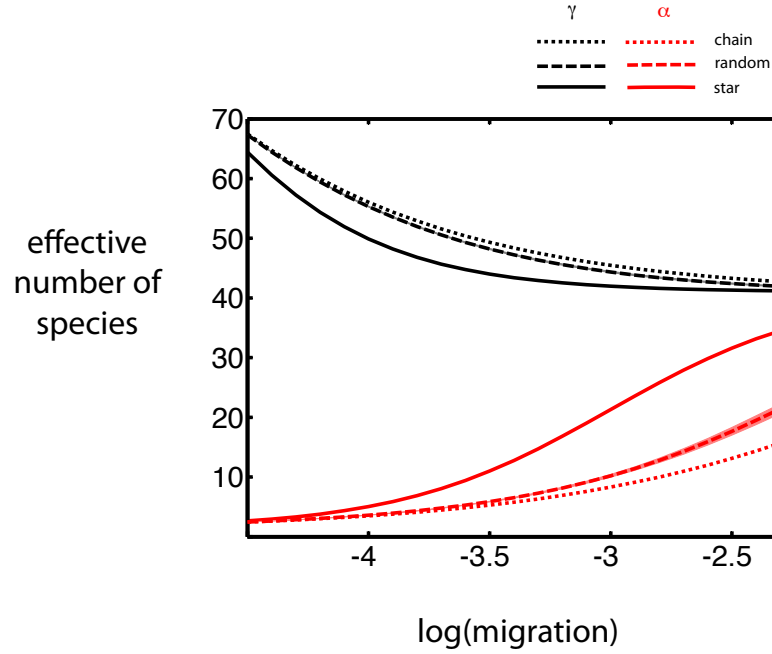


Figure 1.3: The effect of network topology on diversity patterns is demonstrated by examining the diversity levels on networks with otherwise similar parameter values (100 nodes, 99 links, $v = 1 \times 10^{-5}$, local pop. sizes = 20000). a) α diversity (red) and γ diversity (black) in metacommunities with star, chain, or random topologies, are plotted for a range of migration rates. Values for the random network line are averages of ten different networks, and the pink/grey shading reflects standard deviations. The difference between the black and red lines is β diversity using an additive definition. b) $\log(\alpha/\beta)$, an index of geographic differentiation, plotted as a function of network diameter (average minimum path length between all pairs of nodes) for the networks and parameter values considered in figure 3a, with $\log(\text{migration})$ set to -2.5. The curve is a quadratic fitted for visualization purposes.

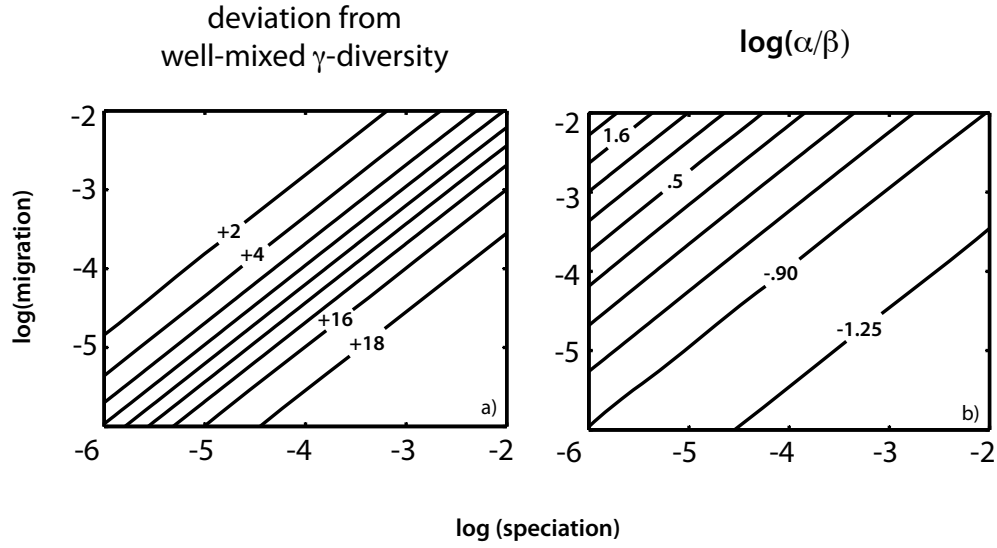


Figure 1.4: Contour plots showing diversity calculated in a range of migration and speciation rates on a chain graph with 20 nodes, and local population sizes set to 20000. a) the deviation of the equilibrium γ diversity in a spatially explicit metacommunity from a well mixed metacommunity of the same size. The units are effective number of species, isoclines depicted in increments of 2. The maximum is expected to be 19 ($n - 1$, see text). b) $\log(\alpha/\beta)$, an index of the allocation of diversity into within and between components, isoclines are in increments of 0.35. Both plots have parallel, linear isoclines, indicating the ratio of m/v is the important driver of these patterns.

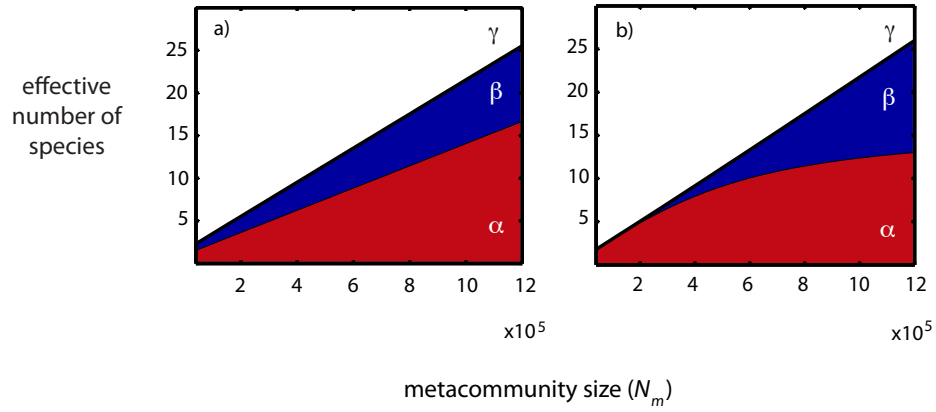


Figure 1.5: Diversity as a function of metacommunity size. a) diversity of a chain graph of length 20, ($m = 1 \times 10^{-3}$) as local community sizes are increased such that total metacommunity size varies between (40000-1.2 million). b) Diversity in a chain graph as nodes are added, so length varies between 1-30 local communities of 40000 individuals each.

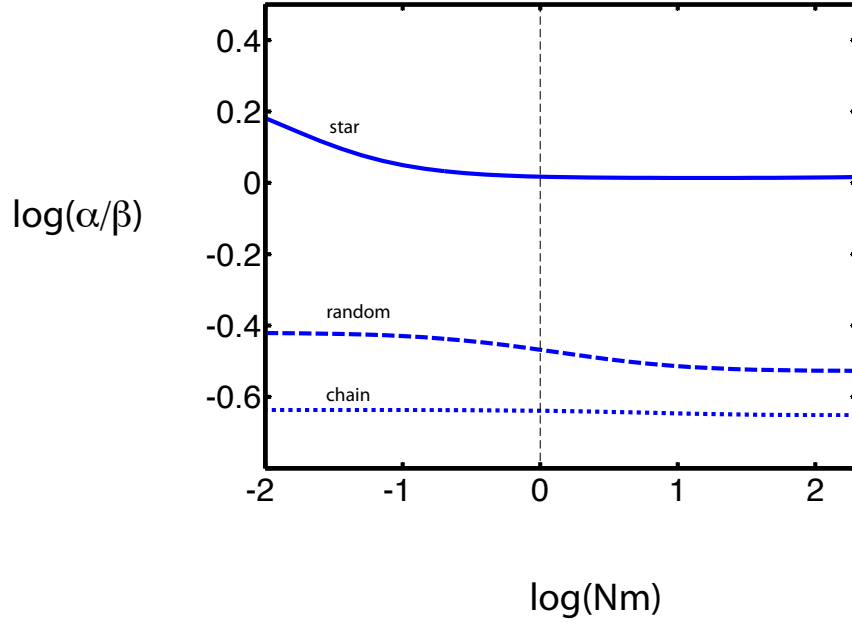


Figure 1.6: The effect of variable Nm , holding m/v constant. Three different networks were examined with the same number of nodes and edges, the chain graph, the star graph, and randomly constructed graphs (Fig. 1). As the number of edges connected to each node (node degree) is variable within these networks, for our value of m , we use the sum of all the edge weights entering each node $\sum_{j \neq i} m_{ij}$, averaged over all nodes. Local community sizes were set to 20000, and migration rates m were varied to produce variation in Nm . Speciation rate was varied with m , keeping their ratio constant $m/v = 100$. Note that as Nm gets smaller, alpha diversity actually goes up slightly, this may be in large part because we are concurrently downgrading v , and overall diversity gets extremely small. Note that in the limit of no speciation and nonzero migration, $\gamma = \alpha = 1$, and $\beta = 0$, using the additive definition.

Chapter 2

Network isolation and local diversity in neutral metacommunities

2.1 Abstract

Biologists seek an understanding of the biological and environmental factors determining local community diversity. Recent advances in metacommunity ecology, and neutral theory in particular, highlight the importance of dispersal processes interacting with the spatial structure of a landscape for generating spatial patterns and maintaining biodiversity. The relative spatial isolation of a community is traditionally thought to have a large influence on local diversity. However, isolation remains an elusive concept to quantify, particularly in metacommunities with complex spatial structure. We represent the metacommunity as a network of local communities, and use network centrality measures to quantify the isolation of a local community. Using spatially explicit neutral theory, we examine how node position predicts variation in alpha diversity across a metacommunity. We find that diversity increases with node centrality in the network, but only when centrality is measured on a given scale in the network that widens with increasing dispersal rates and narrows with increasing evolutionary rates. More generally, complex biodiversity patterns form only when the underlying geography has structure on this

critical scale. This provides a framework for understanding the influence of spatial geographic structure on global biodiversity patterns.

2.2 Introduction

A fundamental task of basic and applied ecology is to understand what determines local community diversity (Brown, 1995; Ricklefs, 1987; Rosenzweig, 1995). Ecological theory increasingly suggests that local diversity depends on spatial dynamics occurring on larger scales. Many ecological communities are embedded in a metacommunity, a network of local communities linked through dispersal. Recent theory has established the importance of these connections for changing and propagating ecological dynamics (Amarasekare, 2003; Holt, 2002; Hubbell, 2001; Leibold et al., 2004; Levin, 1992).

A key variable in most spatial biological theory, including metapopulation (Hanski, 1999), biogeographic (MacArthur and Wilson, 1967), and metacommunity theory (Hubbell, 2001; Leibold et al., 2004) is isolation of a patch or community. However, isolation is a scale dependent concept (Keitt et al., 1997), and the relevant scale for determining local diversity is often unclear. Communities may be isolated relative to their local landscapes, in a regional network of patches, or relative to the rest of their entire biogeographic province. Which scales of isolation control local diversity? And what biological parameters set those scales?

Ecological neutral theory (Chave, 2004; Hubbell, 2001) provides a quantitative, mechanistic framework for understanding biodiversity patterns in

metacommunities in terms of a minimal set of stochastic biological processes. It resides at one extreme in a continuum of metacommunity models that vary in their emphasis on the importance of niche differences, species interactions, and stochastic spatial effects on shaping ecological communities (Alonso et al., 2006; Leibold et al., 2004; Leibold and McPeck, 2006). Despite its limitations, in certain cases it has proven surprisingly capable at predicting community patterns found in nature (Hubbell, 2001; Muneeppeerakul et al., 2008; McGill et al., 2006).

Neutral theory highlights spatial effects due to the central role of dispersal limitation in determining community structure. However, as many of the neutral models explored in the literature are either spatially implicit (e.g. (Etienne, 2005b; Hubbell, 2001)) or constructed with two dimensional landscapes (Bell, 2000a; Chave et al., 2002; Condit et al., 2002; Durrett and Levin, 1996b; Rosindell and Cornell, 2007; Hubbell, 2001), the consequences of spatial complexity for neutral pattern are still largely unknown.

Recent work (Economo and Keitt, 2008; Muneeppeerakul et al., 2007, 2008) has sought to address this limitation by representing neutral metacommunities as networks, with local communities (nodes) linked by the capacity for dispersal (edges). Networks are ideally suited for representing a set of units with complex connections among them, and their utility across disciplines (Strogatz, 2001) has led to the wide application of a common set of quantitative tools (Newman, 2003). In ecology, spatially complex landscapes can be represented as a graph (Economo and Keitt, 2008; Urban and Keitt,

2001; Urban et al., 2009). The structure of the graph could reflect, for example, the arrangements of islands in an archipelago or mountains in a range. An advantage of the network framework is a sophisticated set of quantitative tools available for characterization of network structure (Newman, 2003; Urban and Keitt, 2001). We seek to identify which concepts and tools may be useful to spatially explicit metacommunity theory.

In the spatially implicit neutral model, differences in diversity among local community are primarily driven by migration rates from the metacommunity and the local community size (Etienne, 2005b; Hubbell, 2001; Etienne, 2007). Migration rate is commonly measured by m , or the probability an individual originated outside the local community. This general idea can be traced back to classical island biogeography theory, which emphasized the importance of island isolation on alpha-diversity (MacArthur and Wilson, 1967). In the network model (Economo and Keitt, 2008), the migration rate (m) corresponds to node degree, the number of links a community has with other communities (or the sum of their weights). This places an emphasis on the immediate neighborhood of a node on determining alpha-diversity.

However, in a network of communities, diversity may not simply be a function of connectivity with neighboring patches as those patches may serve as stepping stones to other regions of the metacommunity. If diversity cascades through the patch network in this manner, local diversity would be driven by metacommunity structure at broader scales than the local neighborhood. This requires a more sophisticated implementation of the concept of isolation.

Here we consider equilibrium alpha diversity at different rates of migration (edge weights) and speciation, in two model networks with different types of complex structure. These are a dendritic graph with a tree-like branching topology, and a modular graph with connected clusters of nodes. The dendritic graph allows for relatively easy visualization of node position in the network, and increases variation in topological distance compared to more complex topologies. The modular graph is intended to echo the complexity arising from hierarchically patchy landscapes. To further focus the problem, we only consider symmetric networks, where migration is equal in both directions between two communities.

We use *network centrality* measures to quantify the position of a node in a metacommunity (Newman, 2003). These statistics are used across disciplines to quantify network topology. We use them as different quantitative implementations of the concept of patch isolation in spatial ecology and biogeography. Centrality measures vary in their emphasis on short range or long range connections and how paths between nodes are interpreted. Establishing which of these predict neutral diversity, and under what biological conditions, reveals fundamental properties of how spatial structure drives neutral diversity pattern in complex metacommunities. It also represents the first implementation of network isolation concepts for metacommunities that are applicable well beyond neutral theory.

2.3 Methods

2.3.1 A Network Concept of Isolation in a Metacommunity

We used a variety network centrality measures to quantify the position of a node in a metacommunity with network structure. Node isolation is the inverse of node centrality. Each measure highlights a different aspect of network topology. (i): *Degree centrality* is simply the number of links a node has with other nodes or the sum of their weights. In a landscape, this corresponds to the flux of dispersal directly entering a node from other nodes. (ii): The *geodesic closeness centrality* is the average shortest path length between a node and all other nodes in the network. This measures the position of a node in the broader landscape, literally how close a node is to all other nodes. Note that a node with high closeness can have very low degree, and vice versa. (iii): The *resistance closeness centrality* is identical to geodesic closeness except the resistance distance (McRae, 2006) takes the place of geodesic distance. The resistance distance, which is derived from circuit theory, shortens when there are multiple paths between nodes while geodesic distance is solely determined by the shortest path. (iv): *Eigenvector centrality* scores nodes based not only by the number of connections with neighbors, but also by the importance of their neighbors. The metrics thus far all have a particular spatial scope, with degree centrality a function of local structure and the rest a function of structure of the entire network. As a final metric, it is desirable to have a statistic that can be tuned to reflect structure on intermediate scales. (v): We thus introduce the *k-neighborhood* the number

of other nodes that are within a geodesic distance k from the focal node. The degree centrality is the size of the k -neighborhood when $k = 1$.

As measures of global position of a node in the network, we favored measures of closeness centrality over betweenness centrality (Scott, 2000; Wasserman and Faust, 1994). Betweenness centrality considers how often a node is traversed on either shortest paths or random walks between other nodes, which are important in cases where one may need to identify key connectors in networks of information flow. To understand why we would favor closeness centrality, consider a node that is near the geographical center of the network but is on a cul-de-sac. Such a node would have short path lengths to many other nodes -a high closeness centrality- but would never be intermediate on paths between another pair of nodes. Thus the node would have the lowest possible betweenness score, the same betweenness as a truly peripheral node in the most isolated regions of the network. This makes it a non-ideal measure of the topological position only with regards to the processes of interest in this paper. Here we seek to understand how the global position in the network, which should differ between a cul-de-sac near the center of the network and a cul-de-sac in a peripheral region, affects diversity.

The centrality measures were calculated on the adjacency matrix. Degree centrality is simply the number of edges connected to a node. Closeness centrality is generally a measure of the position of a node relative to the rest of the network, usually calculated as the average distance between a node and all other nodes. We calculate two variants of closeness centrality based on

two measures of network distance (Scott, 2000; Wasserman and Faust, 1994). Geodesic closeness centrality is based on geodesic distance, which is simply the shortest path length between any two nodes. Resistance closeness centrality uses resistance distance in the place of geodesic distance. Resistance distance is a measure based on circuit theory, which accounts for multiple paths between any two nodes (McRae, 2006; McRae et al., 2008). The difference between the two is that geodesic distance is only determined by the shortest path, while resistance distance is shortened when there are multiple paths between two nodes. Resistance distance and geodesic distance are equivalent for tree-like graphs, such as the dendritic network used in this paper. We found geodesic distance (shortest path) between the node and all other nodes, using Dijkstras algorithm, and resistance distance with the method described by Mcrae (McRae, 2006). The closeness measure for node i was then simply the inverse of the mean distance between i and all j , using either distance metric. Eigenvector centrality is the eigenvector associated with the largest eigenvalue of the adjacency matrix, and essentially ranks nodes not only by their immediate connections but the degree of those connections. The size of the k -neighborhood of node i is the number of nodes within a geodesic distance k of the focal node.

2.3.2 Network Construction

We built two networks with complex spatial structure, one with a tree like, dendritic topology (figure 2.1) and one with modular structure (figure

2.2). As the focus of our paper is how the position of a node in a metacommunity affects diversity, we avoided networks that had overly symmetric or entirely random topologies, as in both of those cases, node position tends to be similar across the network. The dendritic network was assembled by randomly connecting nodes, but with the constraints that the 200 node network should have 199 bidirectional edges, and it should be one connected component. The modular network was created by generating subnetworks with random topologies, then haphazardly connecting those. The property we call modular is sometimes called community structure (Girvan and Newman, 2002) in the network literature, but to avoid confusion with the concept of biological community structure, we use the “modular” label.

2.3.3 Neutral Diversity Theory:

The neutral model we examine here is a simple neutral model that assumes a constant metacommunity and local community size. In each generation, an individual is drawn randomly from a parent the same community with probability m_{ii} , from another node j with probability m_{ij} , and is a new species with probability v . We refer to v as the speciation rate, but it also could represent immigration from a large source pool. The set of all m_{ij} , is the migration matrix \mathbf{M} , and describes the structure of the metacommunity. For the purposes of this paper, all migration rates (edges) in the metacommunity are set to the same value and all community sizes N_i are equal.

We used the quantitative method developed in a previous paper (Economo

and Keitt, 2008), for calculating expected neutral diversity in a network of communities under these assumptions. The method adapts equations originally developed from neutral population genetics theory. The quantity we wish to calculate is the probability of identity f_{ij} of two individuals chosen from communities i and j . This probability can then be converted to diversity statistics such as Simpsons index of diversity $1 - f_{ii}$ (Simpson, 1949). In this paper, our measure of alpha-diversity is the Simpson concentration (f_{ii}) converted to an effective species richness, f_{ii}^{-1} that does not converge as diversity becomes large (this is also sometimes called Simpson's index or Simpson's reciprocal index) (Hill, 1973). Probability of identity can be calculated with the following recursive equation (Economo and Keitt, 2008),

$$f_{ij} = (1 - v)^2 \left[\sum_{k,l,k \neq l} m_{ik} m_{jl} f_{kl} + \sum_k m_{ik} m_{jk} \left(1 - \frac{1}{N_k}\right) (f_{kk}) + \sum_k m_{ik} m_{jk} \left(\frac{1}{N_k}\right) \right]$$

Two sampled individuals are the same type if neither has speciated since the previous generation (the first term), and *i*) they were from parents of the same type from different patches (the first summation) or *ii*) they were from different parents of the same type located in the same patch (second summation), or *iii*) they had the same parent (coalesced) in the previous generation (third summation). For a network of n nodes, there are n^2 (i,j) pairs, and thus n^2 linear equations in this form describe the system at equilibrium. Since there are n^2 unknowns in n^2 equations, the system can be solved for the vector \vec{f} of all f_{ij} . For the analyses in this paper, we coded the left side of

equation 4 as a $n^2 \times n^2$ matrix \mathbf{X} , and the right side as a vector \vec{q} of length n^2 , where:

$$X_{(ij),(kl)} = (1 - v)^{-2} \delta_{(ij),(kl)} - m_{ik}m_{jl} + \delta_{k,l}m_{ik}m_{jk}(\frac{1}{N_k})$$

and

$$q_{(ij)} = \sum_k m_{ik}m_{jk}(\frac{1}{N_k}).$$

The formula $X\vec{f} = \vec{q}$ can then be solved for the vector \vec{f} of probability of identities.

Results

Figure 2.1a-b represents the degree and geodesic closeness centrality on the dendritic network, and Figure 2.2 plots resistance closeness centrality and degree centrality on the modular network. Notice that degree centrality is dependent on the local neighborhood of a node, while geodesic closeness integrates the position of the node in the entire metacommunity. Similar plots for both networks and all centrality statistics are presented in Supplemental Figure 2.1.

Figure 2.1b-d plots alpha diversity of each node at different rates of migration. As migration rate increases, alpha diversity increases for all nodes at the expense of beta diversity, as was demonstrated in a previous analysis (Economo and Keitt, 2008). In each panel, color variation was normalized to

the most diverse community. This allows us to visually examine the variation in diversity across the network and across parameter values, which are presented in both Figure 2.1c-f and Supplemental Figure 2.2. When dispersal is low, (Figure 2.1c), it is apparent that node diversity (color) is only a function of the local connectivity, nodes near the center of the network, but only connected to one other node, have a similar diversity to a node that has one connection but is on the periphery of the node. The diversity pattern closely resembles the pattern created by degree centrality (figure 2.1a). As migration is increased by an order of magnitude (figure 2.1d), the most diverse nodes are now not simply those with high degree, but those occurring at a confluence of branches, making them within a few steps of a larger number of nodes than those near the periphery. As migration is increased further (figure 2.1e), the most diverse nodes are those that connect large branches, or major divisions in the spatial structure of the metacommunity. Finally, when migration is highest, the most diverse nodes are those most central to the entire metacommunity.

We examined the correlations of network centrality measures with node position, which should quantify the transition observed in the visual patterns of Figure 2.1. In Figure 2.3, the alpha diversity of each node in the dendritic and modular networks, is plotted as a function of three different measures of node centrality and four different migration rates. For resistance closeness centrality (Fig. 2.3a,d), which integrates the position of the node in the entire network, correlations with alpha diversity are stronger when migration rates

are high, and lower when migration rates are low. Degree centrality (Fig. 2.3b,d), a local measure, is strongly correlated at low migration rates but increasingly becomes less correlated at higher migration rates. Eigenvector centrality is relatively weakly correlated with diversity at any migration rate. This appears to be because eigenvector centrality picks out the most highly connected cluster and assigns nodes within it a higher score than even nodes that have similar connectivity in another section of the network.

These correlations are presented in Figure 2.4, showing the tradeoffs of local vs. network wide controls on alpha diversity. The centrality metrics are not uncorrelated with each other, having a high degree also decreases distance to other regions of the network (particularly in relatively small networks such as these).

At extremes of low and high migration, which can be seen in supplemental figure 2.2, alpha diversity is nearly constant across the metacommunity. This is because each node becomes an independent community (when migration is low) or the metacommunity is effectively panmictic (at high migration). At high migration rates, the metacommunity approaches panmixia, and spatial position of a node has little effect on diversity patterns- alpha diversity is constant across the metacommunity. At the other extreme, when migration is very restricted, each individual node becomes a unique community, and again alpha diversity is basically constant across the metacommunity. Variation in alpha diversity, a proxy for the complexity of spatial pattern, peaks at intermediate migration (figures 2.4c,d).

It is clear in figure 2.4c–d, that this variation peak shifts at different speciation rates. This implies that, given a physical landscape structure, there is a particular combination of migration and speciation rates that produces complex spatial variation in alpha diversity. Or, put another way, for a given taxonomic group with certain propensities for dispersal and evolution, they will form complex biodiversity patterns and respond to geographic features only when there is landscape structure on a particular spatial scale.

Degree and closeness centrality measure node position relative to the local and global structure of the network, respectively, with each predicting alpha diversity when migration is high or low. We use the size of the k -neighborhood as a metric that measures spatial structure as scale is increased. This metric is the number of unique nodes within k steps of the focal node (degree centrality is k -neighborhood when $k = 1$). Figure 2.5 plots the correlation of alpha diversity with the size of the k -neighborhood. When migration is low, $k = 1$ has the most predictive power, while as migration increases, the value of k , which is a surrogate for spatial scale, increases as migration increases.

2.4 Discussion

These results illustrate both the promise and challenges for a network concept of isolation in metacommunities. The centrality measures capture different aspects of network structure, all of which are likely relevant to metacommunity dynamics and should be useful for a wide range of studies. In the neutral scenario considered here, the general idea that more isolated areas

have depressed diversity in a neutral metacommunity is supported. However, it is clear that no single quantitative definition of isolation universally predicts this variation. Rather, isolation predicts diversity only when measured on a critical scale in the network, which is scaled by the relative rates of dispersal and evolution. When migration is more restricted, isolation depresses diversity only when calculated locally. As migration increases relative to speciation, isolation best predicts diversity when calculated at successively greater scales in the network.

This implies that for a given taxonomic group with particular propensities for dispersal and speciation, correlations between isolation and alpha diversity should only be observed at certain spatial scales. This may explain why the isolation component of the island biogeography effect, which is usually arbitrarily defined as a distance to another land mass, is only sometimes observed. In general, more dispersive groups should show a correlation between isolation and alpha diversity on greater spatial scales. For example, the fine scale arrangement of islands in an archipelago would have little effect on diversity variation in a highly dispersive group. For a more sedentary group, diversity levels on an island would be more driven by the position of the archipelago in a broader network of archipelagoes rather than isolation within the archipelago. More generally, for complex biodiversity patterns to form in a landscape due to neutral processes, the geography must have structure on this critical scale.

These results have relevance to several other well-known biogeographic

phenomena. Geometric effects on diversity patterns have been much discussed. These include the peninsular effect, which proposes a decrease in diversity towards the terminal end of peninsulas. This is commonly explained by reduced colonization rates due to the geometry of the underlying spatial template. Neutral theory also predicts a peninsular effect, but only if migration and speciation rates are in the right balance to reflect that geographic feature. Mid-domain effects (Colwell and Lees, 2000) predict diversity to peak in the middle of a domain, a pattern that is sometimes -but not always- exhibited, and explanations have been offered by a number of mechanisms including stochastic neutral effects (Rangel and Diniz-Filho, 2005). This can be generalized to a network, where a network-wide most central node takes the place of geographic center of a domain. Our results suggest that the mid-domain effect does not always hold under neutrality in a spatially complex landscape, as migration becomes more restricted, regional spatial structure overrides the broader metacommunity geometry, so mid-domain effects may be more localized or not present at all. However, the basic conclusion that neutral theory can cause mid-domain effects in some regions of parameter space is supported, and also is in accord with results from population genetics (Wilkins and Wakeley, 2002).

These results also highlight how neutral processes can produce elevated diversity in nodes that connect different regions of the network. In a dendritic network (Fig. 2.1), for certain migration values, the nodes that connected two branches had elevated diversity. These offer a neutral hypothesis for biogeo-

graphic mixing zones (Spector, 2002), instead of an overlap in environments, certain transitional areas may occur due to geometric effects, those patches that connect disparate portions of the network will receive a mix of species from the two areas.

Our understanding of ecological neutral theory is overall still influenced largely by the behavior of spatially implicit models, but this spatially explicit model provides different answers to some basic properties of neutral diversity patterns. The migration parameter m , defined as the fraction of individuals in a local community that originated in another patch, along with the local community size N_k , are often considered to be the two main parameters setting local diversity. The spatially explicit model considered here clearly demonstrates that in many cases local diversity is set not by the number of individuals migrating into that patch, but by its position in a larger neighborhood of patches, or if migration is strong enough, the entire metacommunity. This spatial diversity cascade occurs at regions of higher migration, the local m value is swamped by the flow of diversity through the metacommunity.

2.4.1 A reverse-time perspective

Neutral dynamics can be viewed from equally valid forward or reverse-time (coalescent (Kingman, 1982; Rosindell et al., 2008)) perspectives. In this case of our results, some understanding can be gained by considering the latter. Our model predicts diversity in terms of probability of identities, the probability that two individuals randomly chosen will be the same type.

Conceptually, we are tracing ancestry of two individuals backwards in time and ask if they coalesce before either lineage has speciated. For the case of alpha diversity, we choose two individuals from the same spatial location. This depends on how quickly the two lineages move -via random walks- away from each other in backwards time, because once they become spatially separated they must again enter the same locality before they coalesce. Individuals sampled from nodes that have few connections to other nodes (low degree), or in a region of the network that is not highly connected to the rest of the network, such as a peninsular chain of nodes, will more likely be found in the localized region of the network at more distant times in the past, thus have more opportunity to coalesce before speciation. Increasing migration rate increases the spatial scale that the lineages are likely be found at any time in the past, reducing overall the probability of coalescence (and thus increasing alpha diversity) before speciation, but also making that diversity dependent on the structure of the network in that neighborhood. Thus, at very low migration rates, two lineages are likely to either coalesce or speciate before leaving the node, making spatial location of the node relative to the metacommunity irrelevant. At intermediate migration, lineages may travel some distance before speciation, but will not reach distant portions of the network, so the probability of coalescence is dependent on the structure of the limited local neighborhood of the network. At high migration, the lineages are more likely to explore distant regions of the networks before speciation or coalescence, and so its position in the broader network becomes important.

Finally, when migration is very high relative to speciation, the time scale is so long that the initial spatial position of the individuals becomes irrelevant for the long term probability that the two will coalesce, and diversity is constant across nodes.

2.4.2 Caveats and future directions

The speciation model used here assumes new species arise as a single individual, with equal probability across all individuals. Thus diversity is constantly being added to the metacommunity at all points equally, the patterns are generated by the subsequent flow of that diversity. Note that aside from speciation, this introduction of novelty could be interpreted as migration from a distant, large, source pool. As a model of speciation, there are undoubtedly cases where this is reasonable, such as such as speciation by polyploidy in plants. However, there are probably many cases where spatial structure is important to the process of speciation itself. This implies an additional complexity- speciation rates, not only migration, may depend on spatial location. Future work, building upon recent neutral models (Etienne et al., 2007b; Hubbell, 2005; Moullot and Gaston, 2007), is needed to explore this issue and will likely require a different mathematical approach.

The current analytical methods is limited to relatively small networks (on the order of 200 nodes for sparse networks, much less for highly connected networks on a normal personal computer). One reason for considering network statistics, which can generally be computed easily on much larger networks, is

that they may serve as a surrogate for predicting neutral diversity patterns. We find that they do, but that their performance depends on the parameters of the neutral model. It would be interesting if network statistics were developed that could be used to roughly predict diversity patterns from topology, with migration and speciation rates as parameters, without resorting to the full analytical method.

Our results show that network structure is a strong determinant of local diversity, and that network tools predict that relationship. This is an important step towards a rigorous understanding of the connection between isolation and biodiversity patterns in complex metacommunities. This study also raises important questions about how metacommunity topology affects diversity processes under different models of ecological dynamics than the one considered here. Incorporating spatially explicit model structures into models, which are more realistic depictions of natural landscapes, is likely to change the outcomes of a wide range of metacommunity dynamics. The question is not a trivial one as understanding the processes driving biodiversity pattern is critical for designing effective strategies to maintain it.

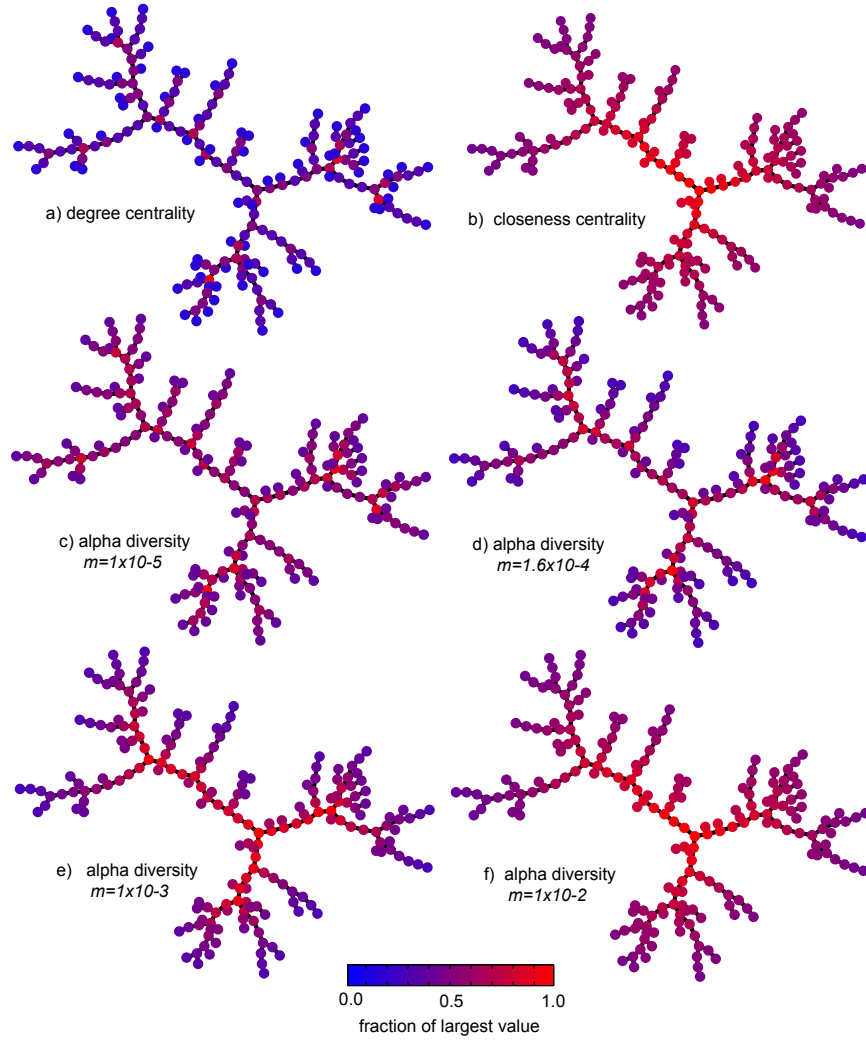


Figure 2.1: Visualization of centrality and diversity patterns in a metacommunity with network structure. node degree (a) and closeness centrality (b), and equilibrium alpha diversity at various migration rates (c-f), across the dendritic network. For the latter, $v = 10^{-5}$ and $N_k = 200000$.

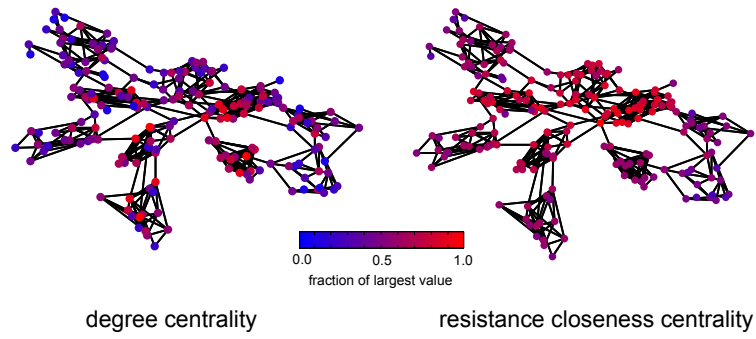


Figure 2.2: The modular network used in this paper with nodes colored by degree centrality and resistance closeness centrality.

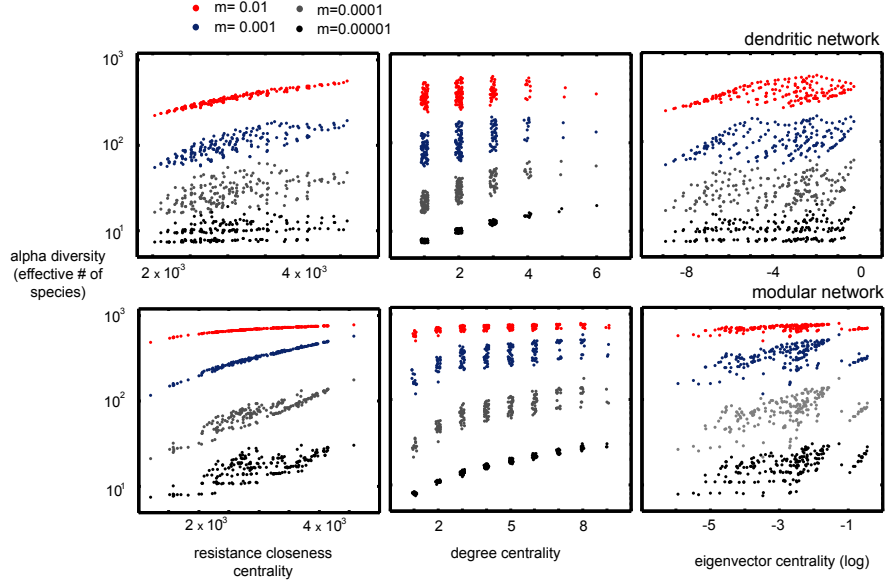


Figure 2.3: Alpha diversity of local communities (nodes) plotted as a function of three centrality metrics for the dendritic and modular networks, at different rates of migration. As migration rates increase, network-scale centrality measures (resistance closeness) better predict diversity, while smaller scale metrics (degree centrality) predicts diversity variation better under restricted migration. Eigenvector centrality only weakly predicts alpha diversity. Speciation rate and local community size were held constant, $v = 10^{-5}$, $N_k = 200000$.

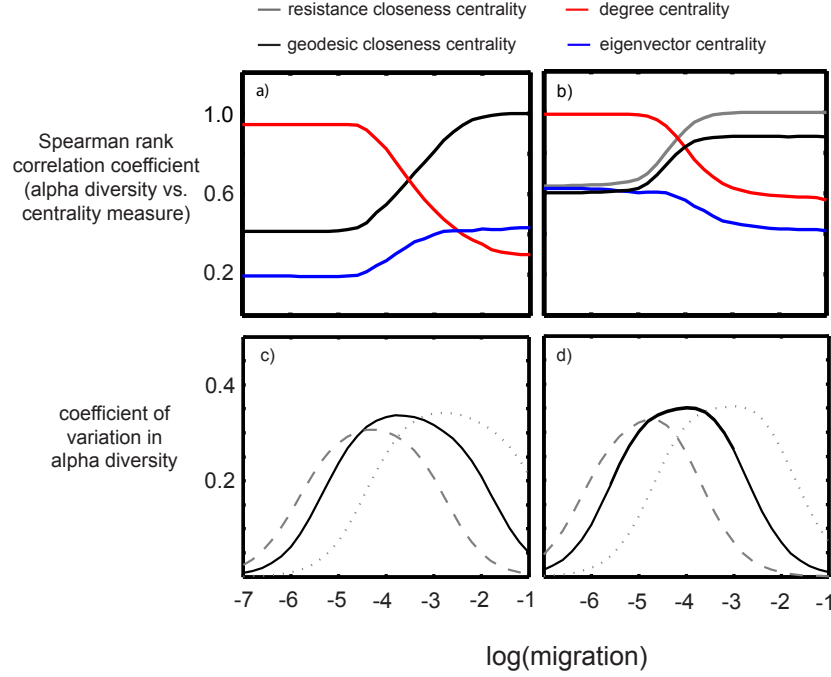


Figure 2.4: Performance of different centrality statistics across parameter values. Spearman rank correlation coefficients of node alpha diversity and network centrality metrics are plotted for the a) dendritic and b) modular network. Variation in alpha diversity across the network, as measured by coefficient of variation, is presented in c-d. For a given speciation rate, variation peaks at an intermediate migration rate. The black line reflects a speciation rate of $v = 10^{-5}$ corresponding to the correlations in a-b, the grey dashed line is $v = 10^{-6}$, and grey dotted line is $v = 10^{-4}$. Thus, for a given topology, variation in alpha diversity depends strongly on the relative rate of speciation and migration.

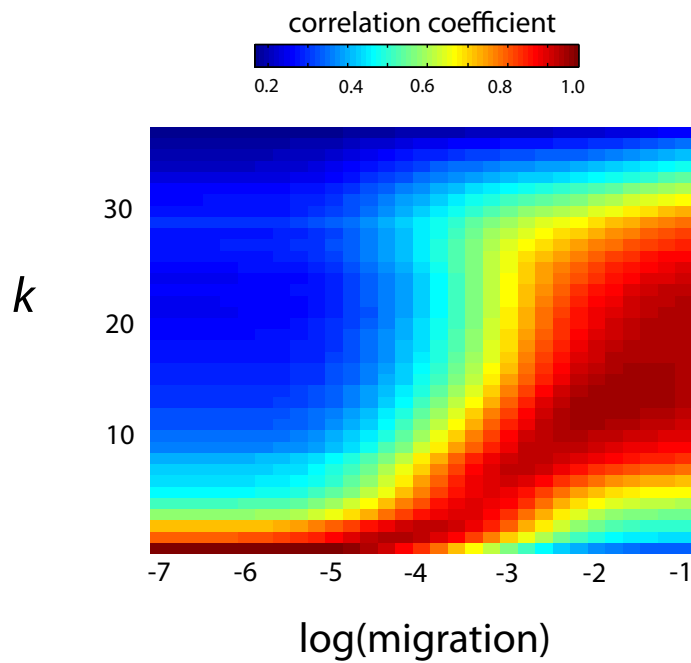


Figure 2.5: Performance of scale-specific centrality Spearman rank correlation coefficient of alpha diversity and the size of the k -neighborhood at different migration rates and values of k . Larger k reflect structure on larger spatial scales, and better predict diversity at higher migration rates. Speciation rate and local community sizes were held constant, $v = 0.00001$, $N_k = 200000$.

Chapter 3

Conservation strategies are ineffective when dispersal drives biodiversity patterns

3.1 Abstract

Modern conservation strategies typically favor habitat units with unique ecological communities, such as those with many endemics, over patches with high similarity to other areas (Margules and Sarkar, 2007; Myers et al., 2000; Possingham et al., 2000; Sarkar et al., 2006; Wilson et al., 2006, 2007). This biodiversity pattern-based approach considers the local community in a given patch and asks what would be lost from regional or global biodiversity if it were degraded. Such methods generally do not account for possible secondary biodiversity losses across the remaining habitat due to loss of the patch. I use spatially explicit neutral theory (Economo and Keitt, 2008; Hubbell, 2001) to investigate the connection between biodiversity patterns such as complementarity and similarity, and both primary and secondary diversity changes due to habitat loss in metacommunities with complex network structure. Surprisingly, losing different habitat units results in a near equivalent long-term loss of biodiversity despite variation in perceived conservation value (complementarity). This is because high connectivity nodes develop high similarity to other communities and appear redundant, but are most important for maintaining

diversity levels in other nodes. More generally, initial biodiversity representation in reserve networks overestimates their long-term diversity capacities due to secondary loss. These results suggest that when spatial biodiversity patterns are driven by dispersal limitation and not environmental heterogeneity, a wide range of conservation concepts and applications are ineffective.

3.2 Introduction

Habitat loss is a widespread consequence of human activities and a global threat to biodiversity (Dirzo and Raven, 2003; Pimm et al., 1995; Rosenzweig, 1995, 2001; Vitousek et al., 1997; Whittaker et al., 2005). A basic premise of conservation biology is that not all habitat units have equal biological value; some are more important than others for maintaining total biodiversity and thus more deserving of protection. Conservation planning traditionally uses biodiversity patterns to prioritize patches for protection, generally favoring patches that harbor biological uniqueness (high complementarity) over those with high community similarity to other areas (Margules and Sarkar, 2007; Margules and Pressey, 2000; Myers et al., 2000; Possingham et al., 2000; Wilson et al., 2007, 2006). With systematic reserve design, large proportions of total biodiversity can often be represented small subsets of total area. This approach often leads to a focus on small areas with many endemics and patch sets with high complementarity at the expense of redundant communities in larger, more homogeneous areas. In part for this reason, diverse areas with low beta-diversity such as the Amazon basin are not considered conservation

hotspots despite ongoing habitat contraction (Myers et al., 2000).

These biodiversity pattern-based approaches evaluate what biotic elements would be lost from the landscape if a given habitat unit is degraded, but implicitly assume that biodiversity patterns across the remaining areas persist at the initial state. However, removing a patch can cause a dynamic response in the rest of the metacommunity and a secondary loss of biodiversity (Cabeza, 2003; Hanski, 1999; Hubbell et al., 2008; Tilman et al., 1994; Bierregaard et al., 1992). These possible effects on biodiversity persistence are increasingly recognized in the conservation literature (Cowling et al., 2003; Margules and Pressey, 2000; Sarkar et al., 2006; Cowling et al., 1999), but their potential conflicts with pattern-based conservation strategies are poorly understood.

Metacommunity theory suggests that spatial patterns of community similarity and differentiation can arise due to environmental heterogeneity or due to the structure of dispersal (connectivity) across the metacommunity (Leibold et al., 2004; Economo and Keitt, 2008; Loreau and Mouquet, 1999). When only properties of the local environment control local community structure, removing a patch should only result in the loss of biotic elements unique to that patch, consistent with the assumptions of conservation planning. When dispersal drives biodiversity patterns, however, removing a patch is more likely to have cascading secondary effects on biodiversity persistence in the metacommunity. From a conservation perspective, a significant problem arises when biodiversity patterns are unstable after habitat loss and in particular when

these secondary effects are correlated with the metrics used for prioritization, such as similarity and complementarity. Because variation in the connectivity of a patch drives both variation in community structure and the contribution of dispersal to other patches, there is reason to suspect that they are.

Here I use spatially explicit ecological neutral theory (Chave, 2004; Condit et al., 2002; Economo and Keitt, 2008; Hubbell, 2001) to investigate the efficacy of the pattern-based paradigm when spatial biodiversity patterns are generated solely by the spatial structure of dispersal across a metacommunity. Real metacommunities are likely to vary in the importance of dispersal versus environmental sorting in driving pattern, but neutral theory serves an important role in highlighting one extreme in the continuum (Alonso et al., 2006; Leibold et al., 2004; Leibold and McPeck, 2006).

Following recent work (Muneepeerakul et al., 2007; Economo and Keitt, 2008; Muneepeerakul et al., 2008), local communities are represented as nodes in a network (the metacommunity), connected by edges reflecting dispersal of individuals. I use this process-based framework to evaluate biodiversity loss in a metacommunity as habitat patches (nodes) are removed and the system dynamically responds to a new equilibrium. The goal is to evaluate the connections between the structure of a local community and its long-term value for maintaining biodiversity.

3.2.1 Diversity Loss in a Metacommunity

Consider the the initial gamma diversity of a metacommunity at neutral equilibrium γ_0 , the initial gamma diversity of all patches *except* node i , γ_i , and the gamma diversity of the metacommunity after i is removed and the rest of the metacommunity relaxes to equilibrium γ'_i (figure 3.1).

The initial, primary cost to gamma diversity of removing a patch i is the complementarity, $c_i = \gamma_0 - \gamma_i$. Complementarity measures the contribution of one patch to metacommunity gamma diversity based on initial biodiversity patterns. This quantity is the main focus of many biodiversity-based conservation analyses as a measure of conservation value. After a patch is removed, secondary biodiversity changes may occur in the remaining patches as the metacommunity relaxes to a new equilibrium. These secondary losses, κ_i , can be written as the difference between the pre- and post relaxation gamma diversity of the reduced metacommunity $\kappa_i = \gamma_i - \gamma'_i$. The total, long-term reduction in biodiversity Λ_i due to node removal is the sum of primary and secondary effects $\Lambda_i = c_i + \kappa_i = \gamma_0 - \gamma'_i$. The main concern of this paper is the correlation of primary (c_i) and secondary (κ_i) biodiversity loss and the relationship between complementarity c_i and total biodiversity loss Λ_i . If removing nodes with a lower complementarity (c_i) leads to greater secondary loss (κ_i), such that c_i becomes a poor predictor of ultimate diversity loss Λ_i , then the logic of many conservation efforts is in question.

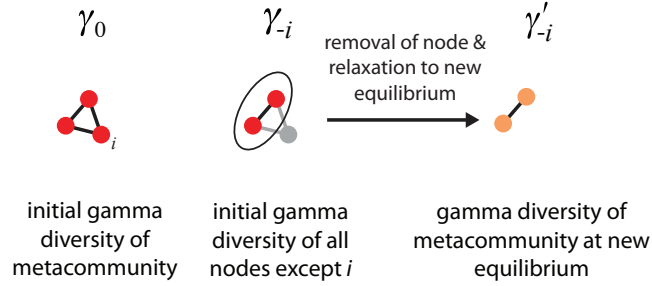


Figure 1

3.3 Results

3.3.1 Single patch removals

A simple metacommunity network is depicted in figure 3.2a. The metacommunity contains one large cluster of highly connected nodes and two smaller, more isolated clusters. In this study, networks are constructed with equal sized nodes for ease of comparison, but highly connected clusters of nodes can be thought of as large habitat units. At initial equilibrium, communities in the smaller clusters (nodes 1-4) have highest complementarity and nodes in the large cluster are more redundant- they share many species with other nearby nodes due to strong dispersal connections. In general, at neutral equilibrium, more isolated nodes have reduced alpha diversity and increased complementarity, while nodes that are highly connected to many others will have high alpha diversity, but low complementarity, as the node is colonized frequently but much of that diversity is shared across many other communities.

Removing each node individually reveals a remarkable regularity- node complementarity holds little information on the ultimate effect on diversity after removal and relaxation (figure 3.2, b-c), in fact all node removals result in a near-equivalent diversity loss. While removing nodes with high complementarity removes more uniqueness from that single patch than removing a redundant node, removing the latter causes a greater reduction in alpha diversity across many other nodes (figure 3.2d). These effects compensate and the diversity loss from node removal (Λ_i) is nearly constant.

To evaluate the generality of these results for larger and more complex networks, and across parameter space, I examined the effects of node removals in 49-node metacommunities with a variety of different network geometries (figure 3.3a-c) and rates of migration and speciation (figure 3.3d-l) (see supplemental methods for more on network construction). These networks all exhibit the same pattern, secondary effects compensate for complementarity such that ultimate biodiversity loss is effectively constant across nodes. The mismeasurement of biodiversity loss by biodiversity pattern is most pronounced at higher migration rates, because nodes appear to be completely redundant but in fact are not. Complementarity is not totally uncorrelated with ultimate diversity loss, it often explains a difference of around 1-2 effective species, which could be important if the metacommunity diversity is very low (see supplemental section). This magnitude of this effect, however, does not scale with increasing diversity implying.

3.3.2 Persistence in reserve networks

It may not be obvious how these secondary effects for single node removals scale to situations involving many patches, which are typical for real-world conservation problems. I thus consider how well initial diversity representation predicts the long term diversity capacity of all 1022 subsets (indexed by k) of the 10-node network (figure 3.2a), which serve as model reserves. The secondary effects occur when the loss of habitat outside the reserve impacts diversity persistence within the reserve. This time I calculate the diversity of a subset γ_k when it is embedded within the initial metacommunity and then after the rest of the metacommunity is removed and the communities in the set relax to a new equilibrium γ'_k . Subsets of nodes (of equal area) that have a high complementarity will have a higher γ_k . Again, regardless of the initial diversity in the reserve, the subset relaxes to an equilibrium diversity that is only dependent on subset size (figure 3.3a-c). When migration is high, small subsets of the metacommunity can represent nearly all of the gamma diversity in the metacommunity, but subsets with disproportionately high representation simply have a greater secondary loss of diversity. Within reserves of a given size, the connectivity of nodes may vary, and alpha and beta diversity levels may vary, but long-term diversity capacity is essentially constant.

3.4 Discussion

In a neutral metacommunity, the secondary effects of habitat loss work in direct opposition to the strategies of protecting unique communities and

representing the most biodiversity in the smallest protected area. Communities with high connectivity to other patches develop high similarity and thus appear to be redundant, but this apparent redundancy correlates with their importance in maintaining diversity across other patches. More isolated nodes have unique diversity within the patch, but removing them has a weaker effect on other nodes in the network. Small subsets of the metacommunity may represent large proportions of total biodiversity, but those will have a greater reduction of diversity after the rest of the habitat is lost. Thus, under these conditions, the assumption that large areas with low beta-diversity can be contracted with little cost to gamma diversity is flawed. This also implies that the empirical form of the species area curve $S \propto A^z$ (with typically $z < 1$) (Rosenzweig, 1995) describing current diversity patterns is a dubious predictor of biodiversity responses to area contraction, for example in future climate change scenarios (Thomas et al., 2004). Instead, equilibrium gamma diversity scales linearly with area $S \propto A^1$, a more rapid decrease of diversity with area.

The secondary loss of diversity may not occur quickly after habitat fragmentation, with the relevant time scales depending on parameters such as speciation rates and community sizes. This implies that there could be a significant extinction debt (Tilman et al., 1994) looming in already fragmented areas such as conservation hotspots (Myers et al., 2000), although diversity reduces in this case because of increased extinction *and* a loss of speciation rate (Rosenzweig, 2001). Likewise, if time scales of habitat change are faster than the community can reach equilibrium, conservation strategies must consider

transient dynamics in addition to equilibria.

These results challenge some of the most fundamental and widely used concepts in conservation biology, but it certainly does not follow that complementarity based approaches should be abandoned or that neutral theory should be used for conservation planning. If beta-diversity in a landscape is due to environmental sorting and not dispersal limitation, ignoring complementarity would be extremely misguided. However, if neutral theory reflects one extreme in a continuum of possible metacommunity dynamics, many conservation analyses implicitly assume another extreme in which community structure is determined entirely by intrinsic properties of a locality.

This analysis suggests that when dispersal processes drive spatial patterns, biodiversity may be in much greater peril than is currently recognized. An urgent task for ecological theory is to link observable biodiversity patterns to the biological dynamics generating them, and use that light to reconcile our conservation strategies with community processes.

3.5 Methods

Here I use an analytic network model of neutral metacommunity diversity that was presented in a previous paper (Economo and Keitt, 2008) and discussed in detail in the supplemental methods. It assumes i): Community dynamics proceeds through zero-sum drift of ecologically equivalent species with. ii) New species arise through point speciation with probability v , which can also be interpreted as migration from a distant, large source pool. iii)

The structure of migration across the metacommunity is set by a migration matrix, and the network is symmetric (dispersal strength is equivalent in both directions between a pair of communities, asymmetric migration is considered in a supplemental section).

The basic procedure for the analyses was to set an initial metacommunity structure and let diversity patterns be predicted by the model. The complementarity was calculated from this initial pattern (see text). Then, one or more nodes were removed and the model was used to find a new equilibrium diversity across the metacommunity. For the figures presented in this paper, speciation rate ($v=0.0001$) and local community size (200000 individuals) were held constant, although other parameter combinations were considered in the supplemental sections.

The diversity values are presented in effective species numbers. Further details on the model, diversity statistics, and network construction are presented in a supplemental methods section.

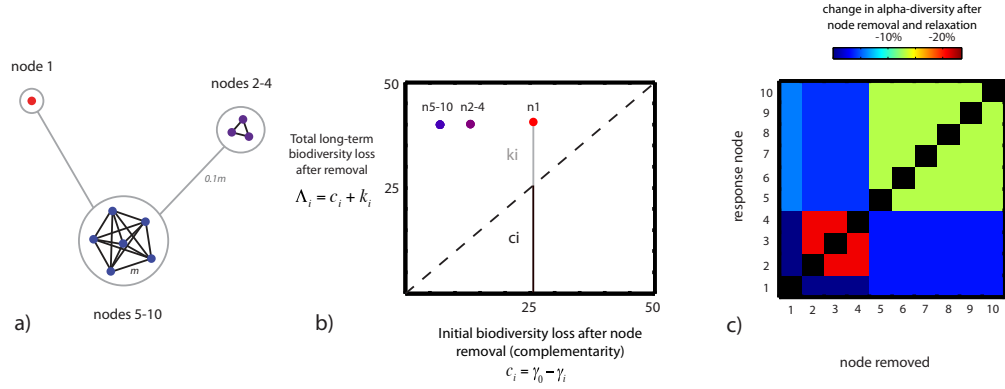


Figure 3.1: Effects of habitat loss on biodiversity in a model meta-community. a) A simple, 10-node metacommunity with three clusters, with the smaller clusters having lower connectivity and higher complementarity. b) Each node was removed and the initial diversity loss (complementarity (c_i)) is plotted against long-term diversity loss (Λ_i) after reduction and relaxation to a new equilibrium with biodiversity is in effective species numbers and $m=0.0001$. Λ_i is nearly invariant because of a trade-off in its components—primary c_i and secondary k_i biodiversity loss. This trade-off occurs because removing nodes from the large clusters (low c_i) results in a greater decrease in alpha diversity across other nodes k_i , which are depicted in c) with the color reflecting the diversity change in the node numbered on the y-axis when the node on the x axis is removed.

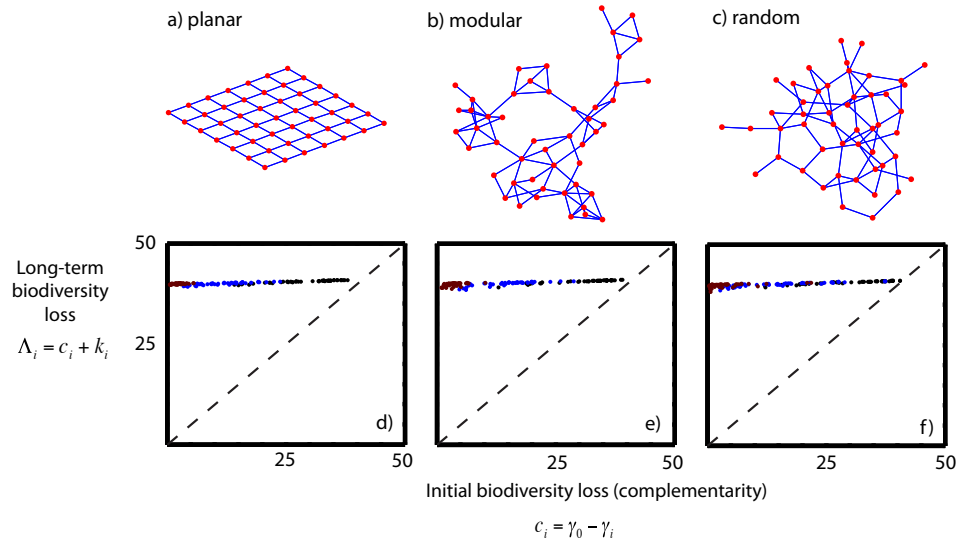


Figure 3.2: Biodiversity impacts of node removals in complex networks with different topologies (a-c) and variable edge weights (see supplemental methods). Migration increases by factors of 10 from black to blue to brown (points with different colors are from different metacommunities). While there may be a good deal of variation in community complementarity, there is very little variation in the effects of removing a community on long term biodiversity loss. Similar plots with more parameter combinations are presented in a supplemental section.

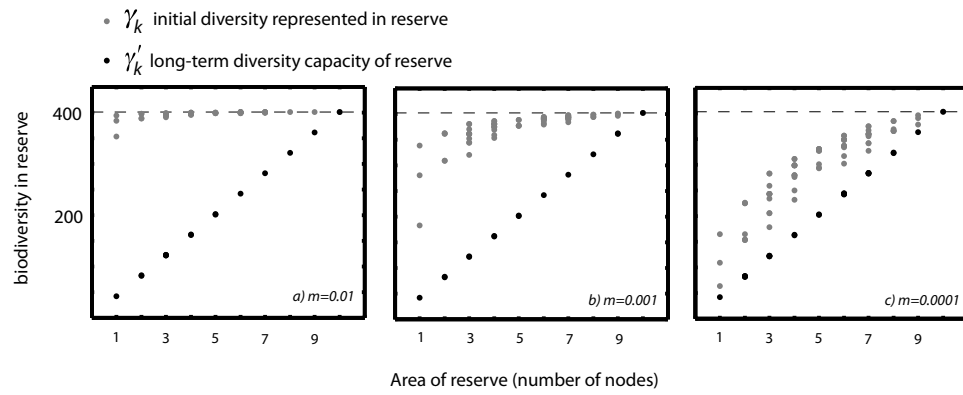


Figure 3.3: Biodiversity representation and persistence in reserves of different sizes. Initial diversity representation (gray dots) and diversity capacity at the new equilibrium (black dots) of all 1022 possible subsets of the 10 node metacommunities in figure 3.2a, measured in effective number of species, plotted as a function of the number of nodes in the reserve with migration rates increasing by an order of magnitude from a to b and from b to c. Diversity capacity is only a function of reserve area and not initial diversity representation- the black dots for a given area are superimposed on each other.

Chapter 4

The role of connectivity in geographic diversification

4.1 Abstract

The pace of speciation emerges from both the rate of genetic divergence of subpopulations and the rate of formation of such subpopulations. These rates are tied to the ecological processes of dispersal and colonization, and the evolutionary processes of gene flow and differentiation, all of which are a function of the flow of individuals across a landscape- the geographic connectivity. Evolutionary divergence rates and colonization rates are hypothesized to both be correlated with connectivity, but in opposite directions, implying the kinetics of the colonization-speciation cycle are maximized at an intermediate connectivity. Connectivity is a function of both life history attributes such as the vagility of a species, and the physical structure of the landscape- the sizes and arrangement of habitat patches. We investigate how both species vagility and landscape structure contribute to speciation rate in model island networks. Speciation rate peaks where the vagility of the species and the physical isolation of patches results in islands being accessible to colonization, but isolated enough to allow evolutionary divergence. This implies for groups with different vagilities, these speciation hotspots will occur in different components

of a landscape, or in different entire geographic regions. This mechanism suggests a hypothesis for differences in macroevolutionary rates among clades and areas, and why certain groups diversify rapidly in a geographic region while remaining depauperate in others.

4.2 Introduction

Biodiversity is distributed unevenly in geographic space and across the tree of life. These patterns are generated in part by variation in macroevolutionary rates (Brown, 1995; Hubbell, 2001; Rosenzweig, 1995). The rate of speciation has been connected to many factors from the body sizes of individuals (Brown, 1995) to the strength of sexual selection (Panhuis et al., 2001), to geographic factors such as range size (Jablonski and Roy, 2003; Rosenzweig, 1995, 2001; Vermeij, 1987) or latitude (Gillooly and Allen, 2007; Mittelbach et al., 2007). When speciation has a spatial component, speciation rate is in part a function of the population structure of a species across its range as the development of genetically and geographically distinct subpopulations is a common route to the evolution of reproductive incompatibilities (Coyne and Orr, 2004; Mayr, 1942). Population structure emerges from the interaction of organismal life histories, such as dispersal ability, with attributes of the physical landscape, the area and isolation of habitat patches. As life history and geographic structure are highly variable among taxa and regions, there may be poorly understood geographic and life history factors driving variation in macroevolutionary rates.

The interactions between the ecological processes of dispersal and colonization, the spatial structure of geographic areas, and evolutionary processes of divergence in determining speciation rate have not been well explored. Previous work has suggested that, at least for some groups, less vagile species have higher rates of speciation as low rates of migration among subpopulations leads to genetic differentiation and speciation (Jablonski and Lutz, 1983). However, vagile species more readily jump barriers and colonize distant, isolated areas, which can lead to speciation. With regards to the physical structure of a landscape, regions with many isolated patches separated by distance or other intervening barriers may promote genetic differentiation and speciation. On the other hand, isolated geographic units may take long time intervals for a species to colonize, which would depress the rate of speciation. These complexities suggest a nuanced relationship between both vagility and geographic structure with speciation rate.

Here we collect these ideas and refocus them around the concept of connectivity, a theoretical keystone of landscape (Brooks, 2003; Taylor et al., 1993), metapopulation (Hanski, 1999), and metacommunity ecology (Leibold et al., 2004). Connectivity generally refers to the flux of individuals among geographic units or across a landscape. It emerges as the properties of a species, such as ecological densities, propensities for dispersal, and habitat affinities, interact with the physical structure of a landscape- the size and arrangement of habitat patches (Brooks, 2003). We ask how connectivity, and its biological and physical components, affects the speciation rate of a clade

in a structured landscape.

Most speciation theory considers the genetic, ecological, or geographic factors that promote the evolution of reproductive isolation among subpopulations (Coyne and Orr, 2004; Gavrillets, 1997, 2004; Schluter, 2000). For example, those species undergoing strong sexual selection may be expected to speciate faster than those that are not, all else equal (Panhuis et al., 2001). Other studies have focused on the effects of different models of population structure on the rate of speciation (Orr and Orr, 1996). It is important to note that this rate refers to how fast subpopulations diverge in a given spatial configuration. The true speciation rate depends on other hidden dynamics, the spatial population processes generating the subpopulations in patches with a given degree of isolation. How this second component, waiting for allopatry, contributes to speciation rate is far less understood (Wiens, 2004).

This is especially relevant because after geographic speciation, the two daughter species have more spatially restricted distributions than the original parent species, and may need to form new subpopulations before another speciation event. Dispersal across barriers into unoccupied geographic units is one mechanism by which a species forms allopatric or near allopatric subpopulations, a route to speciation (Mayr, 1942). Colonization rates correlate with connectivity, a basic premise of island biogeography and metapopulation theory (Hanski, 1999; MacArthur and Wilson, 1967; Hanski and Gilpin, 1998). Thus, while increased connectivity may promote gene flow and inhibit the evolution of reproductive isolation among given subpopulations, connec-

tivity also promotes the colonization of novel areas and the establishment of subpopulations isolated enough for divergence to occur.

This suggests a tradeoff. Both colonization and evolutionary divergence rates are correlated with connectivity, but in opposite directions. As we shall see, elementary assumptions about the quantitative form of those relationships lead to the conclusion that the colonization-speciation cycle, and the speciation rate, is maximized at intermediate levels of connectivity. We investigate how the biological (life history) and physical (geographic structure) components of connectivity contribute to this rate.

Natural landscapes have a diverse array of physical structures. We focus our attention on archipelagoes of discrete habitat patches, where patches are internally homogenous with respect to habitat type, an idealization commonly used in metapopulation theory. This provides a natural spatial scale of speciation: the population of a single patch. We analyze speciation and colonization dynamics with three spatial models, a deterministic model of a simple landscape of two identical islands, a ring of islands with variable distances among them, and a complex network of islands.

4.3 Connectivity and Speciation Rate on Two Islands

A minimal structured landscape is an archipelago of two identical islands. A species inhabiting this landscape can either be found in both islands (BOTH), or in one island but not the other (ONE). Colonization (C) transforms ranges from ONE to BOTH, and speciation (G) transforms one BOTH

into two ONE species. $2G$ is the speciation rate of a species occupying both islands, but the true speciation rate (the focus of this paper) depends also on how fast a species first becomes widespread. For clarity, we refer to the speciation rate of a given subpopulation as the evolutionary divergence rate, and the overall speciation rate (integrating over all subpopulations) as speciation rate. Extinction (E) both transforms one BOTH into one ONE, and removes a localized ONE from the system entirely. The dynamics of species number in the system can be represented by the pair of differential equations,

$$\frac{dS_{ONE}}{dt} = -(C + E)S_{ONE} + (4G + 2E)S_{BOTH} \quad (4.1)$$

$$\frac{dS_{BOTH}}{dt} = CS_{ONE} - (2G + 2E)S_{BOTH} \quad (4.2)$$

which is a deterministic approximation to the stochastic system. E , G , and C are per population rates.

Depending on the biology involved, one might expect several nonlinearities to arise in this situation. For example per capita extinction rates (E) may increase with increasing species number if the new species interact negatively, or may be constant if new species have diverged sufficiently to avoid each other ecologically. Other nonlinearities have been proposed, such as a positive association between divergence rate (G) and species number (Emerson and Kolm, 2005) or extinction rate and speciation rate (Allmon et al., 2001), among others, but those will not be considered here. If E , C , and G

are constant per capita rates, the system is linear and it is this rate of exponential increase or decrease of species number that is our primary concern. If per species extinction rates increase with species number, then the system will reach an equilibrium species richness. We focus here on the speciation rate of an exponentially increasing clade, but the effects of connectivity are similar if extinction is increasing, only for equilibrium diversity instead of rate of overall species increase.

We are primarily concerned with the dynamic interaction of colonization and speciation, and so for purposes of simplicity assume extinction is at some constant and negligible level ($E \ll C, G$). In this case there is a positive eigenvalue describing the rate of species increase.

$$\lambda = \frac{-C - 2G + \sqrt{16GC + (-2G + C)^2}}{2} \quad (4.3)$$

We are now ready to evaluate the effects of connectivity on speciation rate. Connectivity describes the rate in which individuals move among the patches. Both colonization and divergence rate can be expected to be a function of connectivity, but in opposite directions. Colonization, because the higher the rate of individual dispersal into an empty patch, the greater the likelihood a new viable population will be established. Evolutionary divergence, because the greater the gene flow among two populations, the lesser the likelihood reproductive isolation will evolve. In general, for species with different life histories and different assumptions about the genetics of speciation, these functions could take a variety of forms. Our inference only depends

on speciation being an overall decreasing and colonization an increasing function of connectivity. Divergence rate should be near a maximum when patches are completely isolated, and converge to zero as connectivity becomes high. In certain models small amounts of migration have been shown to accelerate speciation (Church et al., 2002) which implies divergence rate may peak at a nonzero connectivity, but the overall tendency should still be a decrease to zero as connectivity gets large. Colonization rate is zero when connectivity is zero, and increases to a very high level when connectivity is high. Figure 4.1a-d plots a variety of possible functional forms describing the relationship between divergence and colonization with connectivity, including exponential (a,d), threshold (b), and linear (c). These functionals can be inserted into equation 2 to extract the relationship between connectivity and overall speciation rate (Fig. 4.1e-f), where the integrated speciation rate G is represented by the eigenvalue (λ) controlling the rate of increase in species numbers.

When connectivity is high, colonization of empty patches occurs rapidly, but divergence is hampered by gene flow, and the result is a widespread cohesive population, and low speciation rates. When connectivity is low, widespread (BOTH) species will speciate and faunas will differentiate among the patches, but colonization is slow to form new isolates and continue the cycle. At some intermediate connectivity, gene flow is weak enough to allow divergence, but after speciation the spatially restricted daughter species can reinvade other patches, and the speciation rate is maximized. The detail of the shapes and magnitudes of the curves, and other such features will be

dependent on the assumed functional forms and the magnitudes of their parameters. Many biological processes contribute in uncertain ways to the forms and magnitudes of the curves depicted in figure 4.1, and the curves are difficult or impossible to measure directly. Thus, like much biogeographic theory, our conclusions must follow from only very general assumptions about the mathematical form of the curves. But constraining the functions to our assumptions, there is always a peaked relationship with speciation rate and connectivity.

Spatial population processes, such as colonization and gene flow, emerge from the interaction of the biological properties of a species, such as habitat affinities, ecological densities, and propensity for dispersal, and the physical characteristics of a landscape, -areas and spatial arrangements of habitat patches. Thus, connectivity is a function of both the physical structure of a landscape and the vagility of the species (Brooks, 2003). A given level of connectivity emerges at a particular combination of species vagility and landscape structure. As connectivity drives the kinetics of the colonization-speciation cycle, this implies the speciation rate of lineages varying in vagility will respond differently to a landscape or component of a landscape. In the next section we break connectivity into its physical and biological components and explore how these dynamics emerge in more complicated landscapes.

4.4 Speciation in a Network of Islands

The dynamics among two patches can be extended to a landscape with many islands. Connectivity can be modeled as a simple function of distance

and a parameter describing the dispersal flux of individuals. Many such models could be applied given different biological and physical assumptions, but we use a simple function for connectivity (K) between two patches i and j ,

$$K_{ij} = \alpha A_i A_j e^{-d_{ij}/\alpha} \quad (4.4)$$

In this model, areas are represented by A_i and A_j , but for simplicity here we assume equal areas and set $A_i = A_j = 1$. In biological terms, K_{ij} can be thought of as the rate in which individuals of a given species move from one patch to another. The distance between islands is given by d , while α is the biological parameter representing vagility. In this formulation, increasing α increases both the total rate of dispersal and the average distance of dispersal (α). Connectivity of a given patch is simply the summation of contributions of all other nodes

$$K_i = \sum_{j \neq i} \alpha A_i A_j e^{-d_{ij}/\alpha} \quad (4.5)$$

At any given time, there may not be a population in each patch, so the summation is simply taken over all patches with a population of the focal species, (6) where $P_j = 1$ if there is a population of the focal species in patch j and 0 if there is not. d_{ij} can be variable in the landscape and α can be tuned as a biological parameter. This is overall quite similar to how connectivity is quantitatively represented in metapopulation theory (Hanski and Gilpin, 1998). Both speciation rates and colonization rates will be a function of this

connectivity measure, and the function could take other forms not presented here.

We model the processes of colonization and speciation in a patch network by assuming those events occur as Poisson processes, the rates of which are functions of connectivity. For each patch that does not have a population of a given species, a colonization rate is calculated, repeated across all species. For all the populations of each species, the divergence rates are also calculated. Here we use a converging exponential function of divergence rate with connectivity (fig 4.1a),

$$G_j = G_{max}e^{-\gamma K_i} \quad (4.6)$$

where G_{max} is the divergence rate under total allopatry, and γ is a parameter. Colonization rate is modeled as a linear function of connectivity (fig 4.1c),

$$C_i = \phi K \quad (4.7)$$

where ϕ is a parameter. These Poisson processes can be modeled transparently with stochastic simulation, see methods for implementation.

Using this approach we can both investigate the overall rate of speciation of the clade in a landscape, and the rate at various specific points in the landscape. As a first analysis, we choose a landscape with regular structure and periodic boundary conditions, a ring. Each node is connected to two other nodes, but distances among nodes vary regularly from a minimum to a maximum. In other words, there is a gradient in distances and thus connectivities in the ring.

With this model landscape, we can investigate the macroevolutionary dynamics of clades with different dispersal rates on the same landscape by tuning the vagility parameter α . It is important to note that per population divergence rates (G) will always be highest in the least connected islands, because connectivity is lowest, and divergence will be lowest in the most connected nodes. But due to the influence of colonization, overall speciation rates may be highest at any region of the landscape, dependent on the vagility parameter α . Fig. 4.2 plots speciation rate for a variety of vagilities. Overall, speciation rate in the landscape is dependent on vagility (Fig. 4.2c), and furthermore the regions of the landscape where speciation proceeds most rapidly change from the most to least connected areas as species become more dispersive (Fig 4.2b). Speciation happens most rapidly where there is an appropriate match between life history and the landscape, where patches are accessible enough to be colonized but not so connected that divergence is inhibited.

We can now examine how this emerges on a more realistic model of landscape structure; an array of patches distributed irregularly in space. In this case, each pair of islands is connected by dispersal, but distance determines the strengths of those connections through equation 5. We randomly generate a landscape (see methods), with patches distributed exponentially around a density center. Certain patches that are close to many others will have higher connectivity, and higher colonization and lower divergence rates.

As we increase species vagility, we again see the centers of speciation moving from the high density to low density areas (Fig 4.3a). When vagility

is very low, colonization events are rare and usually followed comparatively quickly by a speciation event. Overall speciation rate of the clade is thus *colonization limited* and proceeds mostly in the most patch-dense areas of the landscape (Fig. 4.3b). As vagility is increased, connectivity increases and approaches the optimal point in the tradeoff, where patches are connected enough to be accessible to species in the network, but not so connected as to inhibit the evolution of reproductive isolation once colonized. Eventually vagility increases to the point where the central areas become too connected, and while they accumulate most of the species in the system, connectivity is too high to allow divergence and speciation. The speciation hotspots thus move successively towards the peripheral areas of the network, until connectivity is so high that a species quickly colonizes the whole network but cannot diverge enough to evolve reproductive isolation, and speciation rate is *divergence limited*.

4.5 Discussion

On the connectivity axis, the dynamics of all three models broke down into three zones. At high connectivity, species quickly fill the landscape with subpopulations, but divergence rates are low and limit speciation. In the simulations, species moved relatively quickly through these more highly connected areas of the patch network until reaching regions that were connected enough to colonize but isolated enough to allow speciation, where speciation was concentrated. This diversification zone, at intermediate connectivity, maximized the tradeoff between colonization of new patches and evolutionary divergence.

At yet lower levels of connectivity, any species in multiple patches would speciate, but took long time intervals to subsequently colonize other patches and thus speciation rate was colonization limited.

As connectivity has biological and physical components, this implies a novel hypothesis for speciation rate. Speciation rate is maximized when there is a match between species vagility and specific landscape features, resulting in an intermediate, optimal connectivity, and a maximization of the speciation-colonization cycle. This implies that certain geographic features -a few islands of an archipelago or mountains of a range- may be *speciation hotspots* for a given group. Likewise, whole regions where physical structure provides a match with the vagility of a group will promote diversification, while others remain depauperate. This provides insight into the enigmatic relationship between dispersal and speciation rate, its not vagility *per se* that matters, but how vagility interacts with the physical structure of a landscape.

These results are dependent on only minimal assumptions about the form of the relationship between colonization, divergence, and connectivity, but do not imply that this mode of speciation will be most important or even important in any given clade-landscape. Even under ideal connectivities, this speciation-colonization cycle may be slow enough -due to the forms and magnitudes of the colonization and divergence curves- that underlying landscape changes (vicariant processes) are more important for creating allopatric populations. Or, a landscape simply may not contain elements with suitable connectivity for a given clade. For example, a group may freely move among

habitat patches on a continent, but be unable to cross water barriers. In this case, there are areas of very high connectivity (on the continent), and areas of low connectivity (the continent with other geographic areas), but no intermediate connectivity and no speciation hotspots. Clearly many types of speciation may be important to the branching of the tree of life, but modeling speciation by dispersal gives a quantitative way to organize these processes theoretically and understand when speciation by vicariance versus dispersal will dominate.

The current theory took a minimalist approach in its treatment of the process of geographic speciation. This was intentional in order to make a transparent first analysis of the nexus of speciation, colonization, and connectivity. A promising future direction would be to integrate mechanistic models of speciation based on more complicated genetic models (Gavrilets et al., 2000; Kondrashov and Morgan, 2003; Orr, 1995; Orr and Orr, 1996). Integrating dynamics such as genetic snowball effects (Orr, 1995), phenotypic evolution and selection (Garcia-Ramos and Kirkpatrick, 1997; Kirkpatrick and Barton, 1997), metapopulation dynamics (Barton and Whitlock, 1997; Hanski and Gilpin, 1998; Hastings and Harrison, 1994), and the evolution of vagility (Dieckmann et al., 1999; Johnson and Gaines, 1990) would all be relevant extensions of the present model. Furthermore, combining spatially explicit speciation theory with more sophisticated representations of spatial complexity, such as network approaches (Economo and Keitt, 2008; Urban and Keitt, 2001), would be an interesting synthesis.

A basic concept of biogeography is that patch isolation depresses diversity due to reduced colonization rates (Hubbell, 2001; MacArthur and Wilson, 1967). Our results suggest integrating the process of speciation into such models complicates this conclusion; some degree of isolation may promote speciation and diversification. But speciation is only half of the macroevolutionary equation. The diversity of clades and areas is driven by both speciation and extinction rates. It is thus necessary to include extinction in any predictive model of diversity patterns- even if species are generated mostly in one area, they may accumulate fastest in another. Indeed, high connectivity areas, while perhaps not conducive to speciation, are often the most resilient to extinction (Hanski, 1999).

What is needed is an integrated theory of diversity dynamics in structured landscapes, including species generation, colonization, and extinction. The present study, which explores the dynamic interaction of the first two processes, is a step in that direction. The basic, paradigm-changing insight of MacArthur-Wilson (MacArthur and Wilson, 1967) was that the structure of geographic space has consequences for population processes, which in turn have consequences for elementary biogeographic rates. The full potential of this idea for building a quantitative, theoretical biogeography is still unrealized.

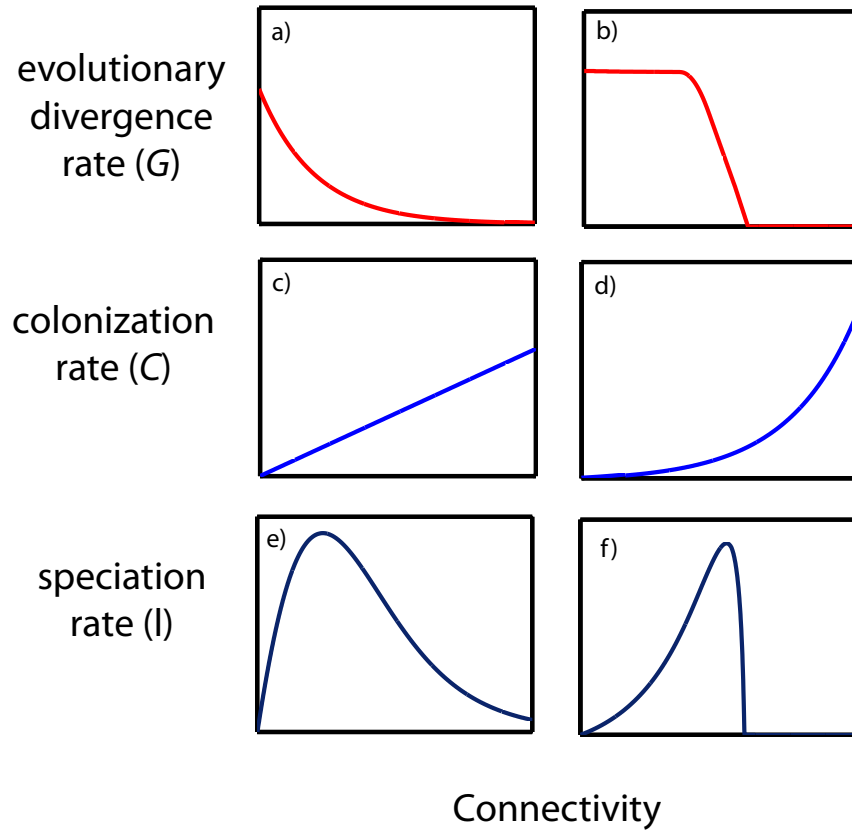


Figure 4.1: Divergence rates, in this case the speciation rate of a species inhabiting both patches in a two patch landscape (BOTH), are hypothesized to generally decrease with connectivity due to increased gene flow, a-b) show exponential and threshold forms of this relationship. Colonization rates, transforming a ONE species into a BOTH species, should generally increase c) linearly, or d) exponentially. The eigenvalue of equation 1 is a measure of overall speciation rate, and has a unimodal relationship with connectivity, e) plots a combination of a) and c), while f) plots b) and d).

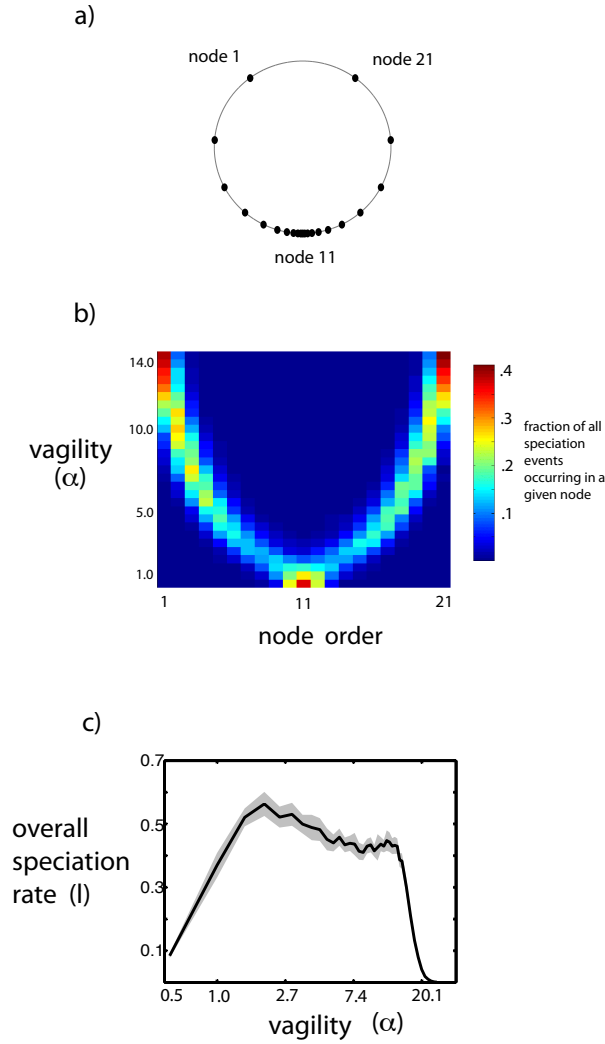


Figure 4.2: A ring landscape (a) is generated with a gradient in connectivity. b) reflects the fraction of speciation events occurring in a given node occurring while a clade diversifies to 300 species through stochastic simulation, for a variety of different species vagilities. The speciation peak moves from the most patch dense to more sparse regions of the landscape as vagility increases. c) The overall speciation rate is depressed at low vagility, increases as vagility matches the landscape elements resulting in optimal connectivity, then decreases as vagility (and connectivity) become very high.

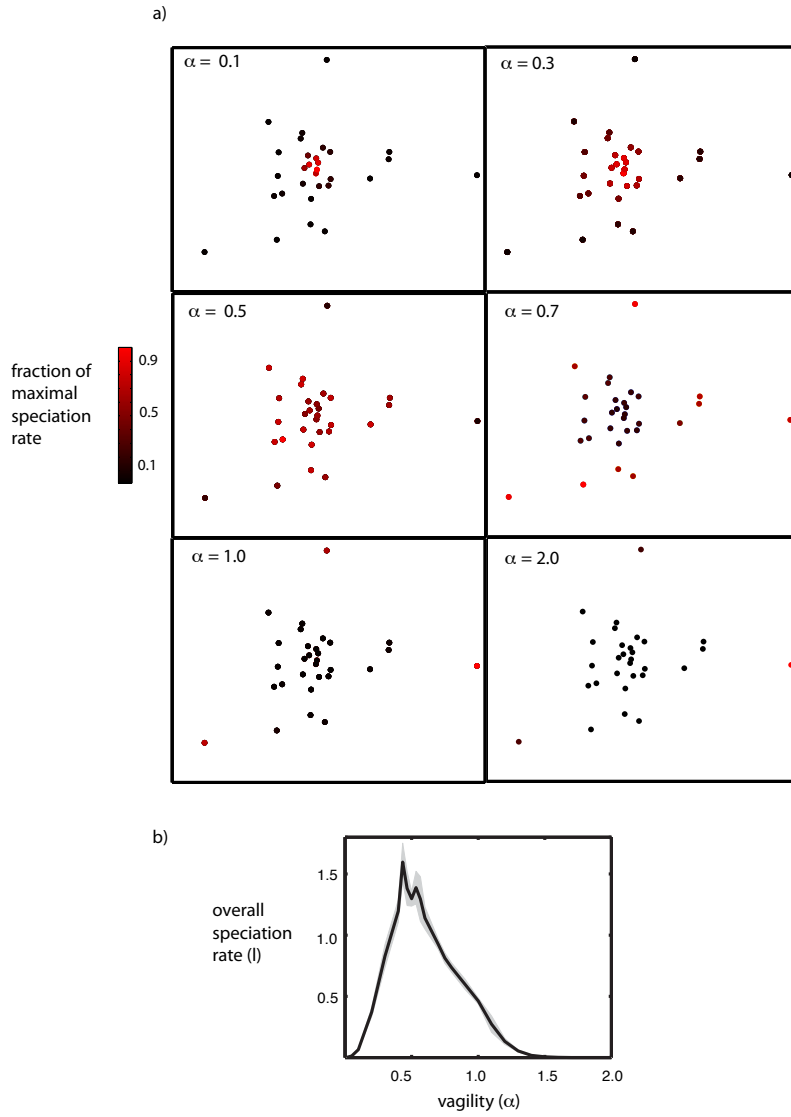


Figure 4.3: a) An archipelago of islands with an exponential density distribution is generated and stochastic simulation is carried out on this model landscape. As vagility is increased, speciation is concentrated in progressively more isolated regions of the landscape, until at the highest vagilities most speciation occurs in the most isolated islands. b) Overall speciation rate peaks at intermediate vagility, where the vagility matches landscape elements, as in fig. 4.2.

Chapter 5

The ants of the Fijian archipelago

5.1 Introduction

The study of biodiversity is entering an era of integration. Community ecology is expanding its spatial and temporal scope to encompass processes occurring on larger scales. Armed with new spatial and phylogenetic methods, biogeographers are increasingly moving beyond descriptive historical studies to ask process-oriented questions. The old boundaries between ecological and evolutionary approaches to biodiversity science are dissolving (Rosenzweig, 1995; Brown, 1995; Hubbell, 2001). An important component of this effort will be case studies that traverse spatiotemporal scales, biological paradigms, and methodologies to understand the origins and maintenance of biodiversity. Insular communities serve as a natural laboratory to inspire and test ideas relating to evolutionary and ecological processes.

This study is intended to be the first steps in developing such a case study, by revisiting one of the classical systems in biogeography. The ants of Melanesia were primary inspirations of theories of taxon cycles (Wilson, 1961, 1959a), and equilibrial island biogeography theory (MacArthur and Wilson, 1967). The ant fauna of Fiji is a mixture of Indo-Australian lineages and

introduced species from around the globe (Ward and Wetterer, 2006; Wheeler, 1935; Mann, 1921, 1919). Similar to other groups in the region, there are no convincing cases of western migration from the neotropics into the Pacific islands. The ants show a filtering effect westward from New Guinea, with most dispersive taxa reaching far into the Pacific. Fiji is recognized as one of MacArthur and Wilson's (1967) "radiation zones", islands that are close enough to be colonized but not so close as to be overwhelmed by continental lineages. The relatively sparse number of colonists to Fiji have diversified into a number of endemic radiations, with over 131 of the 189 species being endemic to the archipelago.

Although myrmecologists have visited Fiji intermittently over the years, knowledge of the myrmecofauna is still dominated largely by the survey conducted by William M. Mann in 1916. Mann's monograph (Mann, 1921) is an impressive piece of work even by modern standards and remains the primary taxonomic reference. A recent compilation of myrmecological records from Fiji suggested undersampling and revealed holes in distributional knowledge. The species occurrences were disproportionately concentrated in Viti Levu, which as the main population center and most accessible island, has received the most attention from collectors (Ward and Wetterer, 2006). Many of the smaller islands have never been visited by myrmecologists and some have never been visited by biologists of any kind.

The primary goal of this project, and a necessary prelude to any sophisticated hypothesis testing, was to develop a reasonably complete picture

of the myrmecofauna and the distributions of the species among the islands and habitats. A massive sampling operation was required to meet this goal, as even sampling the community in a single locality requires a substantial sampling effort. Combining previous unprocessed samples and new collections, we assembled the largest collection of Fijian ants in the world with over 10,000 pinned specimens, representing of over several hundred thousand sorted specimens which remain preserved in alcohol.

As is discussed in the following sections, after initial sampling it soon became apparent that there were many undescribed forms in Fiji. Furthermore, many of the existing species delineations were based on a few samples and did not take into account complex spatial morphological variation. Several “species” were simply forms chosen from disparate points in a morphological continuum, the intermediate forms are now known.

An ideal approach to organizing the biodiversity would be to pursue full taxonomic revisions for all the undescribed or poorly described species. This would involve both a consideration of Fijian species and congeners from the Indo-Pacific region. Eli Sarnat is pursuing such detailed taxonomic revisions, so far producing monographs of the Fijian *Lordomyrma* (Sarnat, 2006) and the *Pheidole roosevelti* (Sarnat, 2008) species complex (previously known as subgenus *Electropheidole*). However, as there are over thirty genera known from Fiji, each requiring separate treatment, it would take decades until all genera were revised in order to complete our picture of the Fijian ant fauna and communities across the archipelago.

Thus, we decided to make an initial evaluation of every form found in Fiji, providing diagnostic characters and in some cases unofficial descriptions for morphospecies we feel are likely to be real undiscovered species. These were assigned temporary codes (e.g. *Cerapachys FJ01*) instead of species names, but treated as legitimate species in all analyses. This “geographic” revision model is somewhat out of fashion, but is important for developing a timely and useful synopsis of the fauna. Without it, a biologist encountering an ant species in Fiji may have no idea the geographic range of that species, what habitats it is likely to be found in, or even whether it is a native or introduced species.

Our inventory establishes many of the general patterns of species distributions across archipelago, and we feel provides a framework within sophisticated ecological and evolutionary studies can proceed, armed with information about each species in the community. An ecologist could now enter a habitat in Fiji, and it is fairly unlikely they would encounter, without some effort, a species that has not been included in our study. There are almost certainly undescribed species in Fiji, and even more island occurrences that have not been detected, but we submit that a researcher would have to work quite hard to discover these, and almost certainly no ecologically dominant species are undiscovered.

In the next three sections, I describe the biodiversity inventory methods used to collect and curate the ants of Fiji. I then describe the numerical results of our inventory- the results in terms of species and population numbers. In

the fourth section, I describe initial analyses of community and biogeographic patterns. Finally, I present a taxonomic synopsis of the entire ant fauna.

5.2 Survey/Curation Methods

Recent inventory efforts focusing on Fijian arthropods accumulated a large collection of unprocessed formicid specimens. These included (i) over a 674 2-week malaise trap samples from the NSF Terrestrial Arthropod Survey (Evenhuis and Bickel, 2005), and (ii) 100 Winkler leaf-litter transects conducted by Dave Olson and the Wildlife Conservation Society. In addition, Hilda Waqa (University of South Pacific) made canopy fogging samples along an elevational gradient on Viti Levu. To these, we added 559 hand collections, and another 75 Winkler transects made across Fiji in numerous trips between 2003-2008. The sampling coverage across Fiji can be seen in figure 5.1. First collections were made by the author on the islands of Moala, Beqa, Gau, and in numerous unexplored localities within the larger islands. The sampling generally followed standard ant survey methods, such as the ALL protocol (Agosti and Alonso, 2000). Our primary goal was to collect the most species from the most localities and habitats, and develop as complete as possible a picture of the ant fauna. Our main bias was toward remnants of pristine forest that were likely to harbor native ants, but many collections were made in human dominated ecosystems.

The ants in each sample were sorted to morphospecies in ethanol, and between 1-4 representative specimens were pinned for each morphospecies.

Representatives of all available castes were pinned. This occurred over several years at UT, UC-Davis, and in Fiji from August 2007-March 2008 in a lab run by the author. An approximate total of 10,000 ants were pinned, representing several hundred thousand individual specimens that remain in ethanol. The pinned ants were then sorted to genus and species. Taxonomic literature as well as previous collections were consulted to make determinations.

5.3 Inventory Results

To assess the impact of our inventory on knowledge of the Fijian ants, we use Ward and Wetterer's 2006 checklist (hereafter, WW) (Ward and Wetterer, 2006) as a benchmark for comparison. WW reported the presence of 33 genera, we collected all of these except one, *Romblonella*, which remains elusive (we have some doubts about these records, and have requested to examine original material). To this list, we added several genera that have never been recorded in Fiji, including *Acropyga* (2 species), *Amblyopone*, *Discothyrea* (3 species), and *Metapone* (2 species). All of these are rare, cryptic, leaf litter ant species. One of the *Acropyga* species, *A. lauta*, was discovered tending subterranean mealybugs, which is a mutualism common to this genus. The other species, an undescribed Fijian endemic (S. Shattuck, *personal communication*), was not observed with mealybugs during the one collection that was made. *Amblyopone*, the so-called "Dracula ant," is exceedingly rare and only known from two specimens. *Metapone*, a specialist inhabitant of termite mounds, is widespread across higher elevation Fijian islands, but only known

from sexual castes caught in malaise traps.

On the species level, WW reported 138 unique species names from Fiji. We identified 183 unique species from our collections, with the additions including many species new to science and several named species unknown to Fiji. That number also accounts for several groups of named species that we determined were actually one species, usually after an accumulation of more specimens, and lumped together.

57 new records were made for Fiji: *Amblyopone zwaluwenburgi*, *Prionopelta kraepelini*, *Cerapachys FJ01*, *Cerapachys FJ04*, *Cerapachys FJ05*, *Cerapachys FJ06*, *Cerapachys FJ07*, *Cerapachys FJ08*, *Cerapachys FJ10*, *Tapinoma FJ01*, *Tapinoma FJ02*, *Acropyga lauta*, *Acropyga FJ01*, *Camponotus FJ04*, *Camponotus FJ02*, *Camponotus FJ03*, *Eurhopalothrix FJ52*, *Lordomyrma curvata*, *Lordomyrma desupra*, *Lordomyrma sukuna*, *Lordomyrma vanua*, *Lordomyrma vuda*, *Metapone FJ01*, *Monomorium FJ02*, *Myrmecina FJ01*, *Pheidole FJ05*, *Pheidole sexspinosus*, *Pheidole FJ05*, *Pheidole FJ09*, *Pheidole bula*, *Pheidole furcata*, *Pheidole pegasus*, *Pheidole simplispinosa*, *Pheidole uncatena*, *Poecilomyrma FJ03*, *Poecilomyrma FJ05*, *Poecilomyrma FJ07*, *Poecilomyrma FJ08*, *Pristomyrmex FJ02*, *Pyramica FJ02*, *Strumigenys FJ01*, *Strumigenys FJ09*, *Strumigenys FJ13*, *Strumigenys FJ17*, *Strumigenys FJ18*, *Strumigenys FJ19*, *Vollenhovia FJ01*, *Vollenhovia FJ03*, *Vollenhovia FJ04*, *Vollenhovia FJ05*, *Hypoponera FJ16*, *Leptogenys FJ01*, *Ponera FJ02*, *Discothyrea FJ01*, *Discothyrea FJ02*, *Discothyrea FJ03*, and *Proceratium FJ01*.

The population level saw the most dramatic change in our knowledge

of the Fiji ants. WW reported 273 unique species-island occurrences. Our survey has produced 777 such records. This is a result of both the survey of new islands (Moala, Gau, Beqa, Koro) and significant increases in the species lists of each previously collected island. Furthermore, within islands, the distributions of many of these species are much better known, as many of the localities we visited were unexplored for ants and some contained restricted endemic species. Figure 5.2 summarizes changes to species richness across the islands from the current survey.

Additions to the fauna in specific localities and for all of Fiji were the greatest from Winkler leaf litter samples. These capture cryptic leaf-litter ants that may be difficult to detect through other methods, particularly species of the diverse genera *Cerapachys*, *Strumigenys*, *Hypoponera*, *Pheidole*, and many less diverse genera.

Malaise samples primarily capture the worker castes of the arboreal ant fauna, dominated by *Camponotus*, *Tetramorium*, and *Pheidole*, but few of even the abundant leaf litter ant species. However, malaise samples were efficient at capturing males and alate queens of both arboreal and leaf litter species, and these samples increased the distributions of many of the species tremendously. For example, *Metapone* is only known in Fiji from sexual castes in malaise traps, and the exceptionally (locally) rare species, *Myrmecina cacabau* has only been collected twice by hand, but the males show up in malaise traps across the archipelago.

After these sampling efforts, what conclusions can be drawn about the

state of knowledge of the Fijian Ant fauna? How many species are likely to remain undiscovered? Biodiversity inventories can be quantified with statistics that estimate the completeness of biodiversity sampling. These methods fit saturating functions to species-accumulation curves and project the “true” richness, with particular attention to how many singletons or doubletons exist in the collections. As ants are social organisms, the concept of “abundance” is somewhat problematic. Thus, multiple individuals collected in a given sample are treated as single individuals for the purposes of species accumulation curves.

Although the theoretical justification of such analyses are somewhat questionable, we used EstimateS (Colwell and Coddington, 1994) to calculate species accumulation curves, and estimate the Chao-2 (Chao, 1984) index of projected richness (figure 5.2). Overall, pooling all sampling methods, accumulation curves are clearly not saturating for Fiji, there are still 19 species that have only been collected once. Relying on the logic that in a well sampled fauna, each species should have been collected multiple times, this implies there are many more species that remain uncollected in Fiji. Breaking it down further by collecting method, hand and Winkler collections are clearly the furthest from saturating, while malaise samples are, if not saturated, closer to capturing the entire arboreal fauna. We estimate Fiji has between 200-225 ant species.

This makes some sense, hand collections are not a random sample of the community, they are biased towards rare and novel taxa, and thus should

not show a strong saturating effect. Winkler samples capture rare and cryptic leaf litter samples, which are much more difficult to detect by collectors than the arboreal fauna that is well collected by malaise samples. Further malaise trapping would probably be less efficient for collecting new taxa, however if more attention were paid to matching males to worker castes, could be very efficient.

In conclusion, while the current inventory has resulted in a complete overhaul in our knowledge of the Fijian ant fauna and distributions across the archipelago, it is by no means complete. There are many rare and difficult to collect species and their spatial distributions are certainly incomplete. This echoes previous work in the Pacific, and elsewhere, finding that while many species are locally and or regionally common and easy to collect, certain species are extremely rare and require intensive sampling to detect, even in relatively species poor communities. In general, future work should focus on hand collections and litter sifting to further uncover the ants of Fiji.

5.4 Community Patterns

5.4.1 Dominance

Although a detailed analysis of Fijian ant communities is beyond the scope of this chapter, we offer a general discussion and a few cursory analyses to characterize the fauna. The five most commonly encountered species are *Camponotus polynesicus* (308 times, Fiji endemic), *Odontomachus simillimus* (277, Pacific native), *Paratrechina vaga* (240, Pacific native), *Tetramorium*

pacificum (202, Pacific native), *Technomyrmex vitiensis* (190, Pacific native). In general, aside from *Odontomachus simillimus*, individual species of introduced ants did not make up a large fraction of the communities surveyed in pristine habitat. However, this ratio would likely change if our survey collected more in disturbed habitats. The most abundant ants were, aside from the notable example of *Camponotus polynesicus*, widespread species found across the Pacific, consistent with empirical and theoretical work finding a correlation between local abundance and geographic range. Introduced ants are present in relatively undisturbed habitat, but generally do not reach high abundances. This latter statement assumes that *Paratrechina vaga*, and *Odontomachus simillimus* which are both ubiquitous and at a very high biomass abundance in the litter, are native to Fiji.

Using number of collections as a rough proxy for relative abundance across Fiji, we can calculate an estimate of the gamma diversity of the native forest metacommunity. Simpson’s index for the entire archipelago is 20.43 effective species, compared with a richness of 189, indicative of a highly skewed abundance distribution.

5.4.2 Species Area Curves

The Fiji islands exhibit a canonical species-area curve, with $S = 12.9A^{0.26}$ ($n = 10, r^2 = 0.797, p < 0.0005, 95\%CI: 0.155-0.371$) for all species (Figure 5.4). This slope is commonly observed across taxa (Rosenzweig, 1995). It remains to be seen how much of the variation around this line reflects real

spatial pattern or sampling effects. Moala (ML), Koro (KR) and Gau (GA) are generally more diverse for their size, and were subject to all three methods of collection. Ovalau (LA) had relatively sparse sampling and no malaise traps, Lakemba (LK) was not hand collected, and Beqa (BQ) did not have any malaise trapping.

Some insight can be gained by breaking down the species-area curve into faunal components. Introduced species also show a species area curve $S = 2.3A^{0.24}$ ($n = 10, r^2 = 0.57, p < 0.012$) with a similar form to line of all species. However, there is much more noise in the exotic group of species than any other. This likely reflects stochasticity in occupancy, due to the vagaries of the invasion process, in addition to sampling effects. Certain exotics, such as *Paratrechina longicornis* for example, are widespread but only occur in the most artificial environments such as villages and homes, making them difficult to detect with Winkler or Malaise samples. All native species show a curve similar to the overall curve $S = 10.98A^{0.27}$ ($n = 10, r^2 = 0.816, p < 0.0003$, 94%CI: 0.16-0.36).

Widespread Pacific natives $S = 6.73A^{0.12}$, ($n = 10, r^2 = 0.82, p < 0.0003$) show the most shallow curve, implying a much weaker area effect in those species. Fijian endemic species show a slightly sharper increase in species number with area ($n = 10, S = 5.39A^{0.33}, r^2 = 0.74, p < .0012$, 95%CI: 0.1726-0.4799), while the sharpest slope is single island endemics, $S = 0.12A^{0.55}$, ($n = 6, p < .016, r^2 = 0.80$, 95%CI: 0.16-0.93).

These patterns are consistent with patterns across different groups -

single island endemics usually have a steeper species area curve than species found on multiple islands. This overall likely reflects differences in connectivity among islands in the different groups. The most connected islands have a shallower species area curve, while the “interprovincial” curve is usually linear (Rosenzweig, 1995).

5.4.3 Elevational patterns

On most Pacific islands, elevation is the dominant environmental gradient. Myrmecologists working in the Pacific have long anecdotally recognized elevation, along with human disturbance, as the main variables determining community composition within an island (Wilson and Taylor, 1967). Conventional wisdom is that lower elevations are dominated by exotic species and widespread Pacific native ants. As elevation increases, the communities become increasingly dominated by endemic species, until at high elevations the fauna consists exclusively of endemic species. Diversity is thought to be reduced at low elevations, perhaps due to the influence of exotics and tramps, peaking at intermediate elevations, and much reduced at high elevations.

However, these patterns have never been demonstrated quantitatively, and our data allows for a preliminary assessment. We found the minimum and maximum elevational range of each species, and made the assumption that the species occur continuously at intermediate elevations between these extremes. This adds the potential for some sampling effects, particularly at the margins. Many species that have an elevation minimum near sea level probably

do actually extend to the ocean, but perhaps collections were made slightly inland, perhaps at 50m elevation (and the same for the higher boundaries). Indeed this is almost certainly what to have caused the apparent precipitous drop in richness near sea level. To mediate this effect, in a second plot we also added a 100m buffer to the ends of each species range, reflecting the assumption that our sampling was unlikely to have detected the exact end of the range.

We plotted richness of different species groups, all (red), endemic (blue), widespread native (black), and exotics (green) (figure 5.5). Fijian endemics peak in richness at intermediate elevation, while widespread natives and exotics both peak at sea level and slowly decline at higher elevations. The unimodal pattern exhibits a “mid-domain effect” (Colwell and Lees, 2000). This is also consistent, although not in any rigorous sense, with a model of high natural connectivity of low elevation forests, and combined with more restricted species forming more differentiated faunas at higher elevation. Also, an open question pertains to how much of an impact introduced ants have had on the native fauna at lower elevations. Future, more targeted work is needed to investigate the mechanistic origins of these community patterns.

5.5 Taxonomic Summary of the Ants of Fiji

This section is a brief summary of a forthcoming monograph on the Fijian ant fauna by E.M. Sarnat and the author.

5.5.1 Amblyoponinae

AMBLYOPONE

Amblyopone zwaluwenburgi is the only species of this genus known from Fiji is represented by a single specimen collected from leaf litter on the island of Gau. It is known to exist in only one other locality in Hawaii (Wilson and Taylor, 1967). This is clearly an exceedingly rare and difficult to collect species that is likely to be much more widespread than is currently known. It is unknown whether this species is native to Fiji or introduced by human activities.

PRIONOPELTA

Prionopelta kraepelini is species is the most widely distributed species of the genus, from Sumatra in the west to Samoa in the east (Shattuck, 2008). It is only known from a handful of specimens in Fiji, but it likely to occur at low abundance in many localities across the archipelago. It is known to occur in marginal habitats, suggesting that it could be spread by human activities. Little else is known about this species.

5.5.2 Cerapachyinae

CERAPACHYS

Cerapachys is one of the more interesting genera occurring in Fiji from a biogeographic and evolutionary perspective. From as few as two individual lineages dispersing into Fiji (Wilson, 1959b), the group has radiated *in situ* to fifteen species, seven of which were uncovered by our sampling efforts. *Cerapachys*

is also an interesting case because, unlike the majority of Fijian genera, it has wingless queens and is not thought to be a good disperser. This probably contributes to the very complex patterns of spatial morphological variation exhibited across the archipelago in the group. Many islands and localities have endemic forms, and it is somewhat difficult to delineate species boundaries. Furthermore, the lack of wingless queens raises the question of mechanism of dispersal to Fiji. For all these reasons, *Cerapachys* would be an interesting test case for further detailed phylogenetic and ecological study.

During the inventory, the group was most readily collected in leaf litter samples, supplemented by few hand collections. The males were captured in abundance in malaise traps, and in some cases can be matched to worker castes. However, due to a lack of nest series, some morphospecies could not be matched and would benefit from a molecular approach. The distributions of the males were much more widespread than is evident in the workers, suggesting they are a potentially fruitful source of data for future inventories.

Most *Cerapachys* species in Fiji can be assigned to two general groupings based on morphology. The *Typhlus* group, with 9-merous antennae, includes three species including *C. cryptus*, *C. fuscior*, and the undescribed *C. FJ06*. Interestingly, FJ06 appears to be widespread and exists in marginal habitats, unlike the other Fijian *Cerapachys*. A possible fourth species, *C. FJ52*, is only known from males from several localities on Viti Levu.

The Melanesian *Dohertyi* group is represented in Fiji by five described species *C. lindrothi*, *C. majusculus*, *C. sculpturatus*, *C. vitiensis*, *C. zimmer-*

mani and a number of undescribed species, *C. FJ01*, *C. FJ07*, *C. FJ05*. The latter emerge from two morphologically difficult species complexes, among the most confusing in Fiji, and likely to be revised in the future with further molecular work and new specimen series.

Three undescribed species, *C. FJ04*, *Cerapachys FJ08*, and *C. FJ10*, the latter two closely allied, do not fit in any of the other groups in Fiji.

5.5.3 Dolichoderinae

IRIDOMYRMEX

Iridomyrmex ranges from South Asia to the Pacific and is often ecologically dominant. In Fiji, it is represented by two species that occur at relatively low abundance. Although they have been collected very occasionally in pristine habitat, they are most commonly collected in transitional to human dominated habitats. The two species *I. anceps*, and *I. ignobilis* are not very common ants, especially the latter which was only collected once during our survey.

OCHETELLUS

Ochetellus, is represented in Fiji by a single species *O. sororis*. The inventory has increased the known range of this species considerably, revealing that it widespread across the archipelago, but locally rare. It generally can be found in low- to mid-elevation intact forest and there is no sign of morphological variation across the archipelago.

PHILIDRIS

Philidris is represented by one species in Fiji *P. nagasau*, although Mann (Mann, 1921) described subspecies level variation between Vanua Levu and Taveuni. Our much more intensive survey found a great deal of morphological variation, there were no clear discrete or spatial aspects to the variation, and we coalesced these forms into one species. It is an example of a genus of ants that has reached Fiji, formed an endemic, but not continued diversification. *Philidris* is the only genus in Fiji that is known to occur only in the smaller islands but not on the largest island, Viti Levu. This is a very odd distribution as Viti Levu is by far the oldest island and the largest target for migrants from the west. It is a dominant member of the mid to high elevation arboreal fauna on Vanua Levu and Taveuni, but only one rogue specimen was found from the coastal Solodamu forest on Kadavu. The nature of the Kadavu population is rather mysterious, and the possibility of a labeling error should not be ruled out until it is corroborated.

One interesting aspect of the biology of *Philidris* is their affinity for nesting in the *Myrmecodia* ant-plants (Shattuck and Barnett, 2000) that are quite common in the islands. The epiphytic plants form an internal cavity ideal for ant nesting, and in return absorb nutrients from materials brought in by the ants. On Vanua Levu and Taveuni, the overwhelming majority of ant-plants are inhabited by *P. nagasau*. On Viti Levu, where *P. nagasau* is absent, the ant-plants are inhabited by a half dozen of other species, many of which are invasive, and many of which can be found living together in the

same plant. Little is known about the association of ants and ant-plants in Fiji and it would be a fruitful area for further work.

TAPINOMA

Tapinoma is represented by four species in Fiji, *T. melanocephalum*, *T. minutum*, *T. FJ01*, and *T. FJ02*. *T. melanocephalum* is one of the most widespread exotic ant species in the world, reaching every tropical region. In Fiji, it is found in high abundance in human dominated areas, and can be readily found in nearly every home. We also collected it in pristine habitats, but less frequently and at low abundances. *T. FJ01* and *T. FJ02* are of different forms that join a host of Pacific *Tapinoma* of uncertain status.

TECHNOMYRMEX

Technomyrmex vitiensis, the only member of the genus occurring in Fiji, is one of the most widespread and locally common species in Fiji. The ultimate ecological generalist in Fiji, it thrives in both pristine and human-dominated habitats and from the coast to the highest mountain peaks. Its ability to survive at high abundance in human-dominated habitat is somewhat unusual for a native ant. It is primarily an arboreal species and both workers and males are commonly found in Malaise traps.

5.5.4 Ectatomminae

GNAMPTOGENYS

Gnamptogenys aterrima, the only representative of the subfamily, is endemic to Fiji. *G. aterrima* belongs to a papuan species group, representing its easternmost extent into the Pacific. This species is widespread across Fiji and commonly collected in litter sifting. It has reached even small isolated islands, such as Moala.

5.5.5 Formicinae

ACROPYGA

Acropyga is one of several genera only recorded in Fiji by our most recent inventory. represented by two species in Fiji, *A. lauta* and an undescribed species *A. FJ01*. *A. lauta*, which has been collected only once in Fiji (Vanua Levu), is also known from other areas of Melanesia. *A. FJ01* is apparently a Fijian endemic. This genus often forms mutualisms with mealybugs, and *A. FJ01* was collected with an associated mealybug species.

ANOPLOLEPIS

Anoplolepis gracilipes, also known as the Yellow Crazy Ant, is widespread across the tropics and occurs across Fiji. In certain low elevation areas, even in otherwise pristine forest, it can form a dominant presence in the leaf litter. *A. gracilipes* can sometimes reach higher elevations (above 700m), but only achieve very low abundances in those areas.

CAMPONOTUS

Camponotus is the most diverse genera in the world (Bolton et al., 2006) and also the most diverse genus in Fiji. It is the most dominant arboreal ant group across the archipelago, both in species numbers, biomass, and ecological extent. There have been at least three independent radiations of *Camponotus*, and possibly as many as five or six, depending on how many independent lineages originally reached Fiji. Across the archipelago, patterns of occupancy are complex and many species form complex patterns of morphological variation. For these reasons and more, *Camponotus* appears to one of the most interesting groups in Fiji for future ecological and evolutionary study.

There are at least eleven species in the *Colobopsis* subgenus. One, *C. oceanicus*, is only known from one queen collected by Mayr in 1870 and never recollected. It is possible that this specimen, which has yet to be examined, is part of the *C. polynesicus* group. The latter is an immensely complicated species complex deserving of much more detailed study. We coalesced several of Mann's subsepecies into *polynesicus*, as our broader collections suggested complex continua of morphological variation. At times, it seems multiple discrete forms occur in the same locality, but in other nearby areas intermediate forms exist. It is possible that this is one globally connected, but at times locally disconnected, network of populations. *C. vitiensis* is one of the more distinctive of the Fijian *Camponotus*, and we have increased its known range from Viti Levu to all the major islands. Finally, *C. FJ04* is a rare, undescribed species of *Camponotus* collected from Kadavu, Taveuni, and Vanua Levu. The

species is distinctive for its dense white pilosity covering the entire body.

The rest of the Fijian *Colobopsis* belong to a very distinctive Fijian radiation, the *Dentatus* group (Wheeler, 1934). The individuals are distinct from other *Camponotus* globally by their heavy armor, petiolar spines, and slow, deliberate foraging habits. They occur in small colonies at low abundances, but at least one species is found on every surveyed island in the archipelago. The most common species is *C. dentatus*, which can be observed in both native and human-dominated habitat. It has a close relative, *C. armus*, which is found in the western and northern areas of Viti Levu (while *dentatus* can be found in the rest of Fiji).

The rest of the species of the broader *dentatus* group fall into what we call the *bryani* complex. These include *C. bryani*, *C. manni*, *C. umbratilis*, *C. FJ02*, *C. FJ03*. The latter two are undescribed species found during the recent survey. This is another group that exhibits complex spatial patterns across the archipelago, and would be interesting for further detailed study.

The subgenus *Myrmogonia* in Fiji can be separated into the *Laminatus* and *Schmeltzi* groups. Each represents a complex of species, again with complicated morphological and occupancy patterns. The *Laminatus* group includes *C. laminatus*, *C. cristatus*, *C. levuanus*, *C. maafui*, and *C. sadinus*. In general, where they occur, these species are at relatively high abundance and are quite conspicuous. Most are confined to intact forest but *C. laminatus* is known to occur in marginal habitats.

We currently have classified three species into the *Schmeltzii* group, *C. schmeltzii*, *C. kadi*, and *C. lauensis*. *C. kadi* is a complex that varies morphologically in space and could be several species. However, there is currently not enough evidence to strongly support species boundaries and we are lumping all into *C. kadi*. *C. lauensis*, interestingly, is the only endemic ant of the Lau group.

PARATRECHINA

P. longicornis and *P. bourbonica* are widespread tropical invasive species and are both present in Fiji. The former is primarily found in villages and urban areas, while *bourbonica* can be found in both human-dominated habitat and marginal/transitional forest. *P. vaga* is among the most abundant ants in Fiji and is found in nearly every habitat in the archipelago. It is unclear whether *P. vaga* is introduced by humans into Fiji, but most likely it is a naturally occurring widespread Pacific species. *P. oceanica* and *P. minutula* are most likely part of a broader species complex and many populations currently classified as *P. minutula* across the Australo-Pacific region are probably multiple species. The group has thus far escaped the focused attention of taxonomists. Both are represented in Fiji, but significant morphological variation suggests there may be other cryptic species in our Fijian samples. *P. vitiensis* is the only known endemic Fijian *Paratrechina*, and is widespread and locally common across the archipelago.

PLAGIOLEPIS

P. allaudi is a very small ant which has been spread worldwide by humans. It has been collected around the archipelago in human-dominated and marginal habitats but does not reach high abundances.

5.5.6 Myrmicinae

ADELOMYRMEX

Adelomyrmex is represented by two species in Fiji, *A. hirsutus* and *A. samoensis*. The two species are most easily collected with litter sifting, although not particularly common. The occurrences of *Adelomyrmex* in the Pacific are something of a paradox, as it is mainly a Neotropical group. Westward dispersal across the Pacific is very rare in many taxa and unknown (so far) in ants. *Adelomyrmex* may be such a case.

CARDIOCONDYLA

Cardiocondyla are small, nondescript species often confused with other small myrmicines. Two *Cardiocondyla* species occurring in Fiji, *C. obscurior*, *C. emeryi*, are globally widespread tramps spread by humans. The three other species in Fiji, *C. minutior*, *C. kagutsuchi*, and *C. nuda*, are all widely distributed across the Pacific. There are no Fijian endemics or evidence of speciation in Fiji.

CAREBARA

Carebara is represented by one species in Fiji, *C. atomus*, which is also distributed across the Pacific. *Carebara atomus* is quite possibly the smallest ant species in Fiji, is widespread across the archipelago, and readily collected in litter samples.

EURHOPALOTHRIX

Eurhopalothrix is a stunning yet cryptic Indo-Australian genus, occurring mainly in high quality intact forest. Two previously described species *E. insidiatrix*, and *E. emeryi*, were collected during the current survey by litter sifting. Alate queens and males were readily found in malaise traps, revealing that *Eurhopalothrix* has a much broader distribution than was previously known. In addition, the males of a relatively small *Eurhopalothrix* species *E. FJ52* were collected in malaise traps, but worker castes are unknown.

LORDOMYRMA

The genus *Lordomyrma* ranges across Japan, Southeast Asia, northern Australia, and east to Fiji. In Fiji a significant endemic radiation has formed. Intensive systematic, phylogenetic, and biogeographic studies on this group are underway (Sarnat, 2006). Our recent inventory brought the total of known species up to eleven, all of which are endemic to Fiji. *Lordomyrma* tends to occur in intact forest, in the leaf litter and on rotting logs, and is readily collected in litter sifting and hand collections (but not malaise). One species,

L. tortuosa, is widespread and across the archipelago. The other species vary in range from localized endemics to those that span several islands. Other Fijian species in the group include *L. curvata*, *L. desupra*, *L. striatella*, *L. stoneri*, *L. sukuna*, *L. levifrons*, *L. polita*, *L. rugosa*, *L. vanua*, and *L. vuda*. Preliminary analyses support a hypothesis of monophyly for the Fijian taxa.

METAPONE

Metapone had not previously been collected in Fiji until recent inventory efforts. The workers have never been collected, probably because they are known specialize on and live primarily in termite colonies. Their distinctive queens and males, however are represented in malaise traps from a number of islands in Fiji. There seems to be some inter-island variation morphological variation, but it is unclear if this reflects inter- or intraspecific variation. Thus, our working hypothesis is that all specimens belong to one undescribed Fijian Metapone species, *M. FJ01*.

MONOMORIUM

The *Monomorium* of Fiji are, with one exception, introduced by humans. *M. floricola*, *M. sechellense*, *M. pharaonis* and *M. destructor* are all globally widespread invasive species and common in the disturbed and low-land transitional areas of Fiji. One additional species, *Monomorium FJ02*, was collected in the port of entry areas of Viti Levu and is almost certainly exotic, although has not yet been identified. The lone endemic Fijian species,

M. vitiense, is mostly confined to lower elevation forest and is quite rare.

MYRMECINA

Myrmecina is exceedingly rare in Fiji. The workers are difficult to detect by hand (only once collected during recent inventory) or litter sifting (zero times). However, males are readily collected in malaise traps, and have extended their known distribution from Viti Levu to all of the major islands. From these males and limited hand collections, we determined there are at least two species of *Myrmecina* in Fiji. One of these, *M. cacabau*, is previously described and occurs on Viti Levu. The other *M. FJ01* appears to be widespread across the other islands.

PHEIDOLE

Pheidole in Fiji, as in the rest of the world (Wilson, 2003), is a hyperdiverse genus. It is unknown how many introductions contributed to the fauna of Fiji, but the majority of the species are endemic. There has certainly been at least one major radiation in Fiji forming the distinctive the *roosevelti* group, and possibly other speciation events producing the other endemics. More detailed phylogenetic work is underway and the genus would be an excellent candidate for future ecological studies. *Pheidole* workers readily collected with hand and litter sifting techniques, and more rarely, in malaise traps. Males and alate queens are common in malaise traps, but often impossible to match to worker castes with morphological characters alone.

Only one of the *Pheidole* species, *megacephala*, is unambiguously introduced to Fiji by humans. This species has spread worldwide and is common in human-dominated habitats in Fiji but does not achieve high abundances in intact forests.

Another class of species, representing a large fraction of the *Pheidole* biomass in Fiji, are found across the Pacific and are thought to be native to Fiji. Three of these, *P. oceanica*, *P. fervens*, and *P. umbonata* are quite common in both disturbed and more pristine habitats. *P. sexspinosa*, while distributed across the Pacific, is exceedingly rare in Fiji and only known from one site on Viti Levu, although likely to occur in low abundance elsewhere in Fiji.

Among the most challenging groups in Fiji, populations of *P. knowlesi* form complex spatial pattern of morphological variation. While there seem to be two distinct forms, with one centered in the Viti Levu highlands and the other in lower elevations and the outer islands, there is no evidence of sympatry of the two forms. Furthermore, there is a point of contact between the two forms near Monasavu Dam on Viti Levu, where the two areas meet and they blend into intermediate states. Thus, for the time being, we consider *P. knowlesi* to be a single species.

P. caldwelli, *P. vatu*, *P. wilsoni* and *P. onifera* are Fijian endemics that had been previously described. These three are all fairly common species, although they do not all extend across the archipelago. *P. FJ05* and *P. FJ09* are undescribed species uncovered by the most recent survey. Determining the

relations between these species and others in the regions remains an important and interesting avenue for future work.

The *roosevelti* group, a radiation that has formed seven endemic species, is one of the most distinctive Fijian groups. Intensive studies are currently underway on the group. The *roosevelti* are characterized by large angulate or bifurcated propodeal spines and a distinctive mesonotal process. The species generally occur in intact native forests, and are often confined to a single island or mountain range. On many islands, two of these species exhibit a parapatric distribution sorting along elevation. Preliminary phylogenetic analysis suggests that there appears to be significant interisland speciation occurring in Fiji, with sister taxa occurring on different islands. The species of the *roosevelti* group include *P. bula*, *P. coalensis*, *P. furcata*, *P. pegasus*, *P. roosevelti*, *P. simplispinosa*, and *P. uncagena*.

POECILOMYRMA

Poecilomyrma, the only genus endemic to Fiji, was discovered by Mann during his 1916 survey (Mann, 1921). Mann originally described one species with two subspecies from Viti Levu. Our recent inventory revealed the genus to be widespread across the archipelago. *Poecilomyrma* is most easily collected by hand, although males are well represented in malaise traps (workers show up in malaise only very occasionally). The genus exhibits complex morphological variation across space, and it is difficult to assign species boundaries. The original categories delineated by Mann do not appear to hold up after further

scrutiny. A good case could be made for calling *Poecilomyrma* either one species or as many as eight species. Due to the significant morphological differences between forms, a lack of variation within a locality, and a lack of intermediate forms, we tentatively sorted *Poecilomyrma* into seven distinct species *Poecilomyrma senirewae*, *P. myrmecodiae*, *P. FJ03*, *P. FJ05*, *P. FJ06*, *P. FJ07*, and *P. FJ08*. Future molecular work will likely be the only route to definitive answers regarding the status of the *Poecilomyrma* of Fiji.

PRISTOMYRMEX

There are two species of this genus in Fiji, *Pristomyrmex mandibularis*, and *P. FJ02*. The former exhibits some morphological variation that could reflect species level variation, but at the present time there is not enough evidence to separate any more species. Both species are widely distributed across the archipelago, broadly sympatric, and collected primarily in litter sifting.

PYRAMICA

Pyramica mebranifera is an introduced species that has been spread worldwide by humans. *P. trauma* and *P. FJ02* are, as far as we know, native to Fiji. They both are widespread in Fiji, but locally rare and difficult to collect.

ROGERIA

Rogeria stigmatica is the only species of the genus found in Fiji and Melanesia in general. The genus is primarily centered in the Neotropics. *R. stigmatica* is often collected in relatively intact, lowland forest. The species exhibits a strange behavior, secreting bubbles from its gaster while under duress. The behavior was discovered by Mann and observed several times during our survey.

ROMBLONELLA

Two species of the genus, *Romblonella scrobiferum*, and *R. vitiensis* were collected by early surveys but eluded both Mann and our most recent survey. Both are apparently endemic to Fiji, but it is unusual that they have not been collected more frequently.

SOLENOPSIS

Solenopsis geminata, the tropical fire ant, has been introduced to Fiji and is common in the drier, westward slopes of Fiji. *S. papuana*, a minute but extremely common species, is widespread in Melanesia and in Fiji. It is readily collected in low to mid-elevation litter samples.

STRUMIGENYS

Aside from one well-known introduced species, *S. rogeri*, most of the diverse *Strumigenys* fauna are considered to be native to Fiji. *Strumigenys* are

generally small cryptic ants that are most efficiently collected with litter sampling. From the great number of new forms revealed by the recent inventory, it is clear that they have eluded capture by predominantly hand collections.

Two species *S. maelli* and *S. godeffroyi* are widespread Pacific natives. The rest of the species *S. basiliska*, *S. chernovi*, *S. daithma*, *S. ekasura*, *S. frivola*, *S. jepsoni*, *S. nidifex*, *S. panaulax*, *S. praefecta*, *S. scelestia*, *S. sulcata*, *S. tumida*, *S. FJ01*, *S. FJ09*, *S. FJ13*, *S. FJ17*, *S. FJ18*, *S. FJ19*, are Fijian endemics.

These species are part of several species complexes, and it is likely that several independent lineages have radiated in Fiji to form the present, diverse fauna. They represent yet another excellent choice for future detailed work.

TETRAMORIUM

Tetramorium is almost unique among the Fiji ants in that it is a quite diverse genus, but most of the species are well known and described. They are a significant arboreal presence in the forests of Fiji, and are often collected in malaise, litter sifting, and hand collections.

The human-introduced species in Fiji include *T. caldarium*, *T. insolens*, *T. lanuginosum*, *T. simillimum*. They are common in marginal and human-dominated areas. While *T. pacificum* and *T. tonganum* are widespread species that have been spread by humans outside their native range, they are thought to be native in Fiji. This assertion deserves further attention with molecular methods.

Fiji's lone endemic member of the genus, *T. manni*, is widespread in the intact forests of Fiji, and exhibits significant morphological variability across the archipelago.

VOLLENHOVIA

There is one previously described species, *Vollenhovia denticulata*, that is also known from other areas of the Pacific. The other four species *V. FJ01*, *V. FJ03*, *V. FJ04*, *V. FJ05*, appear to be undescribed and unknown outside of Fiji. Some or all of them may well be endemics, however, *Vollenhovia* is proving to be one of the more cryptic groups in the Pacific. Several of these species are known from single specimens, indicating they are exceedingly rare. With such rarity, it is difficult to make solid conclusions about distributions of the species both in Fiji and the region. Other recent work (Clouse, 2007) also suggests that *Vollenhovia* may be among the least known elements of the Pacific islands fauna.

5.5.7 Ponerinae

ANOCHETUS

Anochetus graeffei is widespread in Fiji and the Pacific, although generally does not achieve very high abundances. It is regularly collected in litter samples. Although it is considered native, it is unknown whether *A. graeffei* was introduced to Fiji by humans or through natural means.

HYPOPONERA

Hypoponera is one of the more commonly encountered genera in Fiji, and a significant component of the leaf litter fauna. There are several Fijian endemics which vary in abundance across the archipelago. *H. eutrepta* is widespread, fairly common, and morphologically variable. *H. monticola* is also quite common and widespread across the archipelago. Three other endemic species *H. turaga*, *H. vitiensis*, *H. FJ16* are much more rarely collected, although most are widespread across the islands.

H. gleadowi and *H. punctatissima* have likely been introduced to Fiji by humans. *H. opaciceps* occurs has been distributed widely by humans and is present, but not common, in Fiji.

LEPTOGENYS

There are eight known *Leptogenys* species in Fiji, all endemic to the archipelago. All of the species in Fiji are quite rare, and apart from one species *L. letilae*, are only known from one or two localities. The workers are not a common presence in litter nor malaise samples. The males are captured in abundance in the malaise samples across the archipelago, but it is currently impossible to associate males with worker castes. Future molecular work could tap into these data. The other *Leptogenys* species in Fiji include *L. foveopunctata*, *L. fugax*, *L. humiliata*, *L. navua*, *L. vitiensis*, *L. FJ01*.

ODONTOMACHUS

O. simillimus is one of the most common species in Fiji, nearly ubiquitous in the leaf litter at all but the highest elevations. It is thought to be a Pacific native, but has also been spread by humans out of its range.

O. angulatus is a Fijian endemic, mostly confined to the higher elevation intact forests. Originally thought to only inhabit Viti Levu, it is now known to have populations on most of the larger islands.

PACHYCONDYLA

Pachycondyla stigma, the only species of the genus in Fiji, is a globally widespread invasive. It primarily inhabits forest habitats and, while workers are not often observed out in the open, alate queens often are captured in malaise traps.

PLATYTHYREA

Platythyrea parallela is an exotic species in Fiji. It has a fairly restricted presence in Fiji, only known from a few collections on the south coast of Viti Levu.

PONERA

Ponera is a relatively cryptic genus in Fiji, although they can be found at low abundance in litter samples. There are two endemic species of this genus in Fiji, *Ponera manni* and *P. colaensis*. One species, *P. swezeyi*, is widespread

in the Pacific. The recent inventory uncovered one species, *P. FJ02*, that is apparently undescribed.

5.5.8 Proceratiinae

DISCOTHYREA

Discothyrea was not known to occur in Fiji until the most recent inventory. The genus is morphologically distinct and has an interesting ecology, specializing on arachnid eggs (Shattuck, 2008). A handful of workers were collected in litter sifting, and alate queens occasionally were captured in malaise traps. Among these specimens, three species were delineated, *D. FJ01*, *D. FJ02*, *D. FJ03*. Little is known about the distributions of these species as they are locally extremely rare.

PROCERATIUM

At least three *Proceratium* species occur in Fiji, two of which have been previously described. The workers occasionally can be found in litter samples, but the males and alate queens are quite common in malaise traps. *P. relictium* is known to occur in Vanua Levu and Taveuni, while *P. oceanicum* has been collected on Taveuni and Viti Levu. A third, undescribed species, *P. FJ01*, is known from Viti Levu, Kadavu, Taveuni, and Vanua Levu.

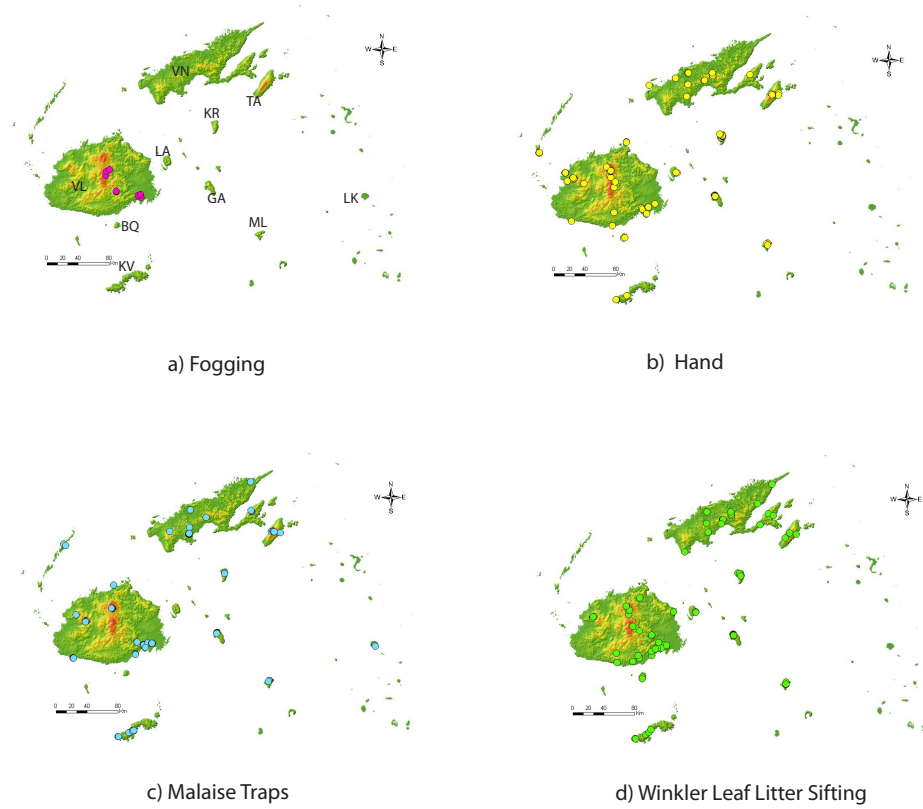


Figure 5.1: Collecting localities in Fiji by collecting method. The island codes are VL: Viti Levu, KV: Kadavu, TA: Taveuni, VN: Vanua Levu, KR: Koro, GA: Gau, ML: Moala, BQ: Beqa, LA: Ovalau.

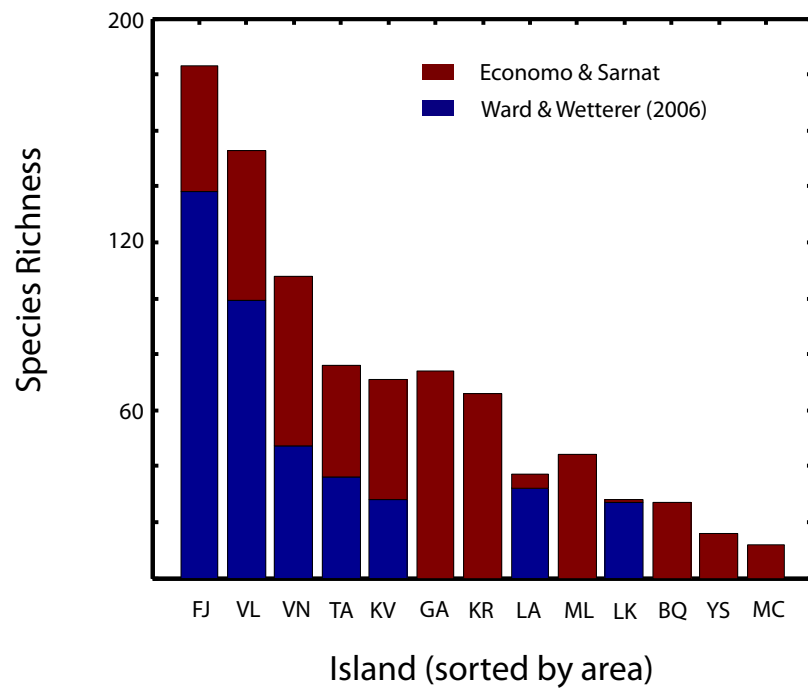


Figure 5.2: Prior knowledge of Fijian island species richness (blue bars) compared with results of this study (red bars).

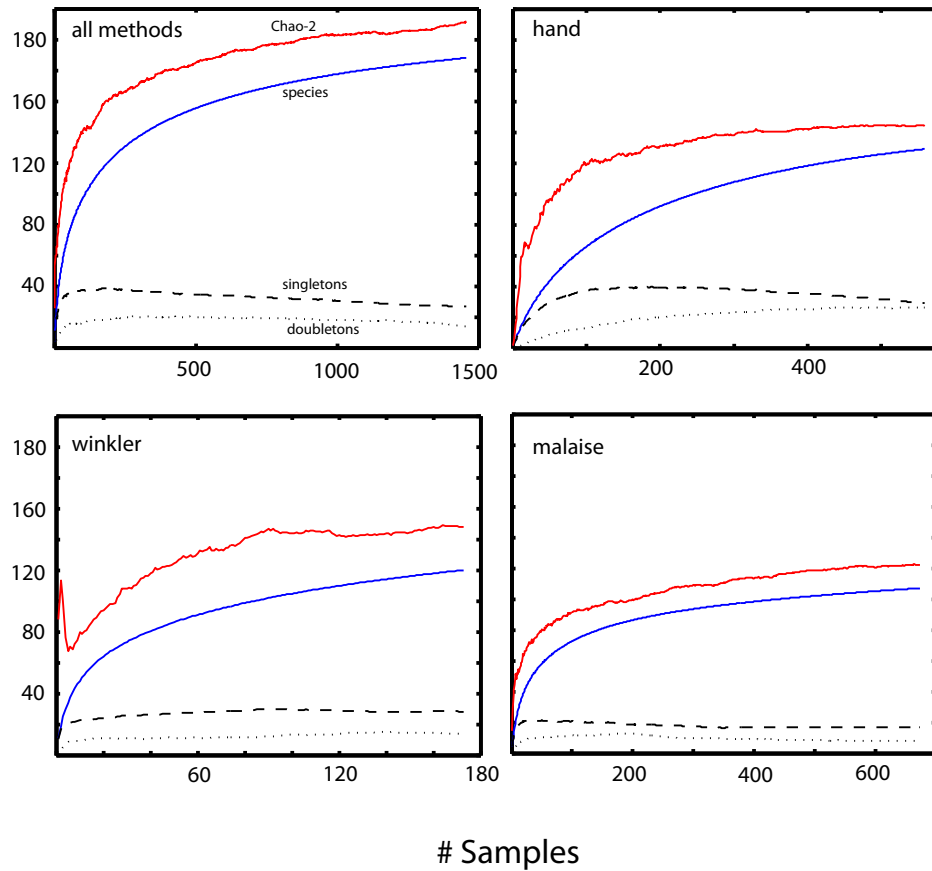


Figure 5.3: Species accumulation curves for different collection methodologies and all methodologies pooled. In addition, singletons, doubletons, and the Chao-2 richness estimator are plotted. Fiji as a whole is not saturated, more collecting is needed. Winkler and hand collections are the most likely to discover further new species with additional sampling.

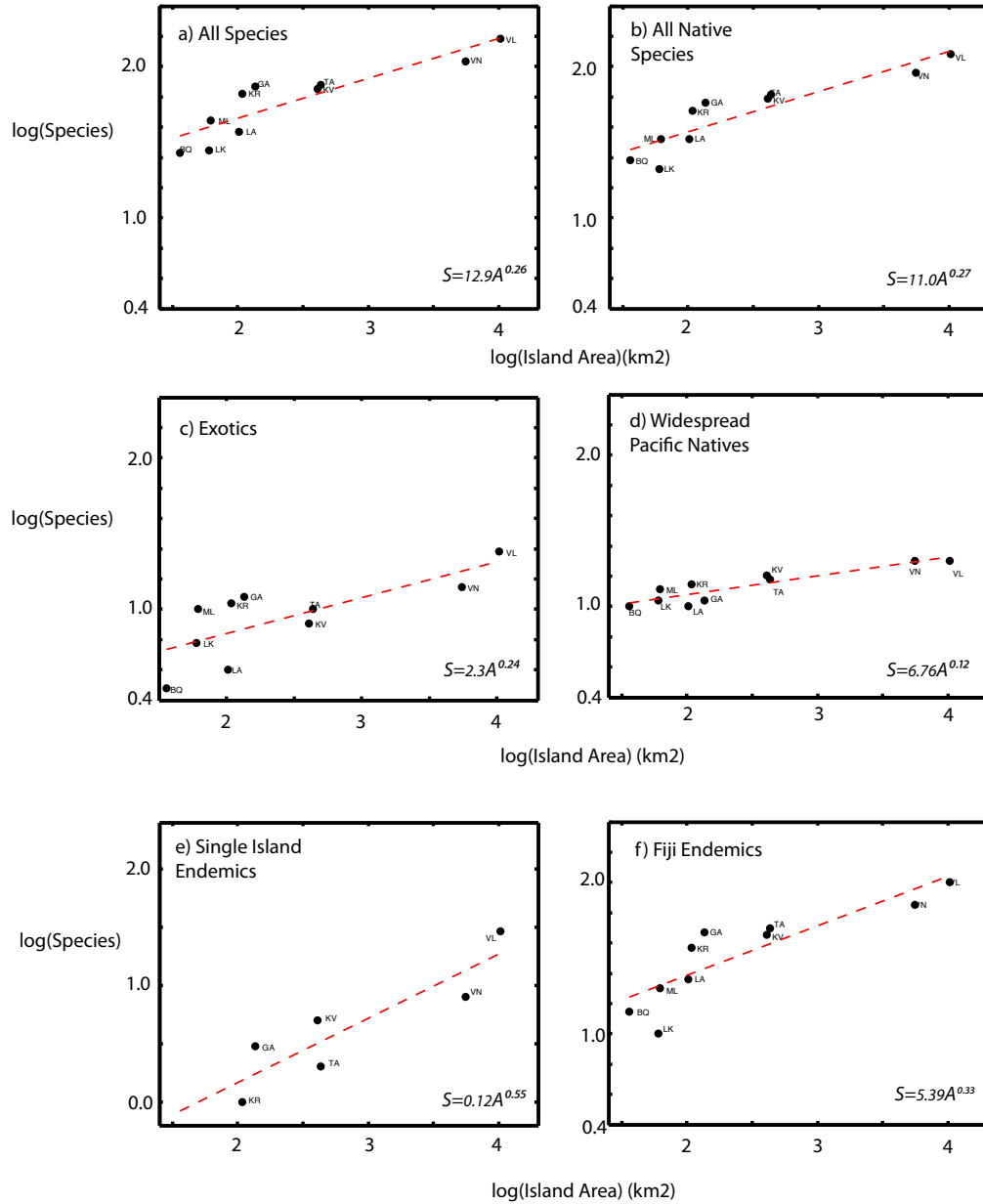


Figure 5.4: Species area curves for the entire ant fauna, and different subsets of the fauna. Widespread species have shallower species area curve than restricted endemic species. Exotic species show the most noisy relationship with area.

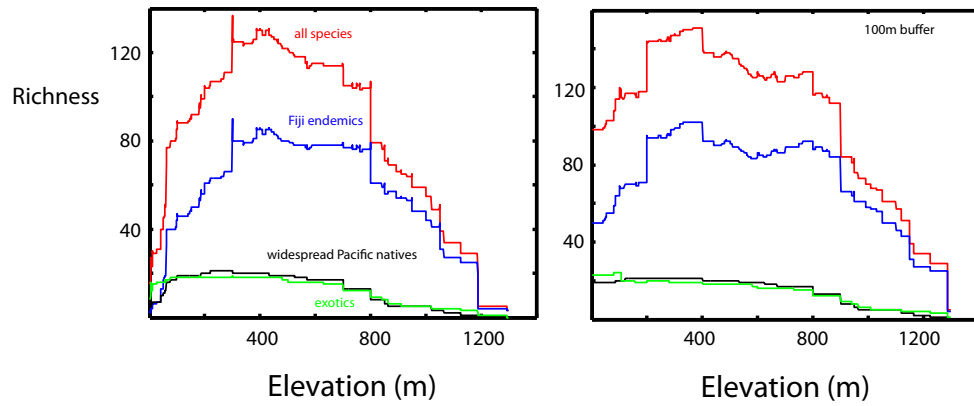


Figure 5.5: Species richness at different elevations in Fiji, and for different subsets of the fauna. In general species richness declines with elevation, while endemics show a unimodal relationship with area, widespread and exotic species show a decreasing richness with area.

Appendices

Appendix A

Chapter 3 Supplemental Information

A.1 Supplemental Methods

Model Assumptions and Implementation

The neutral model used in this paper makes the following assumptions i) constant meta- and local community size in time ii) ecological equivalence of species and iii) point speciation at a probability v per individual-generation. Point speciation could also be interpreted as immigration from a distant (and large) species pool. The model is equivalent to the infinite alleles model in population genetics. The structure of the metacommunity is represented by the migration matrix M , and a vector of local population sizes N_k . The entries of the migration matrix, m_{ij} , are the probabilities that an individual sampled from node i originated from a parent in node j , and $\sum_j m_{ij} = 1$. In this paper, to facilitate unambiguous node comparisons, all local community sizes were set to be equal, although clusters of local communities are effectively large habitat units. The above model was implemented in two ways, by solving a system of linear equations and forward time stochastic simulation.

Simulation Model

In each generation, the metacommunity was replaced with new individuals. These were, for an individual in community i , either a new species with probability v , or an individual of the same species of a randomly chosen individual from community j with probability $(1-v)m_{ij}$. The initial state was each individual as a unique species, and the system was allowed run well past relaxation to diversity steady state before any data on equilibrium diversity were computed.

Analytical Model

For the analytical predictions, we use the method developed in a previous paper (Economo and Keitt, 2008) which can be consulted for further information. The method uses analytical formulas for equilibrium probability of identity \hat{f}_{ij} of two individuals chosen from nodes i and j . The equation for equilibrium probability of identity, from Malécot (Malécot and Yermanos, 1970), is

$$\hat{f}_{ij} = (1-v)^2 \left[\sum_{k,l,k \neq l} m_{ik}m_{jl}\hat{f}_{kl} + \sum_k m_{ik}m_{jk}(1 - \frac{1}{N_k})(\hat{f}_{kk}) + \sum_k m_{ik}m_{jk}(\frac{1}{N_k}) \right].$$

Two sampled individuals are the same type if neither has speciated since the previous generation (the first term), and i) they were from parents of the same type from different patches (the first summation) or ii) they were from different parents of the same type located in the same patch (second summation), or iii) they had the same parent (coalesced) in the previous generation

(third summation).

For a network of n nodes, there are n^2 (i,j) pairs, and thus n^2 linear equations in this form describe the system at equilibrium. Since there are n^2 unknowns in n^2 equations, the system can be solved for the vector \vec{f} of all f_{ij} . For the analyses in this paper, we coded the left side of equation 4 as a $n^2 \times n^2$ matrix X , and the right side as a vector \vec{q} of length n^2 , where:

$$X_{(ij),(kl)} = (1 - v)^{-2} \delta_{(ij),(kl)} - m_{ik}m_{jl} + \delta_{k,l}m_{ik}m_{jk} \left(\frac{1}{N_k} \right)$$

$$q_{(ij)} = \sum_k m_{ik}m_{jk} \left(\frac{1}{N_k} \right).$$

The formula $X\vec{f} = \vec{q}$ can then be solved for the vector \vec{f} of probability of identities. In the following section we describe how to convert those probabilities into diversity statistics.

Diversity Statistics

Diversity in a metacommunity can be measured with raw species numbers or aggregate diversity indices (Magurran, 2003). The analytical methods, which predict probability of identity (f_{ij}), can be converted to a family of diversity indices related to the Simpson concentration. We use the Simpson's index, or effective species numbers, which is the number of species in a community that would produce a given probability of identity if all abundances were equal (Hill, 1973). So, the gamma diversity of the metacommunity (or subset of the metacommunity) is the inverse of the mean probability of identity $(\overline{f_{ij}})^{-1}$, taken over all i and j that are in the set of nodes. So, for example,

to calculate a given γ_h (gamma diversity of the metacommunity without node h), we simply average of all f_{ij} , with $i, j \neq h$. Alpha diversity of node i is f_{ii} .

The pros and cons of using raw species numbers versus diversity statistics for measuring diversity have been previously discussed (Magurran, 2003). Diversity statistics de-emphasize rare species, which are often of interest to conservation. At the same time, two communities may appear identical in terms of presence absences but might have broad differences in abundances reflecting important differences in ecosystem organization.

For our purposes, diversity indices have one big disadvantage- comparing the gamma diversity of two metacommunities with different sizes can have misleading behavior. For example, adding a community that has both low uniqueness and low alpha diversity can actually reduce gamma diversity. In other words, complementarity can be negative, when this is impossible with species richness. While this may be consistent with a definition of gamma diversity based on uncertainty, it is less than ideal as a quantity of interest to conservation (adding individuals to a group should not reduce its conservation value).

Conveniently, under the symmetric migration assumption, alpha diversity and complementarity trade off and this problem does not occur, so we are comfortable presenting complementarity as the difference between metacommunities of different sizes. Furthermore, the x and y values in figures 2 and 3 are both simply subtracted from a constant value (γ_0), so this should not cause a problem. In any case, none of our trials produced a negative complementarity.

ity. For cases of unequal migration, diversity and complementarity can vary independently, and removing a node can cause an increase in diversity (before relaxation). For clarity, in the supplemental section with unequal migration, we simply present the diversity of a subset of the metacommunity (γ_i and γ_k) and the diversity of the subset after relaxation (γ'_i and γ'_k).

Network Construction

The network in figure 2a was constructed with three clusters, within which each node pair was connected with a weight m . All nodes in the two smaller clusters were connected to the larger cluster, with each node pair given a weight of $.1m$. The point of the networks in figure 3 was to represent as much diversity in network architecture as possible, both in topology and patterns of edge weights. The grid network topology is simply a 7×7 lattice. The modular network was generated by randomly assembling sub-networks, then haphazardly connecting them. The random graph is simply an Erdos-Reyni graph (nodes are randomly connected with a probability p , in this case $p = 0.085$). To add more complexity in the metacommunities represented in figure 3, we also varied edge weights. This was accomplished by randomly assigning nodes into three categories of isolation (I-isolated, M-intermediate, and C-connected). If two nodes had an edge between them, were then assigned values based on the categories of each node (I/I: 0.0001, I/M: 0.0005, I/C:0.001, M/M:0.001, M/C:0.005, C/C:0.01). During the trials varying migration rate (figure 3), these edge weights were all reduced or in-

created by a common coefficient, m . In figure 3, the black dots correspond to a metacommunity where $m = 0.01$, blue $m = 0.1$, and brown $m = 1.0$. Asymmetric networks were designed slightly differently, and are discussed in the next section.

A.2 Supplemental Analyses and Figures

Comparison with Simulation

Because the analytical method returns diversity patterns in terms of effective numbers of species, we want to make sure the results are not an artifact of using those statistics. Indeed, many conservation analyses use species numbers, such as number of endemics, to represent diversity patterns. We implemented a stochastic, forward time simulation, to test the effects of node removal on diversity in terms of richness, and compare it to the analytical results. Unfortunately, stochastic simulations are only feasible for metacommunities that are relatively small, which then require a relatively high speciation rate in order to produce much diversity in the metacommunity. Also, at low diversities in small metacommunities, the equilibria are extremely noisy and it is difficult to recover means that may not differ by a great magnitude. We simulated neutral dynamics the 10-node network represented in figure 2a, where $N_k = 20000, v = 0.001$, and calculated the analytical predictions of the equivalent system. The results are depicted in supplemental figure 1. Diversity based on effective numbers of species produces the same pattern as diversity based on species richness, at least in this region of parameter space.

Additional results and discussion of complex network node removals.

Due to space limitations, only figures representing limited parameter space (figure 3) could be presented in the main text. In supplemental figure 3, we present the relationship between biodiversity loss Λ_i and complementarity c_i for a broader range of speciation rates. Notice as speciation rate becomes low, and diversity overall is low (SFig. 3, j-l), relative variation in the effect of node removal becomes higher, and complementarity explains relatively more of that variation. This is due to the fact that nodes do vary to some degree in their effect on biodiversity loss, due to connectivity effects. But these variations usually account for a difference of a few effective species, and that effect does not scale up when the system is more diverse overall, which is why the relative effect becomes reduced in more diverse communities. This is related to a previous result that found that under extremely restricted migration regimes gamma diversity could be inflated by n effective species for an n node metacommunity versus a panmictic metacommunity (Economo and Keitt, 2008), and the importance of that effect depends on the relative diversity of the metacommunity. Removing a node from the metacommunity can reduce connectivity and increase diversity in this way. In conclusion, for metacommunities that support a small number of species, as many systems of conservation interest do, general rules such as maximizing area may break down. However, also note that when diversities are small, neutral equilibria are extremely noisy, implying that the mean values studied here may not be very relevant to a typical realized spatial pattern.

It is important to quantify the strength of secondary biodiversity loss across a range of parameter values. To allow for a standardized comparison when overall diversity levels are changing, we calculate the fraction of total biodiversity loss Λ_i represented by the initial diversity loss (or complementarity, c_i) after removing a single node, at different migration rates. When dispersal is at the lowest value, each node essentially becomes a unique community with maximal complementarity, and the initial pattern correctly predicts the diversity lost from removal (no secondary effects). As dispersal rate increases and begin to move species around, spatial patterns form due to differences in connectivity in different regions of the network. Finally when dispersal is at a maximum, the metacommunity is essentially panmictic and all nodes appear to have a diversity similar to the entire metacommunity (lowest complementarity), dramatically underestimating the cost of removing a node. These results highlight the fact that when dispersal is strong enough to overcome speciation and cause similarity between communities, biodiversity patterns become increasingly misleading in predicting biodiversity persistence.

Asymmetric Network Analyses

While the focus of this paper is on cases where dispersal between communities is equal in both directions (symmetric networks), many real systems have migration that is asymmetric, due to wind or water currents, for example. Offering a full analysis of how asymmetric network structure affects diversity would be beyond the scope of this paper. Here we simply check that our main

result- that current diversity patterns across a metacommunity do not predict well the biodiversity protected, is not sensitive to the assumption of symmetric dispersal.

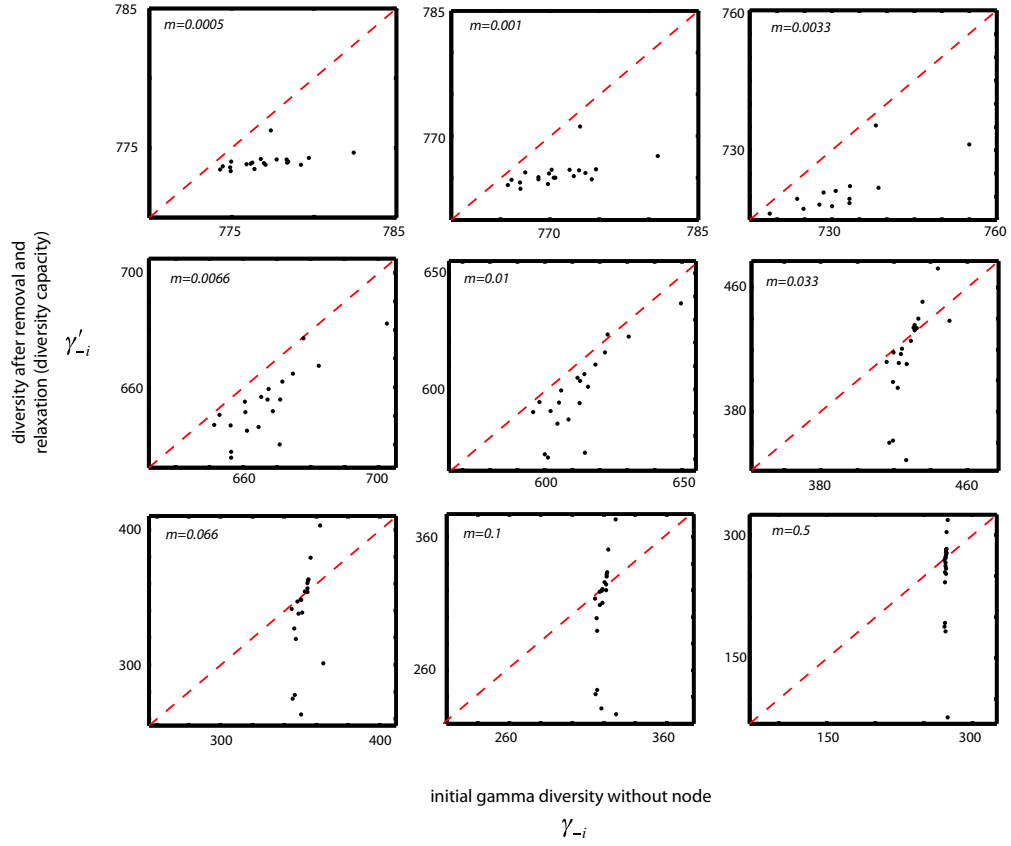
When migration is symmetric (often called *conservative* in the population genetics literature), every individual in the metacommunity has an equal chance of contributing individuals to the next generation, although the locations of the offspring individuals may be more uncertain for some nodes versus others. When migration rate is not symmetric, some individuals contribute a greater or smaller proportion of the individuals in the next generation. In other words, the effective metacommunity size (in analogy to the effective population size from population genetics) is reduced. This depresses metacommunity diversity overall. Individual nodes, through their effects on migration patterns, can be responsible for lowering or increasing the effective metacommunity size, so we can expect that removing them may have a more variable effect on metacommunity diversity than nodes in a metacommunity with symmetric migration.

I consider whether the current diversity of all patches except i in the metacommunity (γ_i) predict long term diversity in that subset (γ'_i), after i is removed and the metacommunity relaxes to a new equilibrium. I generated a random network with 20 nodes, and an average of 4 connections per node. Each edge was assigned a weight at random, either 0.01, 0.005, or 0.0001. The weight for each direction between two nodes were assigned independently. To vary strength of dispersal, I multiplied all weights by a multiplier, m , which

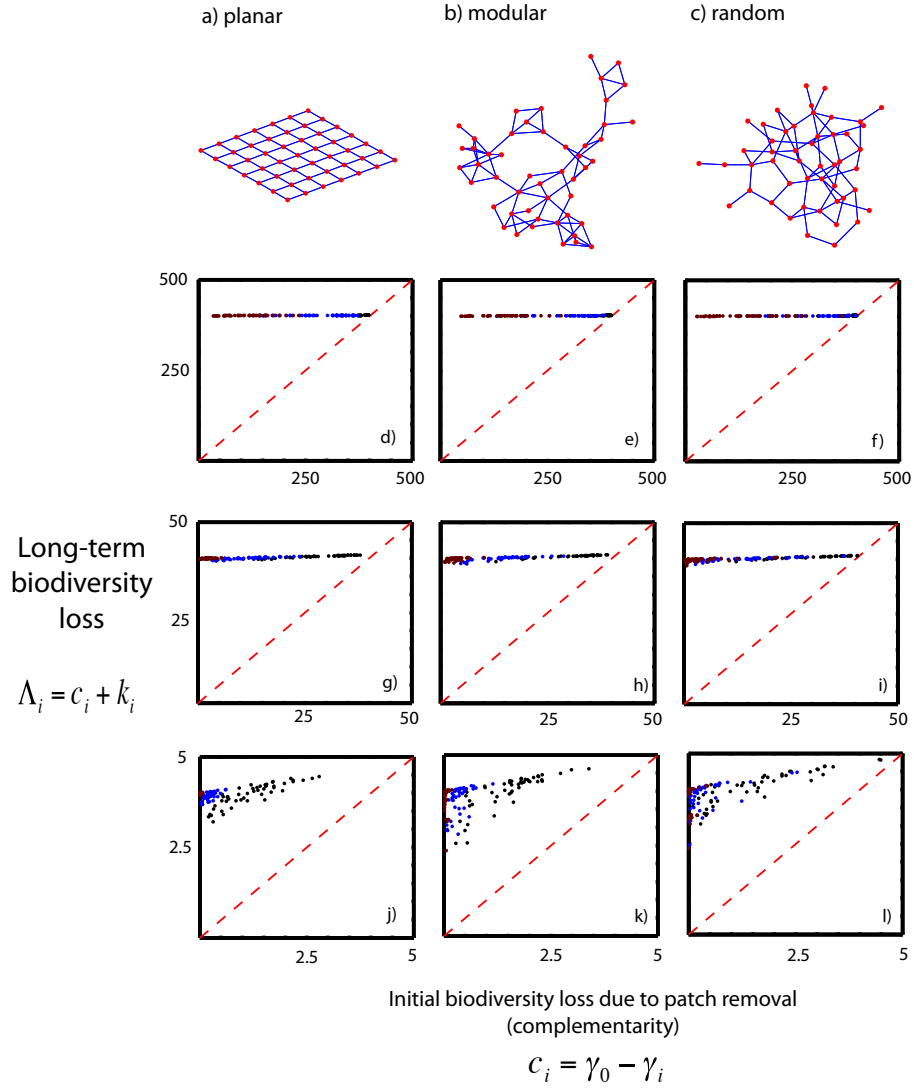
varies among the different trials.

In Supplemental Figure 2, we plot the effects of removing each node in the network, at 9 different migration strengths. The first thing to notice is that unlike the case of symmetric migration, there is a good deal of variation in the effects of removing a node. Removing certain nodes cause a dramatic loss in diversity, while removing others can actually raise effective metacommunity size and promote diversity. For some parameter values, complementarity has moderate predictive value of node removal impact (e.g., panel *e*), while for others complementarity is wildly off (panels *g – i*).

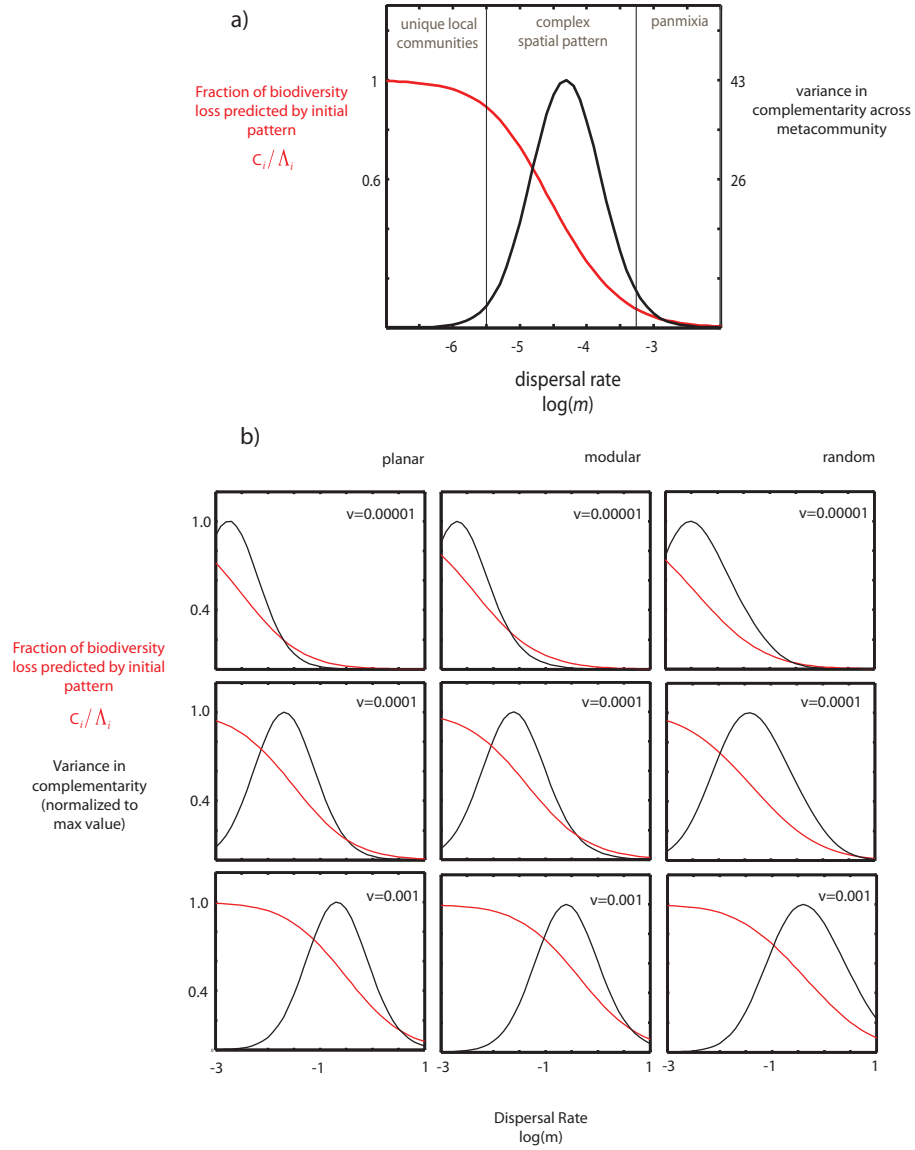
In summary, overall current diversity patterns do not predict well the effects of node removal. However, unlike the case of symmetric migration, individual nodes can vary dramatically in their effects on metacommunity diversity. The extent to which such variation can be predicted by network structure or biodiversity patterns is unknown, and an important goal for future work.



Supplemental Figure A.2: A comparison of the diversity in metacommunity without a single node at initial equilibrium, and then after the node is removed and the subset relaxes to a new equilibrium. The network has 20 nodes and a randomly assembled topology. In each network, migration rates among pairs of nodes are variable, but all the weights are multiplied by a value m which tunes the overall strength of migration in the network.



Supplemental Figure A.3: An expanded version of Figure 3, covering a broader parameter space, showing the effects of node removal on biodiversity in complex networks with different topologies (a-c) and variable edge weights (see supplemental methods). $N_k = 200000$, with migration (all weights) increasing by factors of 10 from black to blue to brown (points with different colors are from different metacommunities). The rows represent different speciation rates, where d-f: $v = 0.001$, g-i: $v = 0.0001$, and j-l: $v = 0.00001$.



Supplemental Figure A.4: The fraction of eventual biodiversity loss Λ_i predicted by the initial complementarity c_i (red), averaged over all nodes i , and the variance in complementarity indicating the degree of spatial biodiversity patterning across the network (black) are plotted as a function of dispersal rate. As migration rates increase, the complementarity predicts a lesser fraction of total diversity loss due to greater secondary effects. Panel a) corresponds to the simple network in figure 2 (at $v=0.0001$), and b) represents the complex networks from figure 3 (random, modular, planar) across different parameter values.

Bibliography

- Agosti, D. and Alonso, L. (2000). The ALL protocol: a standard protocol for the collection of ground-dwelling ants, pp. 204-206. *Ants: standard methods for measuring and monitoring biodiversity. Smithsonian Institution Press, Washington, DC.*
- Albert, R. and Barabasi, A. (2002). Statistical mechanics of complex networks. *Reviews of modern physics*, 74(1):47–97.
- Allmon, W., Morris, P., and McKinney, M. (2001). An intermediate disturbance hypothesis of maximal speciation. *Biodiversity Dynamics: Turnover of Populations, Taxa, and Communities*, page 349.
- Alonso, D., Etienne, R. S., and McKane, A. J. (2006). The merits of neutral theory. *Trends in Ecology & Evolution*, 21(8):451–457.
- Amaral, L., Scala, A., Barthelemy, M., and Stanley, H. (2000). Classes of small-world networks. *Proceedings of the National Academy of Sciences*, 97(21):11149.
- Amarasekare, P. (2003). Competitive coexistence in spatially structured environments: a synthesis. *Ecology Letters*, 6(12):1109–1122.
- Barton, N. and Whitlock, M. (1997). The evolution of metapopulations. *Metapopulation biology. Academic Press, New York*, pages 183–214.

- Bell, G. (2000a). The distribution of abundance in neutral communities. *The American Naturalist*, 155(5):606–617.
- Bell, G. (2000b). The distribution of abundance in neutral communities. *The American Naturalist*, 155(5):606–617.
- Bierregaard, R., Lovejoy, T., Kapos, V., Dos Santos, A., and Hutchings, R. (1992). The biological dynamics of tropical rainforest fragments. *BioScience*, 42(11):859–866.
- Bodmer, W. and Cavalli-Sforza, L. (1968). A migration matrix model for the study of random genetic drift. *Genetics*, 59(4):565–592.
- Bolton, B., Alpert, G., Ward, P., and Naskrecki, P. (2006). *Boltons Catalogue of Ants of the World*.
- Brooks, C. (2003). A scalar analysis of landscape connectivity. *Oikos*, 102(2):433.
- Brown, J. H. (1995). *Macroecology*. University Of Chicago Press.
- Cabeza, M. (2003). Habitat loss and connectivity of reserve networks in probability approaches to reserve design. *Ecology Letters*, 6(7):665–672.
- Cadotte, M. (2006). Dispersal and species diversity: a meta-analysis. *The American Naturalist*, 167(6):913–924.
- Chao, A. (1984). Nonparametric estimation of the number of classes in a population. *Scandinavian Journal of Statistics*, pages 265–270.

- Chave, J. (2004). Neutral theory and community ecology. *Ecology Letters*, 7(3):241–253.
- Chave, J. and Leigh, E. (2002). A spatially explicit neutral model of β -diversity in tropical forests. *Theoretical Population Biology*, 62(2):153–168.
- Chave, J., Muller-Landau, H., and Levin, S. (2002). Comparing classical community models: theoretical consequences for patterns of diversity. *The American Naturalist*, 159(1):1–23.
- Church, S., Taylor, D., and Whitlock, M. (2002). The evolution of reproductive isolation in spatially structured populations. *Evolution*, 56(9):1859–1862.
- Clouse, R. (2007). New ants (Hymenoptera: Formicidae) from Micronesia. *Zootaxa*, 1475:1–19.
- Colwell, R. and Coddington, J. (1994). Estimating terrestrial biodiversity through extrapolation. *Philosophical Transactions: Biological Sciences*, pages 101–118.
- Colwell, R. K. and Lees, D. C. (2000). The mid-domain effect: geometric constraints on the geography of species richness. *Trends in Ecology & Evolution*, 15(2):70–76.
- Condit, R., Pitman, N., Leigh, E., Chave, J., Terborgh, J., Foster, R., Nun˜ez, P., Aguilar, S., Valencia, R., Villa, G., et al. (2002). Beta-diversity in tropical forest trees. *Science*, 295(5555):666–669.

- Cowling, R., Pressey, R., Lombard, A., Desmet, P., and Ellis, A. (1999). From representation to persistence: requirements for a sustainable system of conservation areas in the species-rich mediterranean-climate desert of southern Africa. *Diversity and Distributions*, pages 51–71.
- Cowling, R., Pressey, R., Rouget, M., and Lombard, A. (2003). A conservation plan for a global biodiversity hotspot—the Cape Floristic Region, South Africa. *Biological Conservation*, 112(1-2):191–216.
- Coyne, J. and Orr, H. (2004). *Speciation*. Sinauer Sunderland, MA.
- Dieckmann, U., O’Hara, B., and Weisser, W. (1999). The evolutionary ecology of dispersal. *Trends in Ecology & Evolution*, 14(3):88–90.
- Dirzo, R. and Raven, P. H. (2003). Global state of biodiversity and loss. *Annual Review of Environment and Resources*, 28(1).
- Dornelas, M., Connolly, S., and Hughes, T. (2006). Coral reef diversity refutes the neutral theory of biodiversity. *Nature*, 440(7080):80–82.
- Durrett, R. and Levin, S. (1996a). Spatial models for species-area curves. *Journal of Theoretical Biology*, 179(2):119–127.
- Durrett, R. and Levin, S. (1996b). Spatial models for species-area curves. *Journal of Theoretical Biology*, 179(2):119–127.
- Economo, E. and Keitt, T. (2008). Species diversity in neutral metacommunities: a network approach. *Ecology Letters*, 11(1):52–62.

- Emerson, B. and Kolm, N. (2005). Species diversity can drive speciation. *Nature*, 434(7036):1015–1017.
- Etienne, R. (2005a). A new sampling formula for neutral biodiversity. *Ecology Letters*, 8(3):253–260.
- Etienne, R. (2005b). A new sampling formula for neutral biodiversity. *Ecology Letters*, 8(3):253–260.
- Etienne, R. (2007). A neutral sampling formula for multiple samples and an exact test of neutrality. *Ecology Letters*, 10:608–618.
- Etienne, R., Alonso, D., and McKane, A. (2007a). The zero-sum assumption in neutral biodiversity theory. *Journal of Theoretical Biology*, 248(3):522–536.
- Etienne, R., Apol, M., Olff, H., and Weissing, F. (2007b). Modes of speciation and the neutral theory of biodiversity. *Oikos*, 116(2):241.
- Etienne, R. and Olff, H. (2004). A novel genealogical approach to neutral biodiversity theory. *Ecology Letters*, 7(3):170–175.
- Evenhuis, N. and Bickel, D. (2005). The NSF-Fiji terrestrial arthropod survey: overview. *Bishop Museum Occasional Papers*, 82:3–25.
- Garcia-Ramos, G. and Kirkpatrick, M. (1997). Genetic models of adaptation and gene flow in peripheral populations. *Evolution*, pages 21–28.
- Gavrilets, S. (1997). Evolution and speciation on holey adaptive landscapes. *Trends in Ecology & Evolution*, 12(8):307–312.

- Gavrilets, S. (2004). Fitness landscapes and the origin of species.
- Gavrilets, S., Acton, R., and Gravner, J. (2000). Dynamics of speciation and diversification in a metapopulation. *Evolution*, 54(5):1493–1501.
- Gillooly, J. and Allen, A. (2007). Linking global patterns in biodiversity to evolutionary dynamics using metabolic theory. *Ecology*, 88(8):1890–1894.
- Girvan, M. and Newman, M. (2002). Community structure in social and biological networks. *Proceedings of the National Academy of Sciences*, 99(12):7821.
- Hanski, I. (1999). *Metapopulation ecology*. Oxford University Press.
- Hanski, I. and Gilpin, M. (1998). Metapopulation dynamics. *Nature*, 396(6706):41–49.
- Hastings, A. and Harrison, S. (1994). Metapopulation dynamics and genetics. *Annual Review of Ecology and Systematics*, 25(1):167–188.
- He, F. (2005). Hubbells fundamental biodiversity parameter and the Simpson diversity index. *Ecology Letters*, 8:386–390.
- Hill, M. (1973). Diversity and evenness: a unifying notation and its consequences. *Ecology*, pages 427–432.
- Holt, R. D. (2002). Food webs in space: on the interplay of dynamic instability and spatial processes. *Ecological Research*, 17(2):261–273.
- Horn, H. (1966). Measurement of “overlap” in comparative ecological studies. *The American Naturalist*, 100(914):419.

- Houchmandzadeh, B. and Vallade, M. (2003). Clustering in neutral ecology. *Physical Review E*, 68(6):61912.
- Hu, X., He, F., and Hubbell, S. (2006). Neutral theory in macroecology and population genetics. *Oikos*, 113(3):548.
- Hubbell, S. (2001). *The Unified Neutral Theory of Biodiversity and Biogeography*. Princeton University Press.
- Hubbell, S. P. (2005). The neutral theory of biodiversity and biogeography and stephen jay gould. *Paleobiology*, 31(2_Suppl):122–132.
- Hubbell, S. P., He, F., Condit, R., Borda-de Agua, L., Kellner, J., and Ter Steege, H. (2008). Colloquium paper: how many tree species are there in the amazon and how many of them will go extinct? *Proceedings of the National Academy of Sciences of the United States of America*, 105 Suppl 1:11498–11504.
- Hudson, R. (1990). Gene genealogies and the coalescent process. *Oxford surveys in evolutionary biology*, 7:1–44.
- Jablonski, D. and Lutz, R. (1983). Larval ecology of marine benthic invertebrates: paleobiological implications. *Biological Reviews*, 58(1):21–89.
- Jablonski, D. and Roy, K. (2003). Geographical range and speciation in fossil and living molluscs. *Proceedings: Biological Sciences*, 270(1513):401–406.

- Johnson, M. and Gaines, M. (1990). Evolution of dispersal: theoretical models and empirical tests using birds and mammals. *Annual Review of Ecology and Systematics*, 21(1):449–480.
- Jost, L. (2006). Entropy and diversity. *Oikos*, 113(2):363.
- Keitt, T. H., Urban, D. L., and Milne, B. T. (1997). Detecting critical scales in fragmented landscapes. *Conservation Ecology*, [<http://www.consecol.org/>] 1:4 (online).
- Kimura, M. (1983). *The neutral theory of molecular evolution*. Cambridge University Press.
- Kimura, M. and Crow, J. (1964). The number of alleles that can be maintained in a finite population. *Genetics*, 49(4):725–738.
- Kingman, J. F. C. (1982). On the genealogy of large populations. *Journal of Applied Probability*, 19:27–43.
- Kirkpatrick, M. and Barton, N. (1997). Evolution of a species’ range. *The American Naturalist*, 150(1):1–23.
- Kondrashov, A. and Morgan, M. (2003). Accumulation of Dobzhansky-Muller incompatibilities within a spatially structured population. *Evolution*, 57(1):151–153.
- Lande, R. (1996). Statistics and partitioning of species diversity, and similarity among multiple communities. *Oikos*, pages 5–13.

- Laporte, V. and Charlesworth, B. (2002). Effective population size and population subdivision in demographically structured populations. *Genetics*, 162(1):501–519.
- Leibold, M., Holyoak, M., Mouquet, N., Amarasekare, P., Chase, J., Hoopes, M., Holt, R., Shurin, J., Law, R., Tilman, D., et al. (2004). The metacommunity concept: a framework for multi-scale community ecology. *Ecology Letters*, 7(7):601–613.
- Leibold, M. and McPeck, M. (2006). Coexistence of the niche and neutral perspectives in community ecology. *Ecology*, 87(6):1399–1410.
- Levin, S. (1992). The problem of pattern and scale in ecology: the Robert H. MacArthur award lecture. *Ecology*, 73(6):1943–1967.
- Loreau, M. and Mouquet, N. (1999). Immigration and the maintenance of local species diversity. *The American Naturalist*, 154(4):427–440.
- MacArthur, R. H. and Wilson, E. O. (1967). *The theory of island biogeography*. Princeton University Press, Princeton, N.J.
- Magurran, A. (2003). *Measuring biological diversity*. Wiley-Blackwell.
- Malécot, G. (1948). *Les mathématiques de l’hérédité*. Masson.
- Malécot, G. and Yermanos, D. (1970). *The mathematics of heredity*. WH Freeman San Francisco.

- Mann, W. (1919). The ants of the British Solomon Islands. *Bulletin of the Museum of Comparative Zoology*.
- Mann, W. (1921). The ants of the Fiji Islands. *Bulletin of the Museum of Comparative Zoology*.
- Margules, C. and Pressey, R. (2000). Systematic conservation planning. *Nature*, 405(6783):243–253.
- Margules, C. R. and Sarkar, S. (2007). *Systematic conservation planning*. Cambridge University Press, Cambridge.
- Mayr, E. (1942). *Systematics and the Origin of Species*. Columbia University Press, NY.
- McGill, B., Hadly, E., and Maurer, B. (2005). Community inertia of Quaternary small mammal assemblages in North America. *Proceedings of the National Academy of Sciences*, 102(46):16701–16706.
- McGill, B. J., Maurer, B. A., and Weiser, M. D. (2006). Empirical evaluation of neutral theory. *Ecology*, 87(6):1411–1423.
- McRae, B. H. (2006). Isolation by resistance. *Evolution*, 60(8):1551–1561.
- McRae, B. H., Dickson, B., Keitt, T., and Shah, V. (2008). Using circuit theory to model connectivity in ecology, evolution, and conservation. *Ecology*, 89(10):2712–2724.

- Mittelbach, G., Schemske, D., Cornell, H., Allen, A., Brown, J., Bush, M., Harrison, S., Hurlbert, A., Knowlton, N., Lessios, H., et al. (2007). Evolution and the latitudinal diversity gradient: speciation, extinction and biogeography. *Ecology Letters*, 10(4):315–331.
- Mouillot, D. and Gaston, K. (2007). Geographical range size heritability: what do neutral models with different modes of speciation predict? *Global Ecology and Biogeography*, 16(3):367–380.
- Mouquet, N. and Loreau, M. (2002). Coexistence in metacommunities: The regional similarity hypothesis. *The American Naturalist*, 159(4):420–426.
- Mouquet, N. and Loreau, M. (2003). Community patterns in source-sink metacommunities. *The American Naturalist*, 162(5):544–557.
- Muneepeerakul, R., Bertuzzo, E., Lynch, H. J., Fagan, W. F., Rinaldo, A., and Rodriguez-Iturbe, I. (2008). Neutral metacommunity models predict fish diversity patterns in mississippi-missouri basin. *Nature*, 453(7192):220–222.
- Muneepeerakul, R., Weitz, J., Levin, S., Rinaldo, A., and Rodriguez-Iturbe, I. (2007). A neutral metapopulation model of biodiversity in river networks. *Journal of Theoretical Biology*, 245(2):351–363.
- Myers, N., Mittermeier, R., Mittermeier, C., da Fonseca, G., and Kent, J. (2000). Biodiversity hotspots for conservation priorities. *Nature*, 403:853–858.

- Nagylaki, T. (1980). The strong-migration limit in geographically structured populations. *Journal of Mathematical Biology*, 9(2):101–114.
- Nagylaki, T. (1982). Geographical invariance in population genetics. *Journal of theoretical biology*, 99(1):159.
- Nagylaki, T. (2000). Geographical invariance and the strong-migration limit in subdivided populations. *Journal of Mathematical Biology*, 41(2):123–142.
- Nei, M. (1987). *Molecular evolutionary genetics*. Columbia Univ Pr.
- Newman, M. E. (2003). The structure and function of complex networks. *SIAM Review*, 45:167.
- Orr, H. (1995). The population genetics of speciation: the evolution of hybrid incompatibilities. *Genetics*, 139(4):1805–1813.
- Orr, H. and Orr, L. (1996). Waiting for speciation: the effect of population subdivision on the time to speciation. *Evolution*, pages 1742–1749.
- Panhuis, T., Butlin, R., Zuk, M., and Tregenza, T. (2001). Sexual selection and speciation. *Trends in Ecology & Evolution*, 16(7):364–371.
- Pimm, S., Russell, G., Gittleman, J., and Brooks, T. (1995). The future of biodiversity. *Science*, 269(5222):347–350.
- Possingham, H., Ball, I., and Andelman, S. (2000). Mathematical methods for identifying representative reserve networks. *Quantitative methods for conservation biology*. Springer-Verlag, New York, pages 291–305.

- Rangel, T. and Diniz-Filho, J. (2005). Neutral community dynamics, the mid-domain effect and spatial patterns in species richness. *Ecology Letters*, 8(8):783–790.
- Ricklefs, R. (1987). Community diversity: relative roles of local and regional processes. *Science*, 235(4785):167.
- Rosenzweig, M. (1995). *Species Diversity in Space and Time*. Cambridge University Press.
- Rosenzweig, M. (2001). Loss of speciation rate will impoverish future diversity. *Proceedings of the National Academy of Sciences*, 98(10):5404–5410.
- Rosindell, J. and 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., and Etienne, R. (2008). A coalescence approach to spatial neutral ecology. *Ecological Informatics*, 3(3):259–271.
- Sarkar, S., Pressey, R., Faith, D., Margules, C., Fuller, T., Stoms, D., Mof-fett, A., Wilson, K., Williams, K., Williams, P., et al. (2006). Biodiversity conservation planning tools: Present status and challenges for the future. *Annual Review of Environment and Resources*, 31:123.
- Sarnat, E. (2006). Lordomyrma (Hymenoptera: Formicidae) of the Fiji Islands. *Bishop Museum Occasional Papers*, 90:9–42.

- Sarnat, E. (2008). A taxonomic revision of the pheidole roosevelti-group (hymenoptera: Formicidae) in fiji. *Zootaxa*, 1767:1–36.
- Schluter, D. (2000). *The ecology of adaptive radiation*. Oxford University Press, USA.
- Scott, J. (2000). *Social network analysis: A handbook*. Sage.
- Shattuck, S. (2008). Revision of the ant genus *prionopelta* (hymenotpera: Formicidae) in the indo-pacific region. *Zootaxa*, 1846:21–34.
- Shattuck, S. and Barnett, N. (2000). *Australian ants: their biology and identification*. Csiro.
- Simpson, E. (1949). Measurement of diversity. *Nature*, 163(4148):688.
- Spector, S. (2002). Biogeographic crossroads as priority areas for biodiversity conservation. *Conservation Biology*, 16(6):1480–1487.
- Strogatz, S. (2001). Exploring complex networks. *Nature*, 410(6825):268–276.
- Taylor, P., Fahrig, L., Henein, K., and Merriam, G. (1993). Connectivity is a vital element of landscape structure. *Oikos*, pages 571–573.
- Thomas, C., Cameron, A., Green, R., Bakkenes, M., Beaumont, L., Collingham, Y., Erasmus, B., de Siqueira, M., Grainger, A., Hannah, L., et al. (2004). Extinction risk from climate change. *Nature*, 427(6970):145–148.
- Tilman, D., May, R. M., Lehman, C. L., and Nowak, M. A. (1994). Habitat destruction and the extinction debt. *Nature*, 371(6492):65–66.

- Urban, D. and Keitt, T. (2001). Landscape connectivity: A graph-theoretic perspective. *Ecology*, 82(5):1205–1218.
- Urban, D., Minor, E., Treml, E., and Schick, R. (2009). Graph models of habitat mosaics. *Ecology Letters*, 12(3):260–273.
- Vermeij, G. (1987). *Evolution and escalation*. Princeton University Press Princeton.
- Vitousek, P. M., Mooney, H. A., Lubchenco, J., and Melillo, J. M. (1997). Human domination of earth’s ecosystems. *Science*, 277(5325):494–499.
- Volkov, I., Banavar, J., He, F., Hubbell, S., and Maritan, A. (2005). Density dependence explains tree species abundance and diversity in tropical forests. *Nature*, 438(7068):658–661.
- Ward, D. and Wetterer, J. (2006). Checklist of the ants of Fiji (Hymenoptera: Formicidae). *Bishop Museum Occasional Papers*, 85:23–47.
- Wasserman, S. and Faust, K. (1994). *Social network analysis: Methods and applications*. Cambridge University Press.
- Watts, D. and Strogatz, S. (2006). Collective dynamics of small-world networks. *The Structure and Dynamics of Networks*, page 301.
- Wheeler, W. (1934). Some aberrant species of *Camponotus* (Colobopsis) from the Fiji Islands. *Annals of the Entomological Society of America*, 27(3):415–424.

- Wheeler, W. (1935). Check list of the ants of Oceania. *Occasional Papers*.
- Whitlock, M. and McCauley, D. (1999). Indirect measures of gene flow and migration: $F_{ST} \neq 1/(4Nm + 1)$. *Heredity*, 82(2):117–125.
- Whittaker, R. (1972). Evolution and measurement of species diversity. *Taxon*, pages 213–251.
- Whittaker, R., Araujo, M., Paul, J., Ladle, R., Watson, J., and Willis, K. (2005). Conservation Biogeography: assessment and prospect. *Diversity & Distributions*, 11(1):3–23.
- Wiens, J. (2004). What is speciation and how should we study it? *The American Naturalist*, 163(6):914–923.
- Wilkins, J. and Wakeley, J. (2002). The coalescent in a continuous, finite, linear population. *Genetics*, 161(2):873–888.
- Wilkinson-Herbots, H. (1998). Genealogy and subpopulation differentiation under various models of population structure. *Journal of Mathematical Biology*, 37(6):535–585.
- Wilson, E. (1959a). Adaptive shift and dispersal in a tropical ant fauna. *Evolution*, pages 122–144.
- Wilson, E. (1959b). Studies on the ant fauna of melanesia 5. the tribe cera-pachyini. *Pacific Insects*, 1:39–57.

- Wilson, E. (1961). The nature of the taxon cycle in the Melanesian ant fauna. *American Naturalist*, pages 169–193.
- Wilson, E. (2003). *Pheidole in the New World: a dominant, hyperdiverse ant genus*. Harvard Univ Pr.
- Wilson, E. and Taylor, R. (1967). The ants of Polynesia. *Pacific insects monograph*, 14:1–109.
- Wilson, K. A., McBride, M. F., Bode, M., and Possingham, H. P. (2006). Prioritizing global conservation efforts. *Nature*, 440:337–340.
- Wilson, K. A., Underwood, E. C., Morrison, S. A., Klausmeyer, K. R., Murdoch, W. W., Reyers, B., Wardell-Johnson, G., Marquet, P. A., Rundel, P. W., McBride, M. F., Pressey, R. L., Bode, M., Hoekstra, J. M., Andelman, S., Looker, M., Rondinini, C., Kareiva, P., Shaw, M. R., and Possingham, H. P. (2007). Conserving biodiversity efficiently: what to do, where, and when. *PLoS Biology*, 5.
- Zillio, T., Volkov, I., Banavar, J., Hubbell, S., and Maritan, A. (2005). Spatial scaling in model plant communities. *Physical review letters*, 95(9):98101.

Vita

Evan Philip Economo was born in Montreal, Canada on October 29, 1980 to Helena Economo and George Economo. He grew up in Danville, Virginia and Chapel Hill, North Carolina before moving to Arizona to attend the University of Arizona. He received his Bachelor of Science degree in Ecology and Evolutionary Biology in 2002 where he conducted undergraduate research on a variety of topics including bone cell growth, antbird ecology in Ecuador, and metabolic scaling theory. He then spent a year working as a research technician in the lab of Brian J. Enquist before entering graduate school at the University of Texas at Austin in the fall of 2003.

Permanent address: 1 University Station A6700
Austin, Texas 78712

This dissertation was typeset with L^AT_EX[†] by the author.

[†]L^AT_EX is a document preparation system developed by Leslie Lamport as a special version of Donald Knuth's T_EX Program.