IDENTIFYING EXTINCTION RISK PATTERNS IN POLLINATION NETWORKS
AND
CONSERVATION PLANNING TO REDUCE THE COST OF MANAGEMENT-NECESSITATED TRAVEL

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ABSTRACT

Extinction rates are currently far above background levels, as a result of human activity. Although conservation spending is substantial, there is a shortfall between the cost of meeting biodiversity targets and the resources available to do so. Consequently, decision-makers are faced with the task of identifying which taxonomic groups and geographical regions are of greatest concern, and prioritizing approaches with the greatest conservation benefit. In this dissertation, I develop novel approaches in both of these areas.

First, I take a stochastic, community dynamic approach to modeling extinction risk patterns in pollination networks. Despite the ecological and agricultural importance of pollination and the expectation that environmental variability will increase under climate change, stochasticity is an under-studied driver of extinction risk in the mutualist modeling literature. Here, I demonstrate that extinction risk in a simplified network increases with environmental variability, and that this increase is more rapid for specialists than for generalists. I then examine this pattern over a range of realistic network sizes and structures, using interaction data from 35 empirical networks. Across all networks, extinction risk declines with increasing number of mutualist partners for poorly-connected species, and approaches an asymptote for well-connected species. I use a nonlinear mixed regression to describe how network connectance and nestedness change the relationship between specialization and extinction risk. Highly connected and nested networks showed a significantly steeper decline in extinction risk with increasing partner number, as well as lower extinction risk for the most specialized species.

Second, I develop a method to reduce the operating costs that conservation organizations incur as a consequence of undertaking management activity. Land protection decision-making is well studied, but the question of where to base conservation staff is not. Office locations, however, affect the cost of management-necessitated travel. Here, I estimate the annual over-road travel cost incurred by the management activity of two organizations, both under their current office configurations and configurations that minimize total travel distance. In each case, the reduction in travel cost from either adding an office or reconfiguring current locations is sufficient to protect 171-360 Ha or employ an additional management officer.

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INTRODUCTION

Overview

Human activity has precipitated a biodiversity crisis. Anthropogenic changes in land use are driving habitat loss on a global scale (Newbold *et al*. 2016); human movement and trade introduces predators, competitors and pathogens into new ranges; the introduction of chemical pollutants affects organisms' longevity and reproduction; overexploitation reduces population sizes; and anthropogenic climate change is expected to increase thermal stress and drought (Groom 2005). These threats to biodiversity not only co-occur; there is evidence that they have a synergistic effect on extinction risk (Brook *et al*. 2008). Current extinction rates are estimated to exceed background levels by two orders of magnitude (Dirzo & Raven 2003, Barnosky *et al*. 2011, Ceballos *et al*. 2016), provoking concerns that biodiversity loss may be reaching mass-extinction levels (Barnosky *et al*. 2011, Ceballos *et al*. 2016).

Conservation science and practice seek to prevent the loss of biodiversity. The designation and management of land in the form of protected areas is a dominant conservation strategy (Groves 2003, Cullen 2013), but other approaches include *ex situ* conservation (Kareiva & Marvier 2011) and legislation intended to limit pollution (Stern 1982, Murchison 2005) and overexploitation (Cohen 1995). Each of these actions is costly, and it is widely recognized that resources are often severely limited. For example,the cost of down-listing all globally threatened bird species by a single IUCN threat level is estimated to be US $0.875-1.23 billion annually, but spending is at about 12% of this level; expanding these estimates to include other taxa results in an annual price tag of US $3.41-4.67 billion (McCarthy *et al*. 2012).

Given the mismatch between the scope of the biodiversity crisis and the amount of resources devoted to conservation, it is of paramount importance that conservation scientists and practitioners (a) understand the causes and consequences of population declines, (b) predict where intervention will be necessary and useful before population declines become irreversible, and (c) allocate what limited resources are available to support conservation strategically.

In this dissertation, I identify and address two areas that are unexplored in the literature, and that have the potential to influence conservation decision making. Two chapters focus on understanding unexplored causes and consequences of

species declines and pay particular attention to the relative vulnerability of different groups of species. The third chapter then scales up to focus on habitat conservation efforts broadly and asks how we can target our interventions in more strategically in the face of limited conservation resources.

In the area of understanding and predicting extinctions, the importance of modeling community interaction structure, population dynamics, and stochasticity has been demonstrated (Proulx *et al*. 2005, Simberloff 1998). Despite the ecological and economic importance of pollination, these considerations have not been applied in a unified way to the understanding of extinction risk in mutualist communities. In Chapters 1 and 2, I extend this field to include extinction risk models that take population dynamics and environmental variability into account in a plant-pollinator context. I pay particular attention to the relative vulnerability of specialists and generalists.

In the area of conservation prioritization and strategy, there is a large body of literature dedicated to developing methods to improve the conservation value of cost-constrained decisions. Much of this work focuses on choosing which areas to protect or which management strategy to implement (Cullen 2013). Organizations that manage land, however, incur travel costs each time that staff is sent to work at a protected area. In Chapter 3, I show how conservation organizations can reduce the cost of management-necessitated travel by making strategic choices about the locations of the offices where management staff are based, a previously unaddressed avenue for reducing the conservation costs.

These two topics clearly approach conservation from very different perspectives. Although one focuses on understanding patterns of species-level extinction risk and the other seeks to reduce the operating costs associated with protected area management, each represents what I see as an important frontier topic in current writings on biodiversity loss and how it can be prevented.

Part 1: Stochasticity and network structure affect extinction risk in plant-pollinator systems

In the first part of this dissertation (Chapters 1 and 2), I develop a mathematical model to explore the relationship between the structure of mutualist networks and environmental variability in plant-pollinator communities. This model takes a stochastic, population-dynamic approach that draws together threads from the single-species, food web, and human demography literatures, and applies them to questions about extinction risk in plant-pollinator communities.

Mutualist interactions are crucial to the functioning of ecological communities and to human well-being. The persistence of terrestrial food webs is facilitated by the pollination mutualism, which almost 90% of flowering plants rely on at least in part for reproduction (Ollerton *et al*. 2011). Pollination also increases the yield of 70% of food and commodity crops (Klein *et al*. 2007), many of which are major sources of micronutrients for human populations (Eilers *et al*. 2011). The annual value of pollination services by wild bees in the United States alone is estimated to exceed $3 billion (Losey & Vaughan 2006).

Consequently, pollinator declines constitute a major conservation concern. Wild pollinator declines have been documented in Europe (Biesmeijer *et al*. 2006), and North America (Grixti *et al*. 2008, Burkle *et al*. 2013), where the United States recently designated seven bee species as endangered and has proposed the listing of an eighth (Endangered and threatened wildlife and plants, 2016a,b). Global population trends are less well documented, but patterns in land use change suggest that wild pollinator declines may be widespread (Potts *et al*. 2010).

Because extinction is an outcome of population dynamic processes influenced by species interactions and environmental variability, declines in abundance are associated with elevated risk of extinction. Extinction modeling in plant-pollinator and other mutualist systems is an active area of research, with methods ranging from the use of topological network models (e.g. Dunne *et al*. 2002, Memmott *et al*. 2004, Pocock *et al*. 2012) to those with colonization/extinction (Fortuna & Bascompte 2006) and population (Abramson *et al.* 2011, Bewick *et al.* 2013) dynamics. In topological studies, researchers compare the robustness of a network to different series of species knockouts (e.g. most-to-least connected, random), where each imposed extinction is followed by the loss of all species that rely on the one removed by the knockout. This approach assumes that the presence of a species is sufficient to sustain its mutualists (or other interaction partners that benefit from it), regardless of its abundance.

Population-dynamic models in the trophic literature, however, show that ignoring abundance leads to an underestimate of extinction risk (Curtsdotter *et al*. 2011, Säterberg *et al*. 2013) in trophic networks. This is also the case for extinction risk in plant-pollinator systems, because pollination visits (which provide energy and nutrients to pollinators, and reproductive opportunities to plants) depend on the abundances of the species involved. Simultaneous population declines in plants and their pollinators were documented by Biesmeijer *et al*. (2006), who noted that declines in abundance occurred in animal-pollinated but not wind-pollinated taxa.

Stochasticity is also underrepresented in the mutualist modeling literature (but see Vieira & Almeida-Nieto 2015). Numerous theoretical studies have addressed the influence of stochasticity on the dynamics of single populations (Coulson & Godfray 2007), and this line of inquiry is still active (e.g. Cairns 2009, Klokov 2009) - especially with respect to the autocorrelation structure of environmental noise (Ovaskainen & Meerson 2010). Stochastic dynamics have also been of great interest in the competition literature (Ives & Hughes 2002). From an extinction risk perspective, stochasticity is an important consideration because natural systems are temporally variable, and because it has been shown to reduce persistence times in certain single-species models (Simberloff 1998).

Birth-death models with compensatory density dependent growth and an absorbing extinction extinction boundary do not require *a priori* assumptions about which species is the most vulnerable to extinction. Since these features give rise to dynamics that often tend toward extinction in finite time, such models need not rely on researcher-imposed knockouts, the typical approach in static network studies (e.g. Memmott *et al*. 2004). Rather, in models of this type, primary extinctions arise as a consequence of the system's dynamics. An advantage to applying stochasticity to a population dynamic model rather than a topological one is that the biological relevance of different entry points of stochasticity is readily apparent (Ives & Hughes 2002, Ferguson & Ponciano 2015).

In Chapters 1 and 2, I examine the combined influence of mutualist interactions and environmental variability on extinction risk in plant-pollinator systems. To do so, I develop a model with stochastic community dynamics and a novel approach to representing the effect of mutualist interactions on population growth that incorporates the concept of the birth function (also called the marriage function) from the human demography literature. In human demography, the birth function estimates the size of the next generation by taking into account the abundance of both sexes (Caswell & Weeks 1986). Here, I analogize each species as one 'sex' and its mutualists as the other. In this model, I use a birth function based on the harmonic mean, which has a single, stable, coexistence equilibrium and saturating *per capita* reproductive output.

In Chapter 1, I ask whether environmental variability elevates extinction risk equally across species with different specialization strategies. Prior empirical work looking across specialization strategies generally (McKinney 1997, Brodie *et al*. 2014) and in plant-pollinator systems in particular (Biesmeijer *et al*. 2006, Abramson *et al*. 2011), has also shown that specialists are more likely to decline than generalists (but see Colles *et al*. 2009 for a discussion of how specialization type and scale of study affect this trend).

In this chapter, I apply the model first to a two-species network, as this is the simplest case that can capture species interactions. I then move to four species, the smallest network that can include specialists and generalists of both plants and pollinators. Lastly, I apply the model to two networks from the empirical literature, with >20 species each. Using analytical and numerical methods, I find the equilibria of the two-species system and analyze the stability of each. I then show how the region of parameter space with nonzero extinction risk grows to encompass lower levels of deterministic mortality, as environmental variability increases. I also use numerical methods to simulate population trajectories in the four-species and empirical networks. Results from the four-species model show that all species' extinction risk increases with increasing environmental variability, but the vulnerability of the specialist increases more rapidly than that of the generalist. Simulations of the empirical networks demonstrate that a species' extinction risk is inversely related to its number of mutualist partners. These results suggest that deterministic models underestimate extinction risk in mutualist networks. This result is not uniform across species-- rather, deterministic models underestimate the vulnerability of specialists disproportionately relative to that of generalists.

In Chapter 2, I further examine how the relationship between specialization and extinction risk in stochastic mutualist systems is influenced by the structure of interaction networks. In particular, I focus on connectance and nestedness, which have been shown to affect community-level stability (Okuyama & Holland 2007, Thébault & Fontaine 2010). To do so, I estimate extinction risk across 35 empirical plant-pollinator networks using the stochastic community dynamic model described in Chapter 1. I then use a nonlinear mixed regression to estimate the effects of connectance and nestedness on the relationship between specialization and extinction risk. While all networks followed a pattern of declining extinction risk with number of mutualist partners for poorly connected species and saturating extinction risk for well-connected species, network structure had a significant effect on the shape of this relationship. Species with a single mutualist partner were less prone to extinction, and extinction risk declined more rapidly with partner number, in highly connected and nested networks.

Part 2: Locating human resources to reduce the travel cost of managing networks of protected areas

The second part of this dissertation focuses on a different type of network with importance to conservation-- that of roads. Over-road travel is a costly reality for conservation organizations that engage in protected area management. In

Chapter 3, I demonstrate how the cost of management-necessitated travel can be reduced.

While much has been written about techniques to maximize biodiversity representation in land protection decisions (Ando *et al*. 1998, Myers *et al*. 2000, Groves 2003, Costello & Polasky 2004, Murdoch *et al*. 2007, Cullen 2013), the type and timing of management action (Murdoch *et al*. 2007, Wilson *et al*. 2007), and return on investment (Murdoch *et al*. 2007, Underwood *et al*. 2008), existing literature has largely ignored conservation organizations' other operating costs. Like other for- and non-profit businesses, conservation organizations require equipment, staff and office space. Moreover, the business model of many conservation organizations requires regular travel by staff to protected areas for management and monitoring purposes. Such travel incurs expenses in the form of staff time and vehicle costs, thereby reducing the amount of the budget available for land acquisition and management activity.

In Chapter 3, I ask how the location of the offices where conservation staff are based affects the cost of management-necessitated travel. Using data from protected area networks in the United States and United Kingdom, I find locations that minimize annual over-road travel to each network's protected areas, given the amount of time that management staff spend at each protected area. I then estimate the annual and net present value cost of management-necessitated travel for the existing and travel-minimizing office configurations, both in monetary terms and in terms of carbon output. I also calculate the reduction in travel cost that would follow if each organization opened a new office. In both cases, either adding an office or reconfiguring the locations of existing offices reduces travel costs by an amount similar to that of a management officer's salary. Although travel cost is not the largest expense that conservation organizations face, this analysis can show whether it is more cost efficient to add or move an office, and can reveal the hidden travel costs of office closure.

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CHAPTER 1
SPECIALIZED MUTUALISTS ARE DISPROPORTIONATELY VULNERABLE TO STOCHASTIC EXTINCTION

Abstract

Pollination underpins terrestrial food webs and agricultural systems. This mutualism links the persistence of interacting plant and pollinator populations, propagating the population dynamic consequences of environmental variability across species. Models that exclude stochasticity underestimate extinction risk, but it is unknown whether including stochasticity increases extinction risk estimates uniformly across a community. In this paper, I use a stochastic community dynamic model to (a) link environmental variability and deterministic mortality to extinction risk in a 2-species system, and (b) compare extinction risk between specialists and generalists in a 4-species system and two empirical networks with > 20 species each. I show that increasing the variance of the stochasticity increases the size of the region of parameter space where extinctions occur. I also demonstrate that, at a given variance, extinction risk is greater for specialists than it is for generalists. This relationship holds in the simplified 4-species system as well as in the more realistic networks. My results demonstrate the importance of considering both species interactions and stochasticity when modeling extinction risk in plant-pollinator communities. Models that omit either of these factors are likely to underestimate extinction risk, particularly that of specialists.

Introduction

The loss of pollinators is an issue of pressing ecological and economic importance. About 88% of flowering plants depend upon animals for pollination services (Ollerton *et al.* 2011). The continued persistence of plant populations sustains terrestrial food webs and agricultural systems. Animal pollination increases the annual production of 70% of food crops and commodities globally (Klein *et al.* 2007), with insect pollination valued at €153 billion, or about 10% of the global value of global agricultural production for human consumption in 2005. (Gallai *et al.* 2009). Additionally, animal-pollinated crops are a major source of micronutrients for human populations (Eilers *et al*. 2011).

There is growing evidence of population decline in animal pollinators, particularly bees, both native and introduced. Decreases in the abundance of native bees have been documented in Europe (Biesmeijer *et al*. 2006) and North America (Grixti *et al.* 2008, Burkle *et al.* 2013, Koh *et al*. 2016), and global patterns of land use change suggest more widespread declines (Potts *et al.* 2010). Additionally, Biesmeijer *et al.* (2006) found that plant populations relying on insect pollination

declined in parallel with their pollinators (whereas wind-pollinated plants did not). Such declines have the potential to propagate risk to other species that interact with these plants.

Plants that specialize on a declining pollinator may be more strongly affected than those that rely on a suite of pollinator species. Prior work looking across specialization strategies generally (McKinney 1997, Brodie *et al*. 2014) and in plant-pollinator systems in particular (Biesmeijer *et al*. 2006, Abramson *et al*. 2011), has also shown that specialists are more likely to decline than generalists (but see Colles *et al*. 2009 for a discussion of how specialization type and scale of study affect this trend).

There is a growing body of work modeling extinctions in plant-pollinator and other mutualist systems. These studies range from static topological network models (Memmott *et al.* 2004, Pocock *et al.* 2012) and topological models with interaction switching (Kaiser-Bunbury *et al.* 2010), to those with patch (Fortuna & Bascompte 2006) and population (Abramson *et al.* 2011, Bewick *et al.* 2013) dynamics. Primary extinctions are typically imposed as a series of knockouts, but sometimes arise from environmental drivers (e.g. Fortuna & Bascompte 2006). Previous work in trophic networks has demonstrated that static interaction-based models underestimate extinction risk relative to population dynamic models (Curtsdotter *et al.* 2011).

A further consideration missing in almost all of these models is stochasticity (but see Vieira & Almeida-Nieto 2015). Variability is ubiquitous in natural systems, and has been shown to increase extinction risk in many single-species models that include it (Simberloff 1998). Unlike topological models and those with deterministic dynamics, not all stochastic models need to rely on researcher-imposed knockouts to initiate extinction sequences. In population dynamic models that incorporate mortality, compensatory density-dependent growth and an absorbing extinction boundary, primary extinctions can arise as a consequence of the system's dynamics. In addition to their greater realism in this sense, population dynamic models offer a number of biologically relevant entry points for incorporating stochasticity (Ives & Hughes 2002, Ferguson & Ponciano 2015).

In this paper, I explore how extinction risk in a plant-pollinator model changes when stochasticity in the form of environmental variability is incorporated into community and population dynamics. To do so, I use a discrete time modified community dynamic model with stochasticity applied at each time step. I borrow the notion of the 'birth function' from human demographics as a way to specify different relationships between each species' reproductive output, and its

abundance and that of its mutualists, and show that a birth function based on the harmonic mean increases biological realism and simplifies model dynamics. Using this model, I first explore the relationship between the variance of environmental stochasticity and the size of the region of parameter space where extinctions occur. I then investigate whether environmental stochasticity differentially affects the extinction risk of species in the system, in particular whether specialists' risk increases more than that of generalists.

Methods

The Model

I use a discrete time population model (Equation 1.1) that explicitly considers birth rate, *per capita* mortality, density dependent limits on growth, and environmental variability. I choose the nomenclature of the state variables to loosely represent flowers (*F*) and bees (*B*), while recognizing that many plants produce more than one flower and that many pollinators are not bees (e.g. see Rader *et al*. 2016). The model comprises a system of equations describing plant and pollinator species:

$$F_{i_{t+1}} = F_{i_t} + R_i\left(F_{i_t}, B_t, c_{F_i}, \varphi_{ij}\right)\left(\frac{\kappa_{F_i} - F_{i_t}}{\kappa_{F_i}}\right) - \mu_{F_i} F_{i_t} + \varepsilon_{F_{i_t}} \qquad (1.1a)$$

$$B_{j_{t+1}} = B_{j_t} + R_{B_j}\left(B_{j_t}, F_t, c_{B_j}, \varphi_{ji}\right)\left(\frac{\kappa_{B_j} - B_{j_t}}{\kappa_{B_j}}\right) - \mu_{B_j} B_{j_t} + \varepsilon_{B_{j_t}} \qquad (1.1b)$$

where $F_i(t)$ represents the population size of plant species *i* at time step *t*, and $B_j(t)$ represents pollinator species *j* at time *t.* This system of equations can model an arbitrary number *n* of plant species and *m* of pollinator species, such that $1 \leq i \leq n$ and $1 \leq j \leq m$. The model is written in discrete time, a choice that is well-suited to plant-pollinator systems on an interannual scale, because plants in most environments do not flower continuously (Fenner 1998). I separate the reproductive and mortality components of population growth into different terms because birth rates for all species depend upon the pollination mutualism, whereas mortality rates do not. In this model, I assume that plants reproduce only through seed.

The second term on the right hand side of each equation represents a birth function *R*, that defines each species' reproductive capacity in time step *t* as a function of its own density and that of its mutualists. Below, I expand upon the

choice of a birth function (Equation 1.2) that allows for increasing population growth with available mutualists, with *per capita* saturation in birth rates and a single, stable, coexistence equilibrium. This birth function is multiplied by a density dependence term with carrying capacity κ, to reflect additional constraints (e.g. unshaded spots for plants or pollinator nesting sites) that prevent population sizes from diverging to infinity. The second term on the right hand side of equations 1.1a and 1.1b describes the number of deaths per time step, which in this case is a constant rate that depends both on population size and a mortality rate μ.

The last term, ε, is a value drawn at each time step from a normal distribution centered at zero. I chose to use the normal distribution because it is simple, well-understood, and has properties that do not bias extinction trajectories, on average. First, its mean and variance are independent, making it possible to compare the effects of different levels of variability, while holding the mean effect of stochasticity constant. Secondly, it is symmetric, meaning that values above and below zero are equally likely to be drawn at any time step (Were this not the case, population trajectories would move in a biased way toward or away from extinction).

When a value of ε is drawn that results in a negative population size, the population is considered extinct and its size set to zero from that time step forward. While ε changes the population size directly (e.g. similar to a stochastic immigration/emigration rate), other entry points of stochasticity (and hence scalings) are possible (Ives & Hughes 2002, Ferguson & Ponciano 2015). I explore the introduction of stochasticity on the mortality rate (a *per capita* effect) rather than on absolute population size in Appendix 1.

The choice of birth function R affects the population dynamics in the model. Calculating reproductive rates by multiplying species' abundances, as is commonly done in mutualist Lotka-Volterra models (e.g. May 1981, Bronstein *et al.* 2004, Bascompte *et al.* 2006, Bewick *et al*. 2013), results in a system with two coexistence equilibria and non-saturating *per capita* reproduction (Figure 1.1A), which is biologically unrealistic (DeAngelis & Holland 2006). In real populations, individual reproduction is limited not only by potential mates and mutualist abundance, but also physiological constraints. Individual plants, for example, cannot produce an unlimited number of seeds. Birth functions based on the harmonic mean capture this biological limitation (Figure 1.1B).

For the present study, I use a birth function based on the harmonic mean of the abundance of each focal species and the abundances of its mutualists. The use of the harmonic mean is well-established in human demographic work,

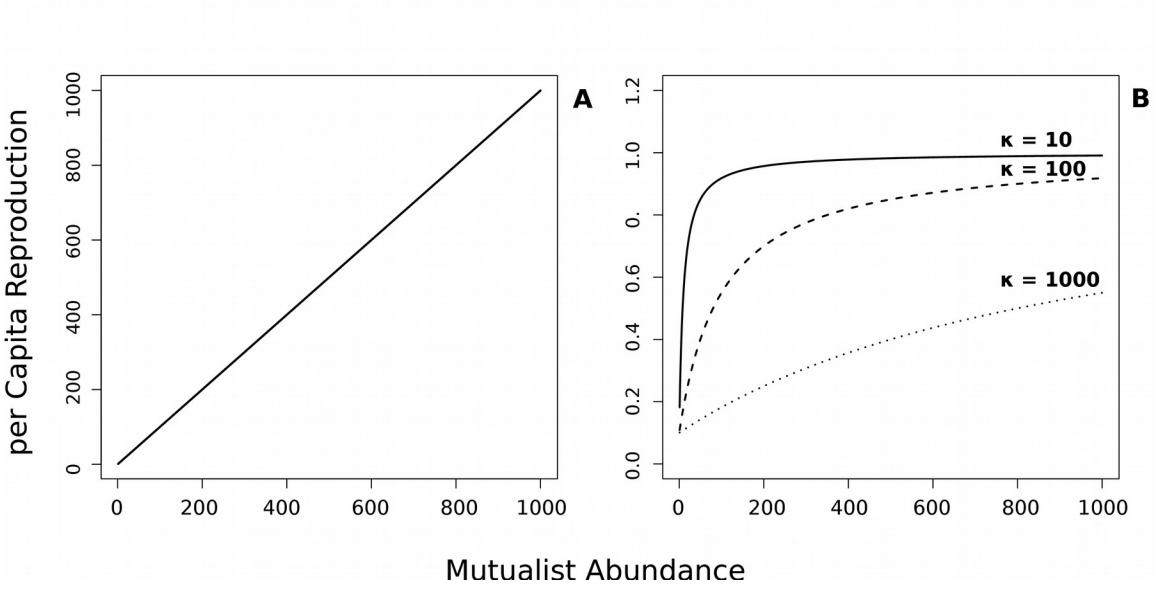


Figure 1.1. *Per capita* reproductive output increases linearly with mutualist abundance when the birth function is a product of species abundances, regardless of carrying capacity (A). For a birth function based on the harmonic mean (B), *per capita* reproductive output saturates with increasing mutualist abundance and decreases with carrying capacity *κ*.

particularly when two-sex models are needed to describe reproductive output (Caswell & Weeks 1986). For the purpose of illustrating the reproductive component of the model, I describe a two-species version of the model (Equation 2a) before generalizing to a case with *n* plant and *m* pollinator species:

$$R_F = c_F \frac{\varphi_{FB} F B}{F + \varphi_{FB} B} \quad (1.2a)$$

where R_F describes the reproductive output of the plant. The birth function for the pollinator (not shown) is analogous. The conversion factor c_F defines the number of seeds produced per floral visit. The interaction strength φ_{FB} determines how strongly the mutualist *B* affects the growth of the focal population *F*.

This birth function is simply half of the harmonic mean of the size of the plant population and its mutualists, scaled by their interactions with the plants. In this case, plant reproduction can be generalized to a community of *n* plant species and *m* pollinator species as follows (Equation 1.2b):

$$R_{F_i} = c_{F_i} \frac{F_{it} \sum_{j=1}^{m} \varphi_{ij} B_{j_t}}{F_{it} + \sum_{j=1}^{m} \varphi_{ij} B_{j_t}} \quad (1.2b)$$

where $1 \leq i \leq n$ and $1 \leq j \leq m$. I represent the reproductive success of pollinators similarly, i.e. assuming a saturating benefit with plant density. In the two-species case, each species is analogous to one 'sex'. The multi-species model accommodates sparse interactions by generalizing the birth function such that the focal species is the analogue of one 'sex', and all of its potential mutualists are aggregated to represent the other.

Analyses

In order to capture the different aspects ways that stochasticity affects extinction outcomes, I ran the model with two species, four species, and with empirical networks (>20 species) taken from the literature. In order to isolate the effect of species interactions, particularly specialization, I hold all parameters except φ constant across all systems and species. For the purposes of this paper, I use κ = 1000, μ = 0.1, and c = 1. When modeling a single plant and pollinator, I assume that and $\varphi_{FB} = \varphi_{BF} = 1$. In the 4-species scenario, I use a nested interaction network such that each specialist depends upon a generalist partner. For the case study model, I parameterize the interaction structure with empirically

estimated values that describe the dependence of each species on each of its mutualists (Olesen *et al*. 2002, Aizen *et al*. 2008).

All numerical analyses and simulations are carried out in MATLAB 2014b. To estimate the extinction risk of the modeled species, I ran 10,000 (2 species), 10,000 (4 species), or 100,000 (case study) replicates of 1000 time steps each, and refer to the proportion of replicates where a species is lost as the extinction risk for that species. Since populations in the deterministic replicates reach equilibrium within 21 time steps under the default parameter set, extinction assessments at t=1000 are unlikely to reflect transient dynamics, even when environmental variability is relatively high.

Extinction risk as I define it here depends both upon the variance of the stochastic parameter ε, and on the length of the replicate. Another possible approach to quantifying the effect of environmental variability on persistence of the species in the modeled communities would be to estimate their extinction times. This, however, would require much longer replicates (and a concomitant increase in computational time), especially in cases with low variance.

A related way of thinking about dynamics in extinction-prone system is to estimate the quasi-stationary distribution of population sizes. This is a time-independent distribution of population sizes, conditional on the population's persistence to time t. The focus of this paper is the relative extinction risk between interacting species rather than on the characteristics of persisting populations; however, I describe the size distributions of extant populations for the 4-species model in Appendix 1.

The 2-Species Model

First, I examine the stability of the two-species model, and explore environmental stochasticity affects the size of the region in parameter space where extinctions occur. Although more species-rich versions could also be used to address the same question, the 2-species model is the simplest model that incorporates mutualism, and it has the advantage of producing results that are straightforward to interpret visually

I use analytical methods to find the equilibria of this model and characterize their stability with respect to the plant mortality parameter μ_F. This deterministic approach provides a baseline of parameter values that allow for persistence or extinction of one or more species, that I compare against the results of the full (stochasticity inclusive) model.

The 4-Species Model

Secondly, I use the two larger models to explore how specialization of the pollination interaction interacts with stochasticity to influence species' extinction risk. The simplest model that can address this question is a two-plant, two-pollinator model, with a specialist and a generalist of each. I find the equilibria of the 4-species system numerically by running the model deterministically, and test whether the system converges on these equilibria for the default parameters (listed above).

I then assess extinction risk over a range of variances and compare between (a) the plant specialist and generalist; (b) the pollinator specialist and generalist; (c) the plant and pollinator generalists; and (d) the plant and pollinator specialists. Because species outcomes are nonindependent due to the model's interaction structure and population dynamics, I compare between-species extinction risk using a McNemar test (McNemar 1947). I use the Bonferroni-Holm method to correct the significance levels for these five comparisons.

Case Study Models

Third, I explore the relationship between specialization and stochastically-driven extinction risk using empirically derived interaction data. I parameterize the model with interaction data from two plant-pollinator networks collected by Olesen *et al*. (2002) on the islands of Flores, Azores and Ille aux Aigrettes, Mauritius. I choose these networks because they are relatively small (22 and 27 species were recorded on Flores and Ille aux Aigrettes, respectively), contain a range of interactions spanning from specialist to super-generalist, and were sampled using similar protocols. Interaction strength between a species and its mutualist is characterized as dependence (Aizen *et al*. 2008), i.e. the proportion of interactions between the species and its mutualist, out of the entirety of that species' interactions. Because I am interested in relative extinction risk, I parameterize the rest of the case study models with the same default parameter set as in the 2-species and 4-species models.

I compare extinction outcomes between systems with a stochastic variance of σ^2_ε=20,000, where the extinction risk of the most and least specialized species diverges substantially in both systems. Species extinction risk calculations are done as before, this time using 100,000 replicates of the model. In order to determine whether these results are in agreement with those of the simpler model, I find the slope of a least-squares linear fit between the number of mutualist partners and stochastically-driven extinction risk for species in each of the case study systems using R 3.2.3.

Results

Equilibria and Stability: Two Species

The two-species model described in (Equations 1.1 and 1.2) has equilibria at (F^*=B^*=0) and

$$F^* = \frac{\kappa_F \kappa_B}{\varphi_{BF}} \frac{\varphi_{FB}\varphi_{BF}(c_F-\mu_F)(c_B-\mu_B)-\mu_F\mu_B}{\mu_F\kappa_F c_B+\varphi_{FB}c_F\kappa_B(c_b-\mu_B)} \qquad (1.3a)$$

$$B^* = \frac{\kappa_F \kappa_B}{\varphi_{FB}} \frac{\varphi_{FB}\varphi_{BF}(c_F-\mu_F)(c_B-\mu_B)-\mu_F\mu_B}{\mu_B\kappa_B c_F+\varphi_{BF}c_B\kappa_F(c_F-\mu_F)} \qquad (1.3b)$$

When equations 1.3a and 1.3b are evaluated with the default parameters, F^* = 800 and B^* = 800. Each of these equilibria is stable when the magnitude of the dominant eigenvalue of the Jacobian is less than 1. The Jacobian for the two-species case is shown below. Analogous Jacobians can be derived for more speciose systems.

$$\begin{bmatrix} 1-\frac{\mu_F\kappa_F(c_F-\mu_F)}{c_F(\kappa_f-F^*)} & \frac{\varphi_{FB}}{\kappa_F}\frac{(\kappa_F(c_F-\mu_F)-c_F F^*)^2}{c_F(\kappa_F-F^*)} \\ \frac{\varphi_{BF}}{\kappa_B}\frac{(\kappa_B(c_B-\mu_B)-c_B B^*)^2}{c_B(\kappa_B-B^*)} & 1-\frac{\mu_B\kappa_B(c_B-\mu_B)}{c_B(\kappa_B-B^*)} \end{bmatrix} \qquad (1.4)$$

Stability of the equilibria depends upon the model parameter values. Here, I vary plant mortality (μ_F) to illustrate its effect on stability. I do not show results for an analogous sweep on μ_B because both species in the model specialize on the other, and consequently their extinction risk is identical.

As μ_F increases from zero, population sizes at the coexistence equilibrium decrease (Figure 1.2A). Both equilibria undergo a stability transition at

$$\mu_F = \frac{\varphi_{FB}\varphi_{BF}c_F(\mu_B-c_B)}{\varphi_{FB}\varphi_{BF}(\mu_B-c_B)-\mu_B} \qquad (1.5)$$

which evaluates to 0.9 with the given parameters. At this value, the coexistence equilibrium becomes unstable and extinction becomes stable (Figure 1.2B).

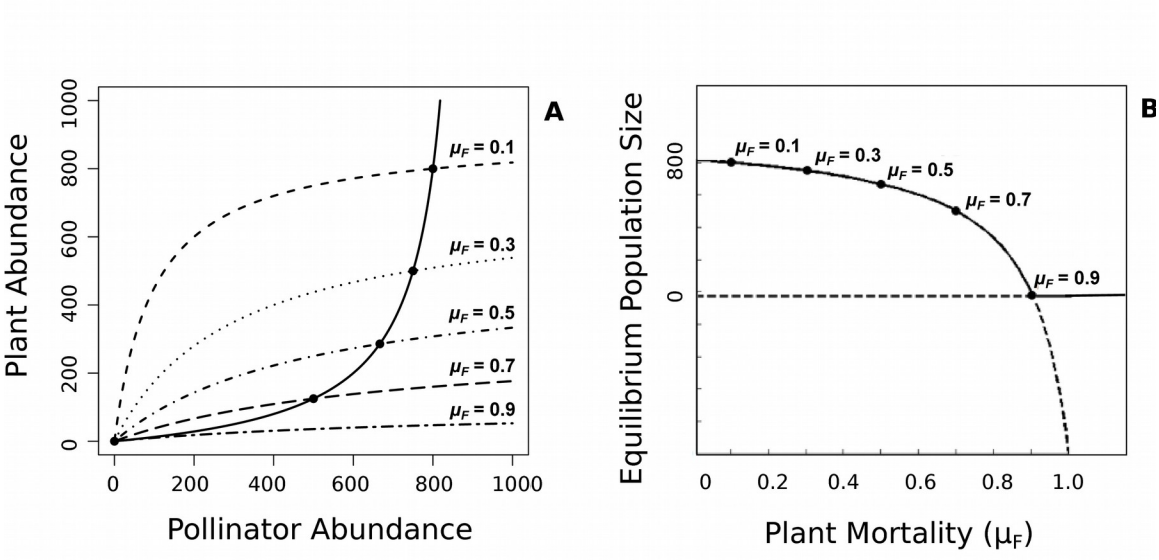


Figure 1.2. The effect of plant mortality μ_F on population sizes and stability. (A) Null clines of the 2-species model under different plant mortality values μ_F. (B) A stability transition occurs at μ = 0.9, where the coexistence of the plant and pollinator becomes unstable and the extinction equilibrium becomes stable. Results are shown for 10,000 replicates using the default values of all parameters except μ_F.

Equilibria and Stability: Four Species

The 4-species model (Figure 1.3A) exhibits full coexistence and extinction equilibria analogous to those of the 2-species model when parameterized with the same values, i.e. $F_1^* = F_2^* = B_1^* = B_2^* = 800$ or $F_1^* = F_2^* = B_1^* = B_2^* = 0$, respectively. Additionally, there are five partial-coexistence equilibria (Figure 1.3B, C). For each partial coexistence configuration shown in Figure 1.3B, the model converges to stable population sizes (Figure 1.3C) from both above and below. Configurations not shown do not have stable coexistence; in these cases, the system converges to the full-extinction equilibrium.

Whether a subset of species characterizes a stable partial community depends upon the interaction structure of the network. In the case of the 4-species model given in Figure 1.3, two different three-species communities and three two-species communities are possible. The model moves from a four-species to a three-species state following the loss of a species that does not interact with a specialist-- in this case, either of the specialists F_2 or B_2. The two-species states may be reached either via stochastic losses from a 3-species community, or the loss of a generalist from the full 4-species community. The system moves from a 3-species to a 2-species equilibrium following the loss of either species of the type that was not previously lost, e.g. a 3-species community that was created through the loss of a pollinator becomes a 2-species community following the stochastic loss of either plant. The system may also move directly from the 4-species to a 2-species equilibrium after the primary loss of a generalist, because it is followed deterministically by the loss of the corresponding specialist.

The bar graphs in Figure 1.3C show the stable population sizes of all extant species at each equilibrium, relative to their population sizes at full coexistence (dotted line). While extinctions reduce the size of all extant populations, generalists undergo the larger decline because the model does not adjust interaction strengths after extinctions. I revisit the role of this assumption in the Discussion.

Variability, Mortality, and Extinction Risk: Two Species

The proportion of replicates where extinction occurred (hereafter 'extinction risk') increased with both increasing plant mortality μ_F and with increasing variance σ^2_ε of the stochasticity applied at each time step (Figure 1.4). In the two-species case, I represent the extinctions of both species in a single graph because the loss of either leads deterministically to a coextinction of the other. Additionally, because the model describes plant and pollinator dynamics in the same way, the

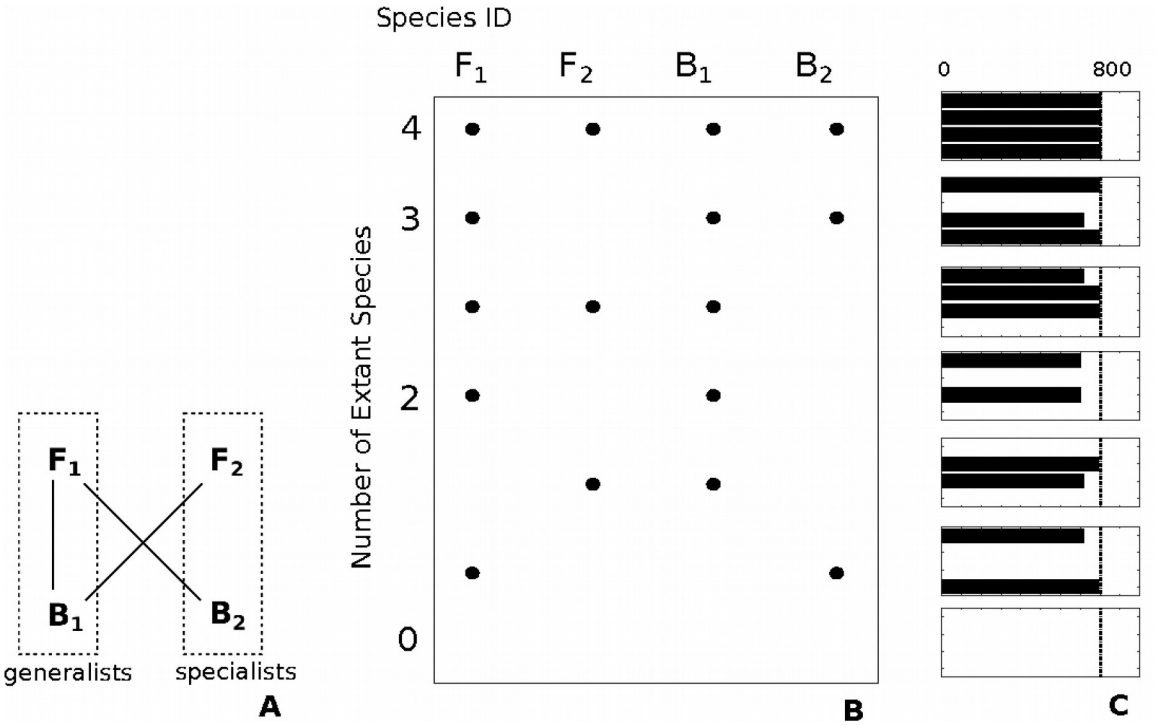


Figure 1.3. Equilibria in the 4-species model. (A) the 4-species interaction network. (B) Species presence at each equilibrium. (C) Species abundances shown relative to population size at the full coexistence equilibrium (reference line). Relative abundances depend upon the interaction structure, whereas absolute abundances are parameter-dependent. Results are shown for the default parameter set.

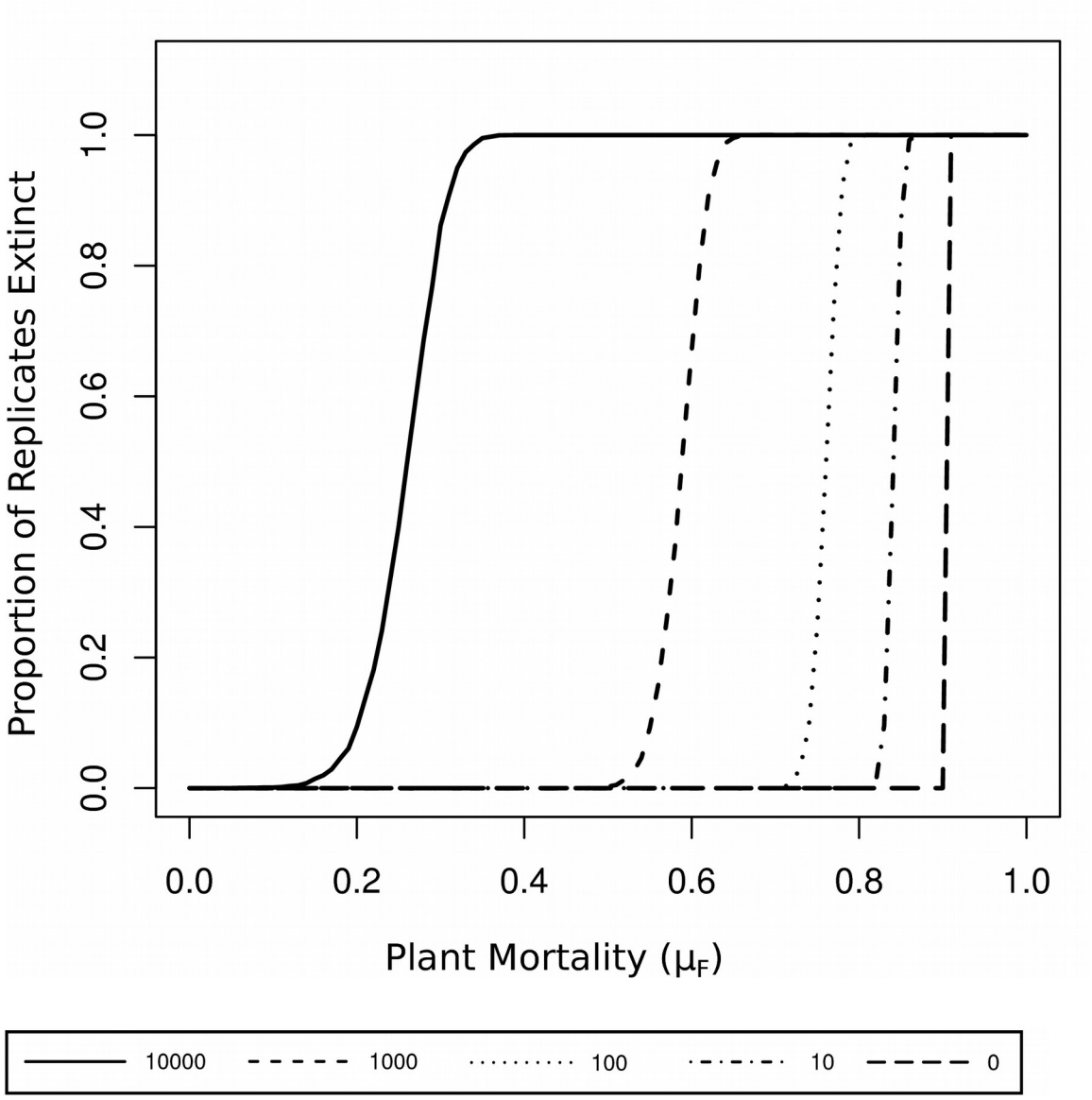


Figure 1.4. Proportion of replicates with extinction increased when stochasticity with increasing variance (0-10,000 individuals per time step) was applied across a parameter sweep on plant mortality μ_F. Increasing the stochastic variance increases the size of the region of parameter space where extinctions occur, as well as the region where persistence/extinction outcomes are unpredictable. Results are shown for 10,000 replicates using the default values for all parameters except μ_F.

effect of increasing pollinator mortality μ_B would be analogous to the results presented here.

In simulations of the deterministic case (σ^2_ε=0), both species persist for values of μ_F < 0.9 and are lost when μ_F> 0.9. As σ^2_ε increased, the transition from persistence to extinction occurred at smaller values of μ_F (Figure 1.4), increasing the size of the region in parameter space where extinction occurs in all replicates. The size of the region of parameter space where population outcomes were variable (i.e. where extinction occurred in some replicates but not others) also increased with increasing σ^2_ε. In larger systems where species interact with more than one mutualist partner, the effect of the parameter sweep is mediated by population dynamics and the strength of the interaction (Appendix 1).

Stochasticity, Extinction and Specialization: Four Species

Increasing σ^2_ε elevated extinction risk for all species, but for a given value of σ^2_ε, specialists were significantly more severely affected than generalists (Figure 1.5). This difference, however, only occurred for variance values where extinction outcomes vary across replicates. When extinction or persistence is rare, all species are at similar risk.

I also tested whether, within each specialization category, plants were more or less vulnerable to stochastically-driven extinction than were pollinators. I found no significant difference under the default parameter set. This follows from my decision to parameterize all species identically. I expand upon the consequences of choosing an asymmetric parameterization in the Discussion and in Appendix 1.

Stochasticity, Extinction Risk and Specialization: Case Studies

In the 4-species model, all species either interact with only one partner, or with all possible partners. In larger, realistic pollination networks, species tend to exist between these two extremes. Here, I demonstrate that the relationship between a species' number of mutualist partners is negatively correlated with its stochastically-driven extinction risk in the two case study pollination networks of Flores, Azores (n = 22 species) and Ille aux Aigrettes, Mauritius (n = 27 species). In these networks, no species interacts with all possible partners, while 6 and 4 species interact with a single mutualist partner in Flores and Ille aux Aigrettes, respectively. In both cases, one of these specialists is a plant and the rest are pollinators.

Linear regressions of the dependence of extinction risk on number of mutualist partners had significantly negative slopes for both pollination networks (Figure

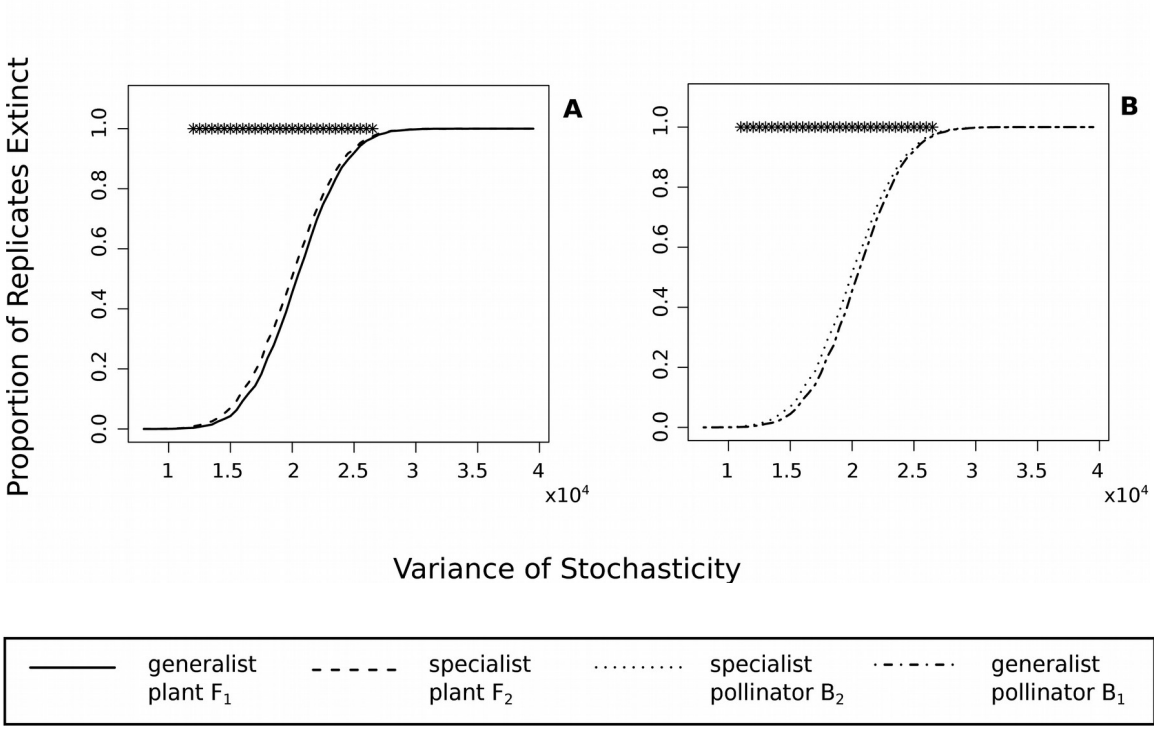


Figure 1.5. Extinction risk comparisons between specialist and generalist (A) plants, and (B) pollinators over a range of variances. Stars indicate significant difference in extinction risk, according to a Bonferroni-Holm corrected McNemar test at each variance. These tests did not find a difference in extinction risk between plants and pollinators in either specialization category (not shown). Results are shown for 10,000 replicates using the default parameter set.

1.6). In the Flores network, extinction risk decreased with number of mutualist partners with a slope of -0.027 (p = 8.91x10^{-7}, R^2 = 0.73). In the Ille aux Aigrettes network, the slope was -0.010 (p=5.07x10^{-5}, R^2 = 0.50). These results are consistent with the direction of the relationship between specialization and extinction risk that I found using the 4-species model. Additionally, the slope of the specialization-risk relationship differed between the two case study networks (p=0.019).

Discussion

Flowering plants, and thus their pollinators, underpin the persistence of terrestrial ecological and agricultural systems. Consequently, it is important to understand the drivers of extinction risk to both groups. In this paper, I explore how environmental variability affects extinction risk in plant-pollinator systems. In particular, I ask whether this stochasticity affects all species equally. To answer this question, I introduce a new population dynamic model that describes the reproductive benefit of the pollination mutualism using a birth function based on the harmonic mean, and apply it to systems with 2, 4, and >20 species. Using a 2-species implementation of the model, I demonstrated that the harmonic mean birth function not only imparts the biological realism of saturating *per capita* reproduction, it produces a system with only one coexistence and one extinction equilibrium. I showed that including stochasticity increased both species' extinction risk. Moreover, increasing the variance of the stochasticity at each time step reduced the deterministic mortality rate that each population was able to tolerate. This result suggests that, where environmental variability is increasing due to climate change (Christensen *et al.* 2013), species may not be able to persist without a favorable change in their life history parameters.

The 4-species network is the smallest version of the model that allows comparison between specialists and generalists of both plants and pollinators. In this case, extinction risk increases with σ^2_ε across all species, but specialists are more affected than generalists over a substantial part of that range. Specialists' disproportionate vulnerability to extinction does not appear to be mediated by small population size: at full community coexistence, all species stabilize with the same number of individuals, and specialists remaining after prior losses stabilize at larger population sizes than do generalists (Figure 1.3). The significant discrepancy in extinction risk between specialists and generalists disappeared when population dynamics were dominated either by the deterministic skeleton (low variance) or stochasticity (high variance), because there was little variation in population outcomes in these cases.

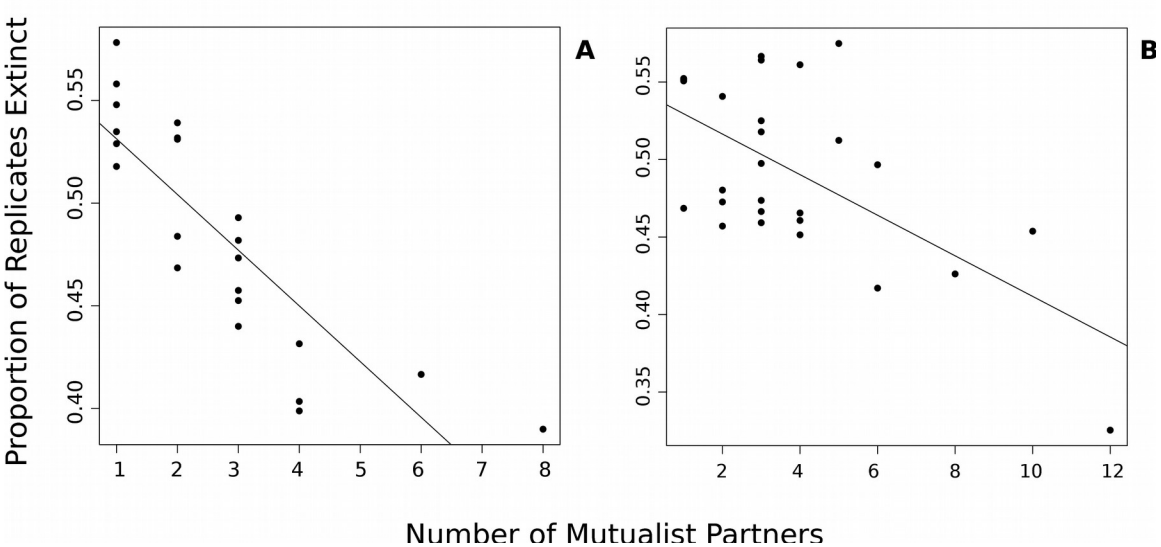


Figure 1.6. Each species' extinction risk plotted against its number of mutualist partners with a least-squares regression fit for sites on the island of Flores, Azores (A) and Ile aux Aigrettes, Mauritius (B). Results are shown for 100,000 replicates using the default parameter set.

This pattern carried over to the two case study networks with realistic empirically derived interaction structures. In both cases, stochastically-driven extinction risk increased with specialization. Because I parameterized each species identically, differences in the slope of the specialization-risk relationship between the two networks are due to differences in network topology, which are driven by the presence of each interaction and its likelihood of being observed.

My findings are in agreement with prior empirical and theoretical work suggesting that specialists are more vulnerable to extinction (McKinney 1997, Biesmeijer *et al.* 2006, Abramson *et al*. 2011). Additionally, Abramson *et al*. (2011) report that the discrepancy between specialists' and generalists' extinction risk in a Levins model is reduced at higher values of habitat loss. My results show a similar trend despite differences in model dynamics, and extinction driver.
My work departs from much of the mutualist network literature in that it focuses on species-level effects. Extinctions are introduced into topology-only models and those that incorporate deterministic population dynamics via knockout sequences and/or parameter sweeps defined by the researcher. Although random losses are often included, they often serve as a comparison against best- and worst-case deterministic sequences in order to assess network-level robustness (Memmott *et al.* 2004, Fortuna & Bascompte 2006, Kaiser-Bunbury *et al.* 2010, Ramos-Jiliberto *et al.* 2012, Santamaría *et al.* 2014, but see Abramson *et al.* 2011 for species-level results from these approaches). Despite the importance of network structure to the persistence of biodiversity, species-level risk remains a major focus of conservation work (ESA 1973, IUCN 2016). My use of stochastic population dynamics allows me to compare risk at the species level, for both primary and secondary extinctions in a given network.

In any ecological model, assumptions are necessary to navigate the trade-offs between specificity and simplicity. Here, I discuss a few major assumptions that affect the present model's deterministic skeleton and stochastic dynamics.

I parameterized the model such that species only differed in their interactions. Consequently, it is unsurprising that extinction risk differed between specialists and generalists, but not between plants and pollinators. Realistically, species vary in their vital rates and ecological role. For example, consider the visit-to-offspring conversion factor c. In plants, c describes the processes of pollen transfer and fertilization. In pollinators, who rely on floral visits for nutrients and energy, the benefit to reproduction is indirect. If I reflect this difference in the model by assigning pollinators a lower value of c, I expect their populations to stabilize at a smaller size, increasing their extinction risk with respect to plants. When I run the model with c=1 for plants and c=0.2 for pollinators, not only is this

the case, but pollinators comprise nearly all of the primary extinctions (Appendix 1).

For mathematical and conceptual simplicity, and because I use the model to explore relative differences in extinction risk, I also assume that interaction strengths do not change after extinctions. Consequently, the loss of species causes an irreversible reduction in its partners' reproductive potential. In the 4-species system, generalists lose ~17% of their density-independent reproductive output when their specialist partner becomes extinct. This leads to a ~10% reduction in equilibrium population size, and a corresponding increase in extinction risk. Scenarios like this one where reallocation of effort does not occur could arise when (a) the presence of the specialist pollinator does not affect the generalist plant's reproductive output, or (b) the generalist plant is fully exploited by pollinators regardless of whether the specialist plant is present. Alternately, reallocation is likely to occur when species compete (an interaction not included in the present model) because the loss of one species frees resources to be used by another. In such cases, reallocation of mutualist effort would mitigate the extinction risk to remaining species.

I also chose to include stochasticity in the model as a random number of individuals added to or subtracted from each population. This is roughly analogous to using a random immigration/emigration term, except that extinct populations are assumed not to re-establish. Other entry points of stochasticity have been explored in the literature (Ives & Hughes 2002, Ferguson & Ponciano 2015). Introducing stochasticity on the mortality rate affects the population in a way that scales with population size, and is less likely to drive populations below zero. When I repeated the analysis on the case study networks applying ε to mortality, the qualitative trend of extinction risk decreasing with number of mutualist partners remained the same (Appendix 1). Because the absolute effect of *per capita* variability decreases with population declines, extinction risk in this case was three orders of magnitude lower than for the absolute additive entry point, and had a gentler slope. My focus is on the relationship between the relationship between specialization and relative extinction risk, and the absolute additive ε emphasizes these differences.

While this model is meant to explore the relationship between stochasticity, specialization and extinction risk in a generic plant-pollinator context, it may be extended in a number of ways to address related questions. For example, I apply this non-spatial model to case study data derived from well-demarcated habitat patches (Olesen *et al.* 2002), but a spatially explicit model may be necessary to answer the same questions of systems where population densities and/or environmental variability are not constant within a habitat. In the time dimension,

I assume that stochasticity is not temporally autocorrelated. Similarly, I assume that species responses to stochasticity are independent, whereas functional and phylogenetic similarities may cause species to respond in a correlated way. I also do not consider differences in the time scales of floral development and pollinator decision-making, interaction turnover within and between seasons, and the effect of multiple interaction types.

Because the majority of flowering plants, including numerous crop species, depend on animal pollination, threats to their persistence are of particular ecological and economic importance. My results demonstrate the importance of considering both species interactions and stochasticity when modeling extinction risk in plant-pollinator communities. Models that omit either of these factors are likely to underestimate extinction risk, particularly that of specialists.

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Appendix 1

Mortality Parameter Sweep in the 4-Species System

In the main text, I show how increasing environmental variability increases the range of values of the plant mortality parameter μ_F where species are lost (Figure 1.4). Here, I repeat this exercise for the 4-species system. In the 2-species simulations, both species either persist or are lost together, because each specializes on the other. In the 4-species system, it is possible to lose only a subset of species. Under the interaction structure described in Figure A1.1, for example, there are five partial-coexistence equilibria (Figure 1.3).

I conducted a parameter sweep on the mortality rate μ_{F1} of the plant generalist species, across a range of variances. As in the 2-species case, both the focal species F_1 and its specialist mutualist B_2 undergo increases in extinction risk (modeled as proportion of replicates extinct) as the mortality parameter μ_{F1} and variance σ^2_ε are increased (Figure A1.2, panels A and D). Compared to the 2-species model at a given value of σ^2_ε, species in the the 4-species network were less at risk of extinction.

In the deterministic model, persistence of both the plant and its obligate mutualist pollinator in the 2-species system was stable for values of $\mu_F < 0.9$. The persistence of plant F_1 in the 4-species model was stable when $\mu_{F1} < 0.996$. Species B_1 and F_2 (neither of which specialize on F_1) did not undergo a bifurcation, meaning that the existence of a stable partial community was possible in the absence of F_1 and B_2.

The stochastic model also showed lower extinction risk in the 4-species system. In the 2-species system, 50% of all replicates went extinct at a value of $\mu_{50} = 0.588$ at $\sigma^2_\varepsilon = 1000$. At the same variance, μ_{50} is 0.609 for F_1 and its obligate mutualist B_2. This higher μ_{50} value indicates that, in the same stochastic environment, F_1 and B_2 are able to persist at slightly higher deterministic mortality rates than are the analogous F and B in the 2-species system.

In the stochastic 4-species model, μ_{F1} indirectly affected the persistence of the non-focal species B_1 and F_2. Extinction risk for these species increased with increasing F_1 mortality, but plateaued for μ_{F1} values at which the focal species was lost with a probability of 1 (Figure A1.2, panels B and C). This is a consequence of population dynamics as well as the likelihood that F_1 is lost in a given replicate. As μ_{F1} increases, the equilibrium size of the F_1 population decreases, which limits the equilibrial population sizes of the other species in the

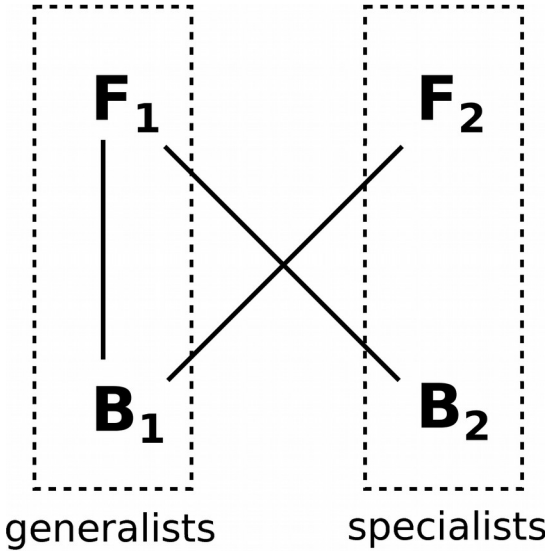


Figure A1.1. Pollination interactions in the 4-species model. Species labeled 'F' are plants, and species labeled 'B' are pollinators. F_2 and B_2 specialize on the generalists B_1 and F_1, respectively. This figure is reproduced from Figure 1.3(A) in the main text.

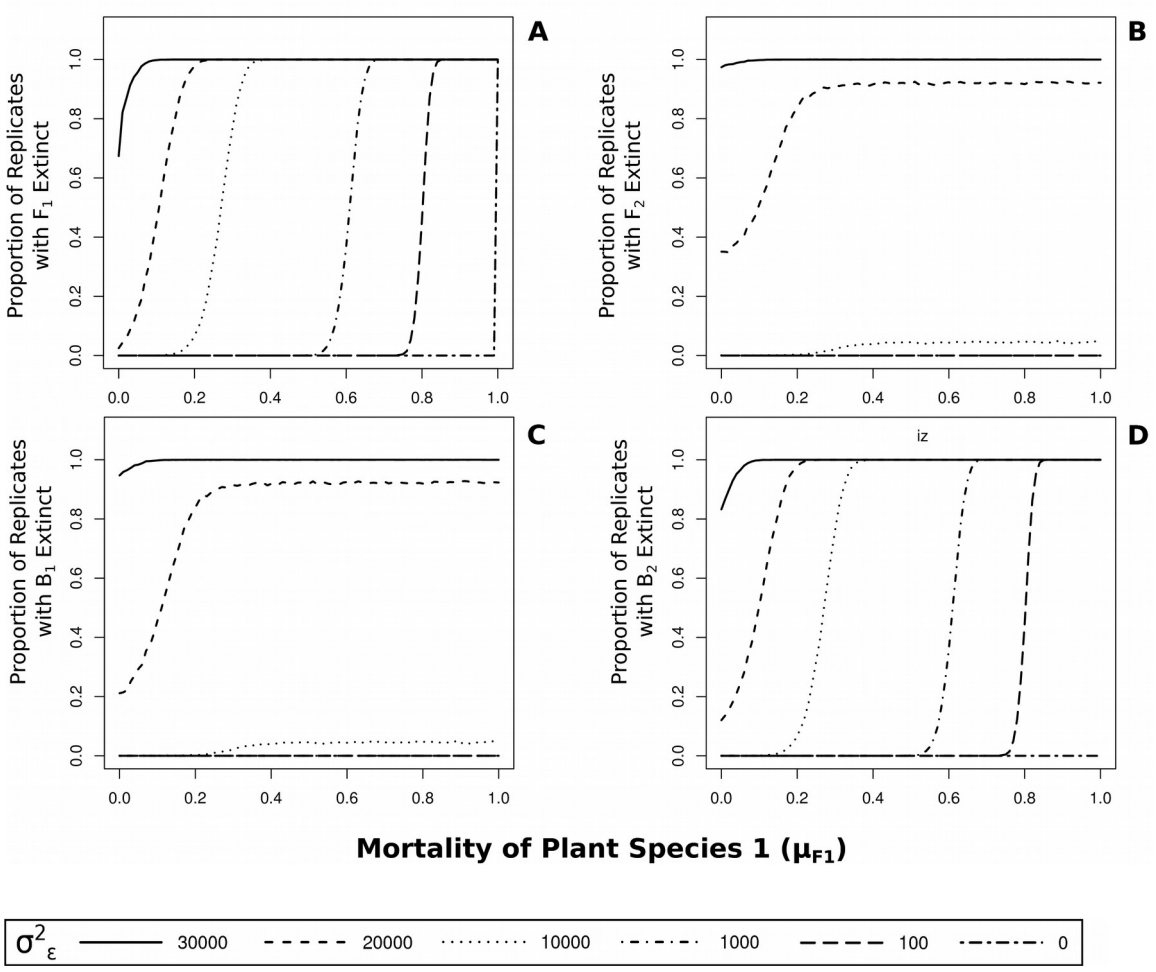


Figure A1.2. Proportion of replicates with extinction increased with variance σ^2_ε (0-30,000 individuals per time step) and the mortality μ_{F1} of plant species F_1. Increasing σ^2_ε increases the size of the parameter space region where F_1 (panel A) and its obligate mutualist B_2 (panel D) are lost, as well as the size of the region where persistence/extinction outcomes are unpredictable. The proportion of replicates with extinctions in species F_2 (panel B) and B_1 (panel C) increases over low μ_{F1}, but plateaus where F_1 is lost with a probability of 1. Results are shown for 10,000 replicates using the default parameter set aside from μ_{F1}.

system. Since stochastically-driven extinction risk is greater in smaller populations, decreasing the equilibrium population size for one species elevates extinction risk for the other species in the system. Because B_1 and F_2 can persist without F_1, their extinction risk plateaus at an elevated level < 1. This elevated risk level is determined by the value of σ^2_ε, with extinction more likely at higher variances. Stochasticity also had a greater effect on specialist than on generalists over the parameter sweep (e.g. see σ^2_ε= 20000).

Stochasticity, Extinction Risk and Specialization: Four Species with Asymmetric Parameters

In the main text, I assigned identical life history parameters to all species, in order to investigate the effect of interaction structure on species' extinction risk. In real systems, however, species vary in both their vital rates and ecological role. Here, I explore the consequences of asymmetric parameterization by assigning different values of the floral-visit-to-offspring conversion factor *c* to plants and pollinators.

This parameter is a natural place to introduce asymmetry because floral visits serve qualitatively different purposes for plants and pollinators. A successful floral visit fertilizes one or more of a plant's ovules and provides the pollinator with energy and nutrients. The effect on plant reproduction is direct, whereas pollinator reproduction benefits indirectly. I reflect this difference in the asymmetrical model by assigning pollinators a lower *c*-value (c=0.2) than plants (c=1) in the 4-species case. I ran 10,000 replicates of the model with these values, leaving the other parameters and the interaction structure unchanged from the main-text (henceforth symmetric) model.

I first found the population sizes at all full and partial coexistence equilibria (Table A1.1). In each case, all pollinator species stabilize at smaller population sizes than the plant species, and all equilibrium populations are smaller than those in the symmetric case. Because smaller populations are more prone to extinction in the presence of stochasticity, I expect pollinators to have elevated extinction risk when compared to plants. Following the main text results, I also expect the specialist pollinator to be at greater extinction risk than the generalist pollinator. I compare extinction outcomes as before, using a McNemar test, corrected for multiple comparisons using the Bonferroni-Holm method to correct for multiple comparisons. Differences in extinction risk under the asymmetric parameterization were significant between specialists and generalists, and between plants and pollinators (Figure A1.3). These differences were especially pronounced between plant specialists and generalists (Figure A1.3, panel A), and

Table A1.1. Full and partial coexistence equilibria for the 4-species community with the asymmetrical parameter set. There is also an extinction equilibrium where all population sizes are zero.

	F_1	F_2	B_1	B_2
4 Species				
	667	667	286	286
3 Species				
	632	0	194	279
	517	656	270	0
2 Species				
	0	583	184	0
	632	0	0	250
	357	0	132	0

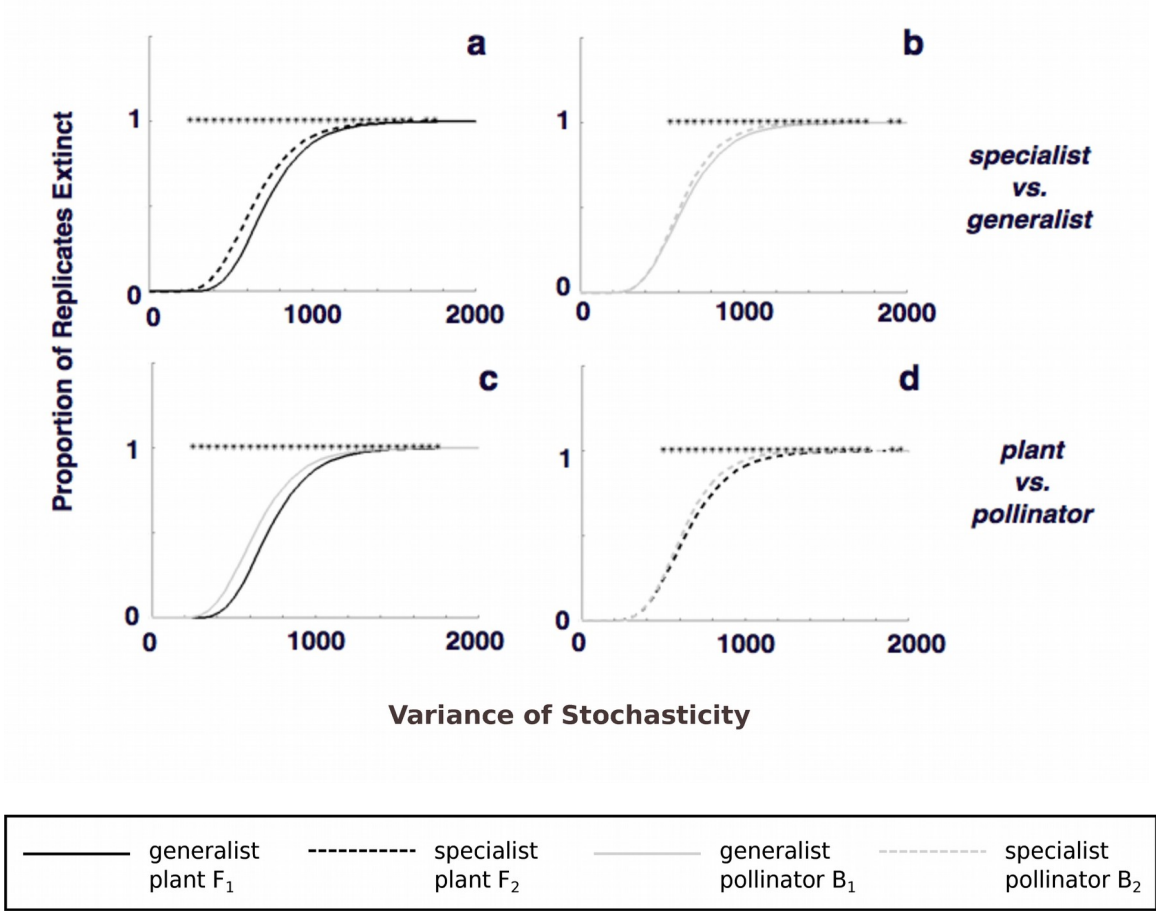


Figure A1.3. Extinction risk comparisons between (a) plant species, (b) pollinator species, (c) specialist species, (d) generalist species, over the entire extinction sequence. Stars indicate significant difference in extinction risk, according to a Bonferroni-Holm corrected McNemar test at each variance. Results are shown for 10,000 replicates using the default parameter set.

between plant and pollinator generalists (Figure A1.3, panel C). Additionally, full-community loss in the asymmetric case occurred at variances an order of magnitude smaller than those causing the same outcome in the symmetric case. This outcome is consistent with pollinators' smaller equilibrium population sizes (Table A1.1), and the assumption that pollination is an obligate mutualism for all species in the system.

These results follow from a simple case of asymmetry, i.e. one where plants and pollinators, as a group, differ in a single parameter value. There is, however, no reason to expect different species in a real system to be described by identical parameter values. Since stochastically-driven extinction risk is mediated by population size, estimates of a species' risk depends upon the cumulative effect of its parameter values on the growth rate and equilibrium size of its population. While I observe a divergence of extinction risks here, it is also possible that asymmetries in parameter values could cancel out and produce similar population growth rates across a system. In that case, I would expect to see less difference in species' extinction risk. Nevertheless, I show here that parameterizing a species for small population size increases the extinction risk for that species as well as its mutualists.

Entry Point of Stochasticity: Two Species

Modeled estimates of extinction risk depend not only upon the presence and variance of stochasticity, but also upon its entry point (Ives & Hughes 2002). Here, I investigate how the additive entry point used in the main text differs in its effects on extinction risk from comparable stochasticity applied to the plant mortality rate in the 2-species model. Additive stochasticity on population size is roughly analogous to variability in immigration and emigration to/from a population, whereas stochasticity applied to the mortality parameter affects population size via *per capita* death rates.

I compare the consequences of these two entry points by repeating the parameter sweep on μ_F with stochasticity applied to the model's mortality terms:

$$F_{t+1} = F_t + R_F(F_t, B_t, c_F, \varphi_{FB})\left(\frac{\kappa_F - F_t}{\kappa_F}\right) - (1+\varepsilon_{F_t})\mu_F F_t \qquad \text{(A1.1a)}$$

$$B_{t+1} = B_t + R_B(B_t, F_t, c_B, \varphi_{BF})\left(\frac{\kappa_B - B_t}{\kappa_B}\right) - (1+\varepsilon_{B_t})\mu_B B_t \qquad \text{(A1.1b)}$$

In Equations A1.1a and A1.1b, ε is again normally distributed about zero, and populations are nonnegative. The magnitude of ε that this system can withstand is much lower than in the additive case because stochasticity is applied to a vital rate (with a range of 0 to 1), rather than the population size (with a full-coexistence equilibrium size of 800 under the default parameter set). In order to compare the influence of different entry points on population dynamics, I chose the variance of the ε in Equation A1.1 such that the whole-population variance was similar to that of the additive model.

The variance of population size in model where stochasticity is applied additively is simply the variance of ε. I calculate population variance in model with stochasticity applied to the mortality parameter using the rule $\sigma^2_g = a^2 \sigma^2_A$ for $g = aA$, where a is a constant and A is a random variable. In this case, $a = \mu_F F$ and A is the stochastic term ε. I rearrange this relationship to find the variance $\sigma^2_{\varepsilon\mu}$ of ε applied to μ_F that results in population variance $\sigma^2_{\varepsilon F}$:

$$\sigma^2_{\varepsilon\mu} = \frac{\sigma^2_{\varepsilon F}}{\mu^2_F F^2} \quad \text{(A1.2)}$$

where μ_F is the mortality parameter of Equations A1.1a and A1.1b, and F is plant abundance. In order to compare population dynamics between models with the additive and multiplicative entry points of stochasticity, I set $\sigma^2_{\varepsilon F}$ in equation A1.2 equal to the population variance in the additive model at equilibrium abundance $F=F^*$.

I compared population outcomes using the summary statistic μ_{50}, the value of μ_F where 50% of replicates are lost at a given variance σ^2_ε. For all levels of variance, μ_{50} is higher when stochasticity is applied to the mortality rate (Figure A1.4), because the absolute effect of of this *per capita* stochasticity decreases with population decline. In other words, the value of μ_F where the system moves between persistence and extinction is higher when stochasticity is applied to the mortality rate than when it is applied directly to the population size.

Entry Point of Stochasticity: Case Study

In order to explore the influence of the entry point of stochasticity on realistic systems, I also compared the consequences of the different entry points on persistence for the two case study networks. As in the main text, I carried out this analysis using a variance of 20,000 for the model with stochasticity applied to population size. This translates to an input variance of 3.125 for the model with stochasticity applied to the mortality parameter (Equation A1.2).

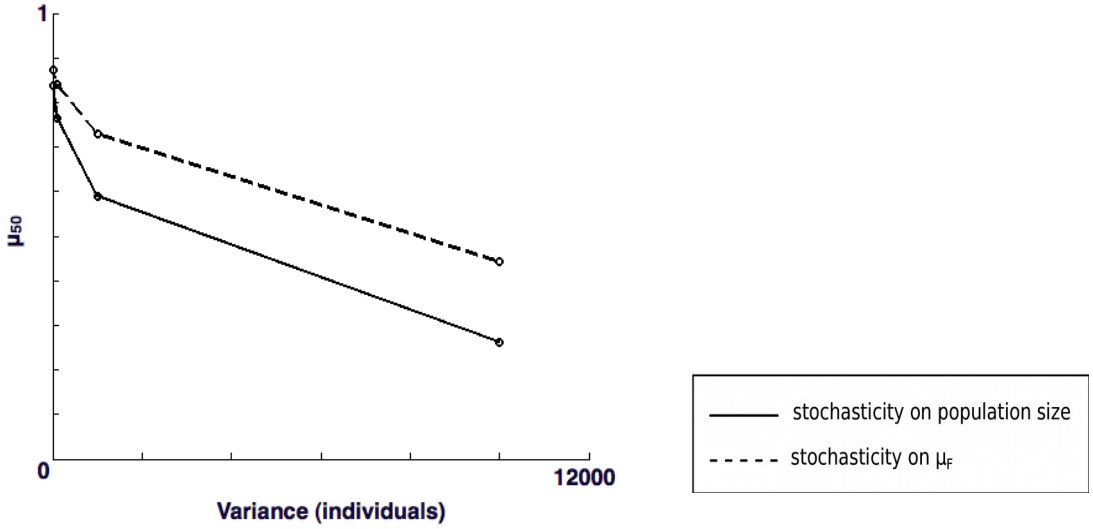


Figure A1.4. The effect σ^2_ε (in numbers of individuals) on μ_{50}. The solid line shows the effect of an additive entry point of stochasticity (i.e. adding/subtracting a random number of individuals). The dashed line shows the transformed effect of stochasticity applied to the mortality parameter. this is the result for 100 replicates and the default values for all parameters other than μ_F.

In both cases, the overall trend was the same: species extinction risk increases as the number of mutualist partners decreases (Figure A1.5). The relationship between number of mutualist partners and extinction risk with stochasticity applied additively to population size was -0.034 (n = 22, p = 8.91x10^{-7}, R^2 = 0.73) for Flores and -0.010 (n = 27, p=5.07x10^{-5}, R^2 = 0.50) for Ile aux Aigrettes. When the model was instead run with applied to the mortality parameter, these slopes became -0.034 (n = 22, p = 8.91x10^{-7}, R^2 = 0.73) and -8.92x10^{-6} (n = 27, p = 0.034, R^2 = 0.168) for Flores, and Ille aux Aigrettes, respectively.

While the entry point of stochasticity did not affect the qualitative relationship between specialization and extinction risk, it affected extinction rates themselves. For a comparable level of variance, extinction risk was three orders of magnitude greater in the model where stochasticity was applied directly to population size. Consequently, the regression line fits less tightly to the data, and the confidence intervals are much larger.

Size Distributions of Extant Populations

The main text of this chapter focuses on the relationship between stochasticity and extinction in communities of interacting mutualists. A related but different approach to describing extinction-prone populations is to characterize the behavior of those populations that have not yet been lost. Since population models like this one (with mortality, compensatory density dependent growth, and an absorbing boundary at zero) commonly give rise to dynamics that tend to extinction in finite time, the likelihood of observing a population with > 0 individuals declines with time t. It is often possible, however, to derive a probability distribution describing the size of populations extant at t, conditional on their persistence up to that point. When this distribution is independent of t, it is termed quasi-stationary. There is a large body of literature discussing the properties of quasi-stationary distributions in single-population models, as the concept is useful for summarizing stochastic behavior over long time periods (Méléard & Villemonais 2012).

Here, I summarize the distributions of population sizes (conditional on non-extinction) for the model described in this chapter (Equations 1.1-1.2) at different levels of variability. All replicates are initiated with population sizes of 700 for all species. In the absence of stochasticity, all populations reach their equilibrial value of 800 within 21 time steps. I record the size distributions of non-extinct populations at times t=100, t=500, and t=1000.

The size distribution of populations of the generalist plant species F_1 extant after 1000 time steps appears broadly normal over a range of values of the model's

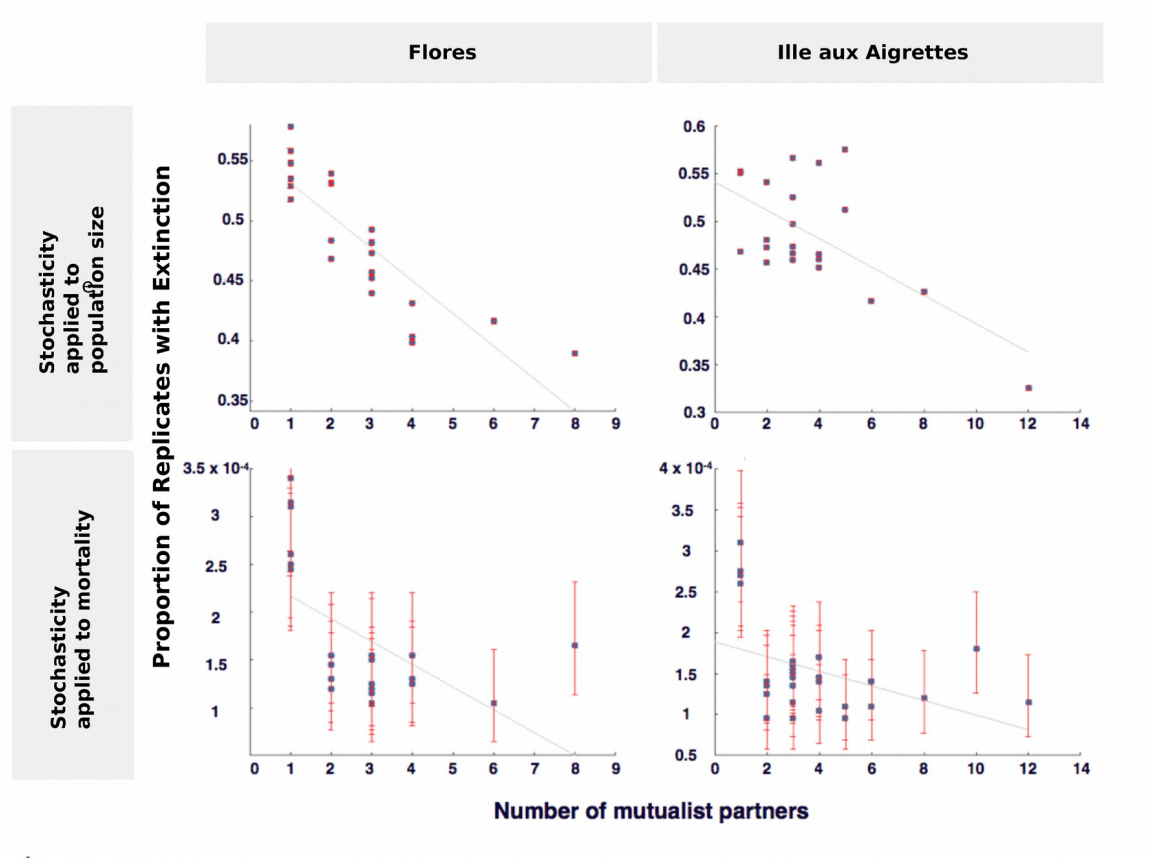


Figure A1.5. The entry point of stochasticity affects the magnitude of extinction risk in both pollination networks. (A) Flores with stochasticity applied to population sizes. (B) Ille Aux Aigrettes with stochasticity applied to population sizes. (C) Flores with stochasticity applied to each species' mortality parameter. (D) Ille Aux Aigrettes with stochasticity on each species' mortality parameter. Results are shown for 200,000 replicates of the default parameter set.

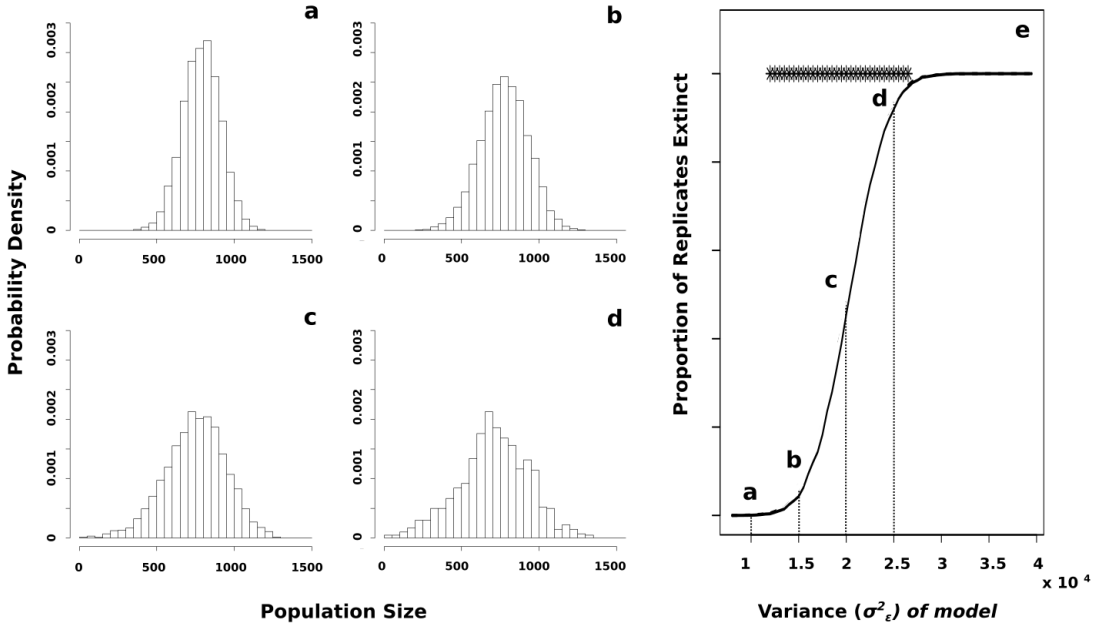


Figure A1.6. Size distributions of generalist plant populations extant at the end of each replicate, normalized such that each graph has an area of 1. Histograms are shown for population variances (a) σ^2_ε = 10,000, (b) σ^2_ε = 15,000, (c) σ^2_ε = 20,000, and (d) σ^2_ε = 25,000. These values correspond to persistence at t = 1000 of ~99%, ~95%, ~55%, and ~8% of 10,000 replicates (e).

variance parameter σ^2_ε (Figure A1.6). As σ^2_ε increases, fewer populations are extant at t=1000 (Table A1.2), and the distribution becomes wider as more populations undergo larger excursions from their equilibrial size. In the two most variable cases (Figure A1.6 panels c and d), small populations appear to be overly represented relative to a normal distribution; however, these distributions are the least certain because the sample size of the data generating these histograms decreases with variance (e.g. the number of extant populations contributing to Figure A1.6d is less than a tenth of the number making up Figure A1.6a).

The graphed distribution shows population sizes of the generalist plant species F_1 at the end of each replicate. Results for the specialist plant F_2 are similar (Table A1.2). Since these distributions are taken from simulations using the default (symmetric) parameter set, the pollinator species are analogous to those of the plant species. Furthermore, the size distributions of extant populations change very little over each replicate. Even in the most variable case, the mean size of extant populations changes by less than 6% between t=100 and t=1000 (Table A1.2).

The shape, mean, and variance of the size distributions of extant populations are influenced by the assumptions of the model. That the distributions in this case have a broadly normal shape (Figure A1.6) is related to the choice of a normal distribution to represent environmental variability at each time step. Since stochasticity is represented as the addition or subtraction of a random number of individuals to or from the population, the total number of individuals added stochastically should take on a normal distribution given enough time, regardless of which distribution is applied to each time step. But additions at each time step also contribute to nonlinearly to reproductive output in the next. Thus it cannot be assumed that using another distribution to model stochasticity at each time step would result in a broadly normal size distribution of extant populations.

Parameters affecting population size and growth (including the visit-to-offspring conversion factor c and carrying capacity κ) affect the mean of the resulting population size distribution. Populations with high capacities and fast growth are more likely to be large at any given time than those with low growth and low capacity. Lastly, the variance of the distribution of population sizes is affected by the variance of the stochasticity introduced at each time step. Systems with more variable trajectories are more likely to show a wide distribution in population sizes.

Table A1.2. Number, mean size and standard deviation of populations extant at times t = 100, 500 and 1,000 (conditional on non-extinction). These metrics are shown for one generalist (F_1) and one specialist (F_2); results for B_1 and B_2 are analogous under the default (symmetric) parameter set. Results are shown for 10,000 replicates of the model.

σ^2_ε	Species	t	n	Mean	Standard Deviation
10,000	F_1	**100**	10,000	786	123
		500	9,998	788	123
		1000	9,996	788	121
	F_2	**100**	9,998	786	124
		500	9,993	787	124
		1000	9,991	788	123
15,000	F_1	**100**	9,968	782	154
		500	9,820	778	153
		1000	9,571	774	155
	F_2	**100**	9,937	782	152
		500	9,665	777	155
		1000	9,301	778	154
20,000	F_1	**100**	9,705	769	180
		500	7,902	759	187
		1000	5,452	749	195
	F_2	**100**	9,539	770	183
		500	7,311	765	184
		1000	4,921	762	185
25,000	F_1	**100**	8,914	750	209
		500	3,598	724	220
		1000	807	708	228
	F_2	**100**	8,419	754	209
		500	3,186	759	214
		1000	691	734	235

Due to the use of a symmetrical parameterization across all species in this chapter, the size distributions of extant populations are unlikely to reflect those in nature. This is a difficult comparison to draw, however, because to do so requireseither calculating abundance distributions from empirical measurements of demographic parameters for all species in the network, or estimating model parameters from time series data of each species' abundance. In either case, data collection would take several field seasons of intensive observation on numerous taxa. Moreover, a comparison to empirical quasi-stationary distributions would apply only to scenarios with no directional change expected in the model parameter values. Climate change and anthropogenic land conversion render this an unlikely assumption. I discuss directional change in more depth in the Conclusion to this dissertation.

References

1. Méléard, S., & Villemonais, D. (2012). Quasi-stationary distributions and population processes. *Probab. Surv.* **9**:340-410.

CHAPTER 2
INTERACTION STRUCTURE AFFECTS THE RELATIONSHIP BETWEEN SPECIALIZATION AND STOCHASTICALLY-DRIVEN EXTINCTION RISK

Abstract

Population dynamics, environmental variability, and interspecific interactions are ubiquitous in natural systems and affect species' persistence. There is a recognized relationship between the community-level stability of species interaction networks and their structural properties. In mutualist networks, connectance and nestedness are associated with greater stability. Similarly, species-level properties such as specialization are thought to affect persistence. Here, I investigate how network properties affect the strength of the relationship between specialization and extinction risk. I calculate the connectance and nestedness of 35 plant-pollinator networks, and estimate species-level extinction risk for the 3794 species represented therein, using a stochastic, community-dynamic model. I then link the network-level properties to species-level extinction risk using a nonlinear mixed regression. In all networks, extinction risk decreased with number of mutualist partners for poorly-connected species, and approached an asymptote with increasing partner number. While specialists are more vulnerable than generalists to stochastic extinction, the regression shows that they experience lower extinction risk in highly connected and highly nested networks. Moreover, this extinction risk decays more rapidly with number of mutualist partners in highly connected and highly nested networks. These results demonstrate that network structure contributes to species-level extinction risk in dynamic, stochastic systems. Given the ecological and economic importance of pollination, it is crucial to understand the factors that contribute to ongoing wild pollinator declines.

This chapter builds on Chapter 1. The aims of Chapter 1 were to (a) show that stochasticity increases extinction risk in networks of interacting mutualists (thus extending the known single-species result to the community level), and (b) show that this stochasticity-introduced risk varies with number of mutualist partners. Here, I show how interaction structure in realistic networks can mitigate or exacerbate the relationship between partner number and extinction risk, for poorly connected species.

Introduction

Within the past decade, declines in wild pollinator populations have been documented in Europe (Biesmeijer *et al*. 2006) and North America (Grixti *et al*. 2009, Burkle *et al*. 2013). In the United States, such declines have prompted the listing of seven yellow-faced bees (*Hylaeus* spp.) as endangered (Endangered

and threatened wildlife and plants, 2016a), as well as a proposal to list a formerly widespread bumblebee species (*Bombus affinis*) as endangered (Endangered and threatened wildlife and plants, 2016b). Although less is known about population trends globally, land use patterns suggest that widespread pollinator declines are likely (Potts *et al*. 2010).

The potential impact of declining pollinator abundance extends beyond the elevated extinction risk that these species face. Because animal pollinators enable or increase the reproductive output of nearly 90% of flowering plant species (Ollerton *et al*. 2011), pollinator scarcity may limit plant population growth. While the importance of pollen limitation to reproductive success varies between plant species (Ashman *et al*. 2004, Biesmeijer *et al*. 2006), it has been shown to contribute to plant population declines.

The potential for extinction risk to propagate between species via their interactions motivates a large segment of the extinction risk modeling literature. Because ecological communities typically consist of numerous interacting species, the role of network structure in this process is of particular interest. In topological models that describe interaction structure but not population dynamics, extinction is introduced through a series of primary knockouts, which may be followed by the secondary loss of species whose prey and/or mutualists were previously removed. This approach has been used to compare the robustness of trophic (e.g. Dunne *et al*. 2002), mutualist (e.g. Memmott *et al*. 2004), and mixed-interaction (e.g. Pocock *et al*. 2012) networks to knockout sequences representing different types of pressures. Additionally, there is a growing body of work that incorporates additional considerations such as interaction switching (Kaiser-Bunbury *et al*. 2010), population dynamics (Abramson *et al*. 2011, Curtsdotter *et al*. 2011, Bewick *et al*. 2013) and stochasticity (Ives & Hughes 2002, Vieira & Almeida-Nieto 2015, Chapter 1 of this dissertation) into community network models.

This work has yielded insights about patterns in the relationship between interaction structure and persistence both at the community and species levels. At the community level, the network properties that are associated with greater stability differ by interaction type. For example, community stability improves with modularity in trophic networks and with nestedness in mutualist networks (Jordano *et al*. 2006, Okuyama & Holland 2007, Thébault & Fontaine 2010). At the species level, specialization is associated empirically with greater extinction risk (McKinney 1997, Biesmeijer *et al*. 2006, Brodie *et al*. 2014).

In Chapter 1, I demonstrated that environmental variability increases species extinction risk in a community-dynamic model. While this was true for all modeled

species, stochasticity increased the vulnerability of specialists more than that of generalists, over a wide range of environmental variability. This was true in the simplified four-species model, and for two empirically derived case studies. Here, I extend that work by modeling this relationship for 35 plant-pollinator networks from the empirical literature. I ask, at a given level of variance, (a) what is the shape of the relationship between specialization and extinction risk, (b) how general is this shape across networks, and (c) how is it influenced by network-level properties such as connectance and nestedness?

Methods

In order to investigate how realistic values of connectance and nestedness affect the relationship between specialization and extinction risk, I used a data set of 35 empirical plant-pollinator networks. I calculated extinction risk by parameterizing a stochastic, community dynamic model with each network, and simulating population trajectories over 1000 time steps. I then fit the relationship between specialization and extinction risk with a nonlinear, mixed regression model that takes into account the network-level properties of connectance and nestedness, as well as unknown network-level effects that influence species' extinction outcomes (Figure 2.1). Community dynamic simulations are carried out in MATLAB 2014b, and all other analyses take place in R 3.2.3.

Plant-Pollinator Networks

I simulated extinctions in 35 plant-pollinator interaction networks published in the peer-reviewed literature, accessible via the Interaction Web DataBase and R's Bipartite package (Dormann *et al*. 2008). I calculated the connectance and nestedness of each network using the Bipartite package in R 3.2.3 (Dormann *et al*. 2008, R Core Team 2015). Although these networks also vary in other ways, connectance and nestedness are more likely to have a direct bearing on the relationship between specialization and extinction than properties (e.g. modularity, web asymmetry) that constrain maximum partner number.

Connectance and nestedness are measures whose values reflect the number and identity of links in a network. Importantly, both have been identified as structural properties that affect the stability of mutualist networks (Okuyama & Holland 2007, Thébault & Fontaine 2010). Connectance is defined as the proportion of realized links, which is calculated here as the number of nonzero cells in the interaction matrix, divided by the product of the number of plants and the number of pollinators (Dunne *et al*. 2002). Possible values for connectance range from zero, where species do not interact, to one, where each species

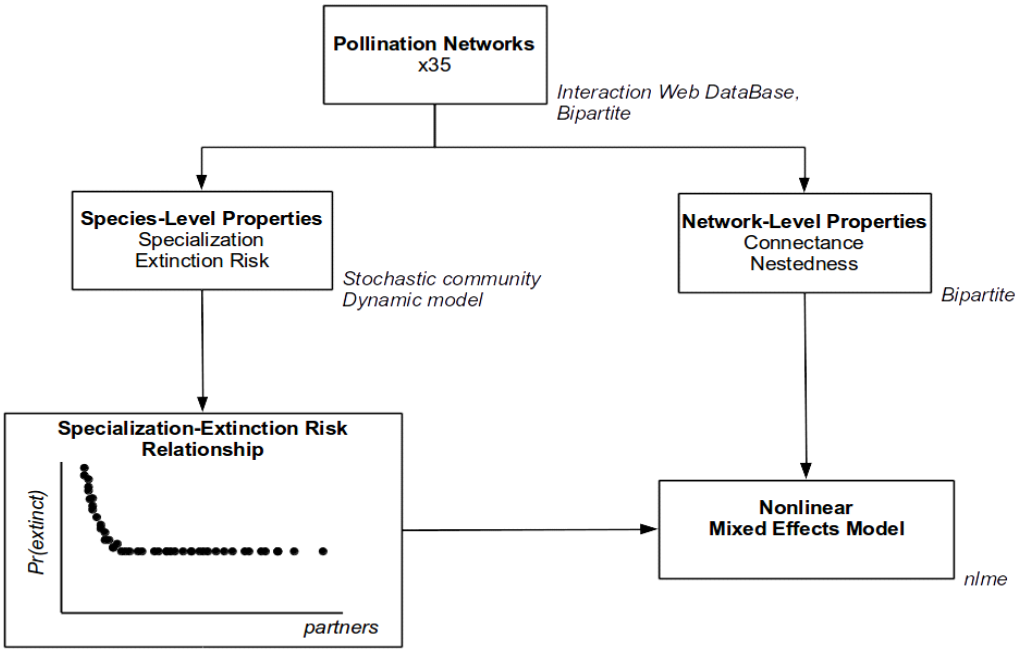


Figure 2.1. Methodological approach to assessing the influence of connectance and nestedness on the relationship between specialization and extinction risk.

interacts with every other. Nestedness describes the tendency of specialists to interact with generalists. In a perfectly nested community, a specialist plant (or pollinator) interacts with the most generalized pollinator (or plant) available, i.e. the one that interacts with the greatest number of other species. A plant with two mutualists interacts with the most- and second-most well connected partner available, and so forth. A network's degree of nestedness is expressed as a unitless 'temperature' between 0 and 100 that represents its relative disorder compared with perfect nestedness. Lower values thus signify greater nestedness (Rodríguez-Gironés & Santamaría 2006).

Table 2.1 summarizes the medians and interquartile ranges of network-level (network size, connectance, nestedness) and taxon-level properties (number of mutualist partners). Networks are composed of between 22 and 770 taxa, with a range of 7-104 plants and 9-679 pollinators. The median network size is 65, and the median number of plants and pollinators is 14 and 44, respectively. Taxa interacted with a minimum of 0 and a maximum of 189 mutualist partners, with a median of 2 partners. Connectance ranges between 0.02 and 0.42, with a median of 15% of possible links realized. The presence of more than one self-contained compartment in about half of the networks may explain in part why median connectance is fairly low-- median connectance for the 17 single-compartment networks is 0.22. Networks tend to be highly nested, with median nestedness of 11.5 and values ranging between 0.702 and 33.9.

Community Dynamics

I use a stochastic, discrete-time population model (Equation 2.1) to estimate the extinction risk of each species in each network. This model comprises a system of equations describing *n* plant and *m* pollinator species:

$$F_{i_{t+1}} = F_{i_t} + R_i\left(F_{i_t}, B_t, c_{F_i}, \varphi_{ij}\right)\left(\frac{\kappa_{F_i} - F_{i_t}}{\kappa_{F_i}}\right) - \left(1+\varepsilon_{F_{i_t}}\right)\mu_{F_i} F_{i_t} \qquad (2.1a)$$

$$B_{j_{t+1}} = B_{j_t} + R_{B_j}\left(B_{j_t}, F_t, c_{B_j}, \varphi_{ji}\right)\left(\frac{\kappa_{B_j} - B_{j_t}}{\kappa_{B_j}}\right) - \left(1-\varepsilon_{B_{j_t}}\right)\mu_{B_j} B_{j_t} \qquad (2.1b)$$

where $F_i(t)$ represents the population size of plant species *i* at time step *t*, and $B_j(t)$ represents pollinator species *j* at time *t.* These state variables loosely represent "flowers" and "bees" respectively. I assume that birth rates for all species depend upon the pollination mutualism and are density dependent with carrying capacity κ, and that mortality is density independent at a constant *per capita* rate of μ. In contrast to the entry point of stochasticity in Chapter 1, I

Table 2.1. Median and interquartile range for network-level properties and species-level properties (number of partners).

Properties		Median	Interquartile range	Minimum	Maximum
Network Level	Number of species	65	80.5	22	770
	Connectance	0.15	0.13	0.020	0.420
	Nestedness	11.5	14.5	0.702	32.9
Species Level	Number of partners	2	3	0	189

introduce stochasticity $\varepsilon(t)$ to this mortality term at each time step. This entry point maximizes the contrast between the analyses I undertake here and in Chapter 1; more importantly, it emphasizes the nonlinear shape of the relationship between partner number and extinction risk. As in Chapter 1, $\varepsilon(t)$ is drawn from a normal distribution centered at zero, and uncorrelated temporally and between species. Population sizes are constrained to be equal to or greater than zero. Once a population falls to or below zero, it is set to zero for the remainder of the replicate.

The first term on the right hand side of each equation is the population size of each species at time t. The second represents a birth function R, that defines each species' reproductive capacity in time step t as a function of its own density and that of its mutualists, whose identities are given by the interaction network used to parameterize the model. Here, I choose a birth function based on the harmonic mean of the abundance of a focal species and the sum of the abundances of its mutualists (see Chapter 1 for further elaboration on this choice). The birth function for plant species i is:

$$R_{F_i} = c_{F_i} \frac{F_{i_t} \cdot \sum_{j=1}^{m} \varphi_{F_i B_j} B_{j_t}}{F_{i_t} + \sum_{j=1}^{m} \varphi_{F_i B_j} B_{j_t}} \quad (2.2)$$

where R_{Fi} describes the reproductive output of plant i. Pollinators have an analogous birth function (not shown). The parameter c_{Fi} is the conversion rate between the number of floral visits made to species i and its reproductive output. The interaction strength φ_{FiBj} defines whether and how strongly each potential mutualist j affects the growth of the focal population i. I populate φ with a binary version of the empirical networks described above, where φ_{FiBj} takes a value 1 if plant i interacts with pollinator j, and has a value of 0 otherwise.

In order to isolate the effect of partner number and network topology, I hold all parameters except φ constant across all systems and species. For the purposes of this chapter, I use $\kappa = 1000$, $\mu = 0.1$, and $c = 1$. Asymmetries in these parameters lead to differences in equilibrium population size and population growth rate, potentially obscuring the influence of interaction structure on extinction risk (Appendix 1).

In environments with little variability, population dynamics are dominated by the deterministic skeleton of the model, and few extinctions result. In highly variable environments simulated at the same time scale, stochasticity drives most

populations extinct. Therefore, variation among species in their vulnerability to stochastic extinction only reveals itself at intermediate levels of environmental variation (see Figure 1.5)

For the baseline parameters, extinction outcomes vary greatly between species when stochasticity applied to the mortality parameter μ has a variance $\sigma^2_\varepsilon = 9$, something determined by initially scoping multiple possible variance levels (Appendix 2).

I simulated this model numerically using MATLAB 2014b. As in Chapter 1, I simulated the community dynamic model for 1000 time steps, and refer to the proportion of replicates where a species is lost as its extinction risk.
I ran 50,000 replicates simulating community dynamics for each of the 35 networks.

Nonlinear Mixed Effects Model

Species extinction risk has a nonlinear relationship with number of partners in both the linear and log-log plots, steeply decreasing with increasing partner for poorly-connected species, and saturating at an apparent minimum extinction risk for well-connected species (Figure 2.2a). This relationship was not apparent for the two community models considered in Chapter 1 (Figure 1.6) where I relied on linear fits. However, nonlinearity emerges more clearly when a larger set of networks is considered, as these span a greater range of size and structure. Applying stochasticity to mortality parameter μ emphasizes this nonlinearity.

To model the relationship between extinction risk and network structure, I used an exponential function that decays to an asymptote:

$$Pr(ext)_{ij} = a + b * \exp\left(-\left(c_0 + c_1 conn_j + c_2 nest_j\right) partners_{ij}\right) + \alpha_j + \epsilon_{ij} \quad (2.3)$$

where $Pr(ext)_i$ is the proportion of replicates where species i is lost from network j, $partners_{ij}$ is the number of species in network j that interact with species i, $conn_j$ is the connectance of network j, and $nest_j$ is nestedness of network j, α_j is a random effect shared by species within the same network and ϵ_{ij} is the species-specific error term. The parameter a defines the location of low-extinction-risk asymptote, and b defines the maximum distance between this asymptote and the intercept $a+b$. The c parameters determine how quickly $Pr(ext)$ changes with increasing partner number. At high values of c, specialists' extinction risk is close to the intercept; risk drops rapidly with increasing partner number; and most species have extinction risk near the value of the asymptote (Figure 2.2b). When

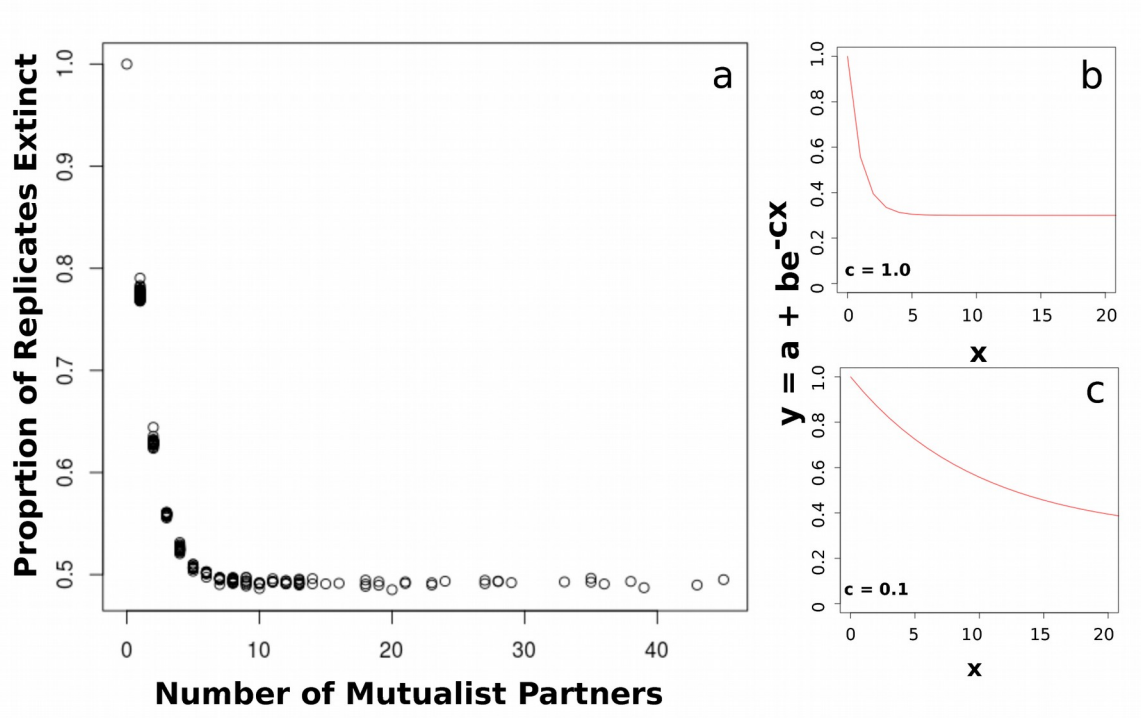


Figure 2.2. The relationship between number of mutualist partners and extinction risk in the output of the community dynamic model (a) and modeled by equation 2.3 (b,c). Panel (a) shows the proportion of replicates extinct for species with <= 20 mutualist partners, from the Kaiser-Bunbury control network (Kaiser-Bunbury *et al*. 2010), simulated using the default parameters. Panels (b) and (c) illustrate the shape of equation 2.3 when *c*=1.0 (b) and *c*=0.1 (c). Panels (b) and (c) are plotted using parameter values *a* = 0.3 and *b* = 0.7.

c takes a low value, specialists' extinction risk drops more slowly with partner number, and fewer species have *Pr(ext)* near the asymptote (Figure 2.2c). Because I am interested in how network properties affect the relationship between specialization and extinction risk, I treat them here as modifications to the *c* parameter.

When hypothesizing how network properties will affect the relative extinction risk of specialist and generalist species, it is important to recognize that connectance and nestedness increase the likelihood that poorly-connected species interact with well-connected ones. Nestedness measures this directly, while connectance increases species' average numbers of partners. Specialists interact with few species regardless of network connectance; therefore, increasing connectance implies that specialists' partners are increasingly connected. Since specialists rely on fewer mutualist partners than generalists do, their persistence relies more strongly on that of each partner. Generalists' robustness to partner loss is evidenced by the saturating relationship between extinction risk and number of partners in the community-dynamic model output (Figure 2.2). Because generalists' extinction risk is not substantially reduced with added partners, increasing connectance and nestedness should lead to a smaller difference between the extinction risk of generalists and specialists, and to a steeper drop toward the asymptote.

In the both the data sets and the community dynamic simulations, species are grouped by network. In order to reflect this structure in the analysis, I used a mixed regression model including a random effect associated with each community. One implication of this grouping is that extinction outcomes of species with the same number of partners in different networks may vary with network membership. This is the case both for the network properties that I model in equation 2.3, and for other known and unknown effects due to differences in structure and geography, as well as data collection protocol and date. Because the model assumes that species with no mutualist partners decline in a deterministic way, I assume that the unknown network-level differences affect the asymptote rather than the intercept. Consequently, I include nestedness and connectance as fixed effects, and treat all other network-level variation as a random effect on the asymptote *a*, denoted by α_j in equation 2.3. I carried out the model fit using the nlme package (Pinheiro *et al*. 2016) in R 3.2.3.

I first checked for collinearity among the different predictor variables, noting that the tolerance was 0.55, well within acceptable levels to proceed. An examination of the residuals from the regression fit revealed no evidence of bias, although there was some evidence of possible heteroscedasticity due to a greater spread of residuals for the most specialized species.

Results

Extinction Risk

In this chapter, I hypothesize that stochastically-driven extinction risk declines with partner number in a unified way across plant-pollinator networks, and that this relationship can be described with a decaying exponential function (Equation 2.3) when life history parameters and environmental variability are held constant. I also hypothesize that increasing connectance and nestedness increases the rate at which extinction risk drops toward the asymptote as partner number increases.

When fitted, all parameters in equation 2.3 are significantly different from zero (n=3794 species, $p < 0.001$) (Table 2.2), where the strong significance likely reflects in part the large sample sizes involved. At the median values of connectance and nestedness (Table 2.1), species that interact with a single partner have a predicted extinction risk of 0.77. Adding a partner reduces extinction risk to 0.63, halving its distance to the asymptote. Adding a third partner does the same ($Pr(ext)$= 0.56). Risk declines more slowly thereafter.

Extinction risk approached an average asymptote a of 0.49 (Table 2.2) with increasing partner number, meaning that well-connected species persist in about 50% of replicates. Network-specific a values were very consistent, ranging between 0.488 and 0.495.

While extinction risk behaves consistently across networks, the regression identifies significant effects of nestedness and connectance. The connectance coefficient c_1 significantly increases the steepness of the partners-risk slope for poorly-connected species, meaning that extinction risk drops more quickly with partner number for poorly-connected species in networks with high connectance. Specialists are also less likely to be lost in networks with high connectance: The model predicts that species with one partner have 1.3% lower extinction risk in the network with the highest connectance than those in the network with the lowest connectance.

By contrast, the nestedness coefficient c_2 significantly decreases the slope of the relationship between specialization and extinction risk. To interpret this result, it is important to remember how nestedness is measured across networks--specifically that nestedness decreases with increasing nestedness temperature. Therefore, the sign here indicates that specialization-extinction risk slope is greater at high nestedness, when controlling for connectance. Specialists are

Table 2.2. Parameter estimates, standard error and p-values for the fit of Equation 2.3 to the data (35 pollination networks) with a as a random effect.

Parameter	Estimate	Standard Error	*p*-value
a	0.49	0.0004	<0.001
b	0.57	0.0009	<0.001
c_0	0.70	0.0020	<0.001
c_1	0.09	0.019	<0.001
c_2	-0.001	0.0002	<0.001

also less vulnerable to extinction in highly-nested networks. The risk of extinction for a species with a single partner is predicted to be 1.2% less in the most nested network in the data set than in the least-nested network.

Discussion

In this chapter, I ask how the structure of plant-pollinator networks influences the relationship between specialization and extinction risk. In order to capture a range of realistic values of these properties, I analyzed a set of 35 empirical pollination networks taken from the peer-reviewed literature. First, I exploited the large variation among empirical networks (Table 1) to reveal more fully the shape of the relationship between specialization and species level extinction risk. Then, I explored variation between networks in this relationship, focusing in particular on the effects of connectance, which summarizes at the network level species' tendency to interact, and nestedness, which describes the tendency of poorly-connected species to interact with well-connected ones.

As in Chapter 1, I found that, at a particular level of variance, specialists went extinct more frequently than generalists. Although species' extinction risk decreases as number of mutualist partners increases, simulating a set of larger networks revealed that this relationship approaches an asymptote. For well-connected species, the addition or loss of a partner has little effect on extinction risk. This relationship was robust across all 35 networks. For poorly connected species, extinction risk decreases with increasing number of partners.

The rate at which extinction risk decays with partner number increases both with increasing connectance and increasing nestedness. Increasing connectance and nestedness also reduces the risk that a species with a single partner will be lost. These results are consistent with the hypothesis that interacting with well-connected partners reduces extinction risk in poorly-connected species. Nestedness addresses this relationship directly, by describing the propensity of poorly-connected species to interact with well-connected ones. In contrast, interactions between specialists and generalists are more likely in networks with high connectance because non-specialists interact with a greater number of partners (Note that in the regression fit the number of partners that a specialist interacts with does not itself increase with connectance; otherwise it would cease to be a specialist).

These outcomes are in concordance with expectations in the literature that connectance and nestedness confer stability at the network level (Okuyama & Holland 2007, Thébault & Fontaine 2010). But to date, this literature has focused

on deterministic stability properties of the community. In contrast, the approach I take here links these findings to species-level processes and to the possibility of stochastic extinctions arising from environmental variability.

Connectance and nestedness in mutualist networks have also been shown to follow geographic patterns. For example, Olesen & Jordano (2002) demonstrated that lowland networks have higher connectance than highland networks, and that plants are more generalized at higher latitudes and less so in the tropics. Consequently, the relationships I describe in this chapter predict that extinction risk drops more rapidly with partner number in lowland networks and that the loss of mutualist partners may be a more important contributor to extinction risk in tropical plants than temperate plants.

Like all ecological models, this one makes a number of simplifying assumptions. Here, I discuss three that I think were particularly important. Each of these three assumptions was made in order to try to isolate the relationship between network properties, specialization, and extinction risk, specifically. The three assumptions concern the choice to find extinction risk at a single variance; the decision to hold all life history parameters constant between species; and the use of binary networks to describe extinction risk. In Chapter 1, I showed how extinction risk in simplified networks increases with increasing σ^2_ε, a result that agrees with established theory (Simberloff 2008). While that remains true here (Appendix 2), the relationship between specialization and extinction risk only exists when extinction outcomes vary by species. Consequently I model extinction risk in this paper using a variance where these differences are particularly strong. Incorporating a wider range of variability into the understanding of how network properties change the relationship between specialization and extinction risk is an important next step.

Similarly, I also hold all life history parameters constant across species in this model. This has the effect of removing species-specific influences on equilibrium population size, thereby emphasizing the role of network structure, following the example of Bewick *et al*. 2013 (See Appendix 1 for a discussion of how asymmetric life history parameters influence relative extinction risk through differences in equilibrium population size). In natural systems, however, life history parameters do affect species' equilibrium abundances. In the data sets I use here, annual (e.g. *Helianthus petiolaris*, Clements & Long 1923), biennial (e.g. *Echium wildpretii*, Dupont *et al*. 2003)), and perennial (e.g. *Sanguinaria canadensis,* Schemske *et al*. 1978) plants are all represented, as are insect (e.g. bees such as *Apis mellifera*, Olesen *et al*. 2002) and vertebrate (e.g. hummingbird species including *Clytolaema rubricauda*, Vizentin-Bugoni *et al*. 2016) pollinators. While this information is important in assessing particular

species' vulnerability to extinction, that is not the aim of this chapter. Rather, I focus here on how network structure contributes to that vulnerability.

Another simplifying assumption that I make here is that each species interacts equally with each of its mutualist partners. In other words, the interaction strength between a species and one of its partners is the reciprocal of its total number of partners. While more sophisticated metrics exist, (e.g. Blüthgen *et al*. 2006), they are often affected by abundances, which are (a) controlled in the model by the parameter choices described above, and (b) not reported in the network data sets. It is nevertheless possible for species to be 'cryptic' specialists, i.e. interacting weakly with several partners and strongly with only a few (Brodie *et al*. 2014). For example, in the Flores data set, wild carrot *Daucus carota* is visited by three pollinators, but 84% of those visits are by a single species of fly, *Musca domestica* (Olesen *et al*. 2002). Because the relationship between specialization and extinction risk described in this chapter has the steepest slope for species that rely on very few partners, the results of this chapter underscore the importance of identifying cryptic specialists for conservation.

It is important to note, however, that the results of this chapter reveal that the relationship between specialization and extinction risk is robust over a range of realistic connectance and nestedness values. Much of the theory that models extinction risk in interacting communities emphasizes the role of network structure on community-level stability. I show in this chapter how the structure of plant-pollinator networks affects the relationship between a risk factor and extinction outcomes at the species level. Moreover, I demonstrate that these patterns exist when population dynamics and environmental variability are present (as they are in natural systems).

Pollination is essential to the maintenance of terrestrial ecological and agricultural systems. Consequently, it is important to understand the factors that contribute to pollinator declines, and their community-level consequences. In Part 1 of this dissertation, I show that stochasticity is one such factor that should be taken into account. Although it has long been known that stochasticity reduces persistence times, I show here that not all species are affected equally. Rather, specialists' vulnerability increases more rapidly than that of specialists, and that network structure mediates the shape of this relationship.

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Appendix 2

Choice of Variance

I demonstrated in Chapter 1 that extinction risk increases with increasing environmental variability (Figure 1.5) for all species in a simplified network. Extinction risk increased more quickly for specialists than for generalists, such that the proportion of replicates where specialists were lost was always at least as high as that where generalists were lost. This gap is the largest at intermediate variances, and disappears at very low variances (where nearly all replicates persist) and very high variances (where most species go extinct).

This pattern is also present in the 35 empirical plant-pollinator networks that I simulate in Chapter 2 (Figure A2.1). At $\sigma^2_\varepsilon = 4$, extinction risk was near zero for all species, and there was little difference in specialist and generalist outcomes. At a variance of $\sigma^2_\varepsilon = 12$, extinction risk ranged between 0.85 (generalists) and 1.0 (specialists with a single mutualist partner), a difference of about 0.14. At $\sigma^2_\varepsilon = 9$, the difference in extinction risks was about 0.51.

Since the questions I address in Chapter 2 deal with the relationship between number of mutualists partners and extinction risk and how network properties change that relationship, I focus my efforts on the case of $\sigma^2_\varepsilon = 9$, where this relationship is the most pronounced.

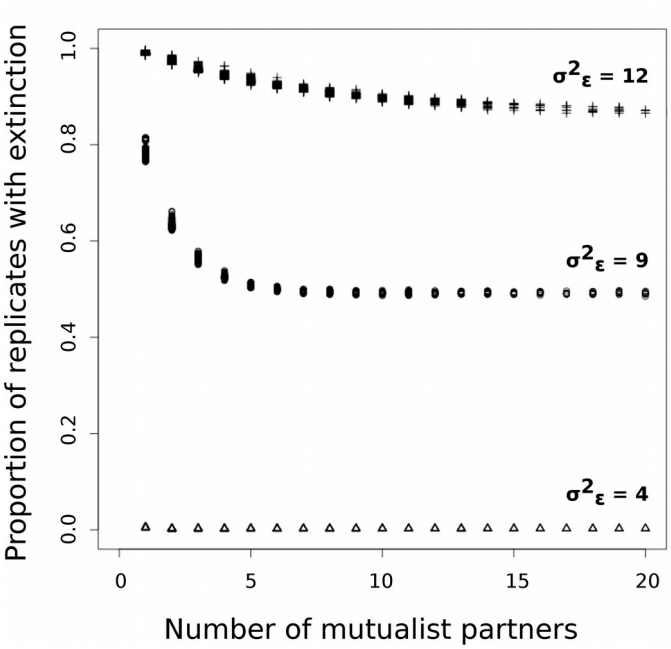


Figure A2.1. Extinction risk (proportion of replicates where a species goes extinct) plotted against mutualist partner number for all species in the 35 empirical networks, when simulated using stochasticity with variance σ^2_ε = 4, σ^2_ε = 9, and σ^2_ε = 12 (and the default parameter set as defined in the main text). Here, I show only species with <=20 mutualist partners. Although many of the networks contain species with more partners, extinction risk approaches and asymptote.

CHAPTER 3
LOCATING HUMAN RESOURCES TO REDUCE THE COST OF MANAGING NETWORKS OF PROTECTED AREAS

A version of this chapter was originally published by Christine E. Dumoulin, Tyler Macmillan, Rob Stoneman, and Paul R. Armsworth:

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CED wrote the software model, ran analyses and was the lead author on the manuscript. CED and PRA designed the research. TM and RS provided data. PRA, TM and RS contributed substantially to manuscript revisions.

Abstract

Conservation organizations that manage networks of protected areas commonly require staff to travel to those areas for management and monitoring purposes. I examine how conservation organizations can reduce the resulting travel costs by locating human resources effectively. Specifically, I focus on the problem of siting the home offices of management staff, in a way that minimizes the travel costs involved. I illustrate the importance of travel cost using two case study applications, the Yorkshire Wildlife Trust (YWT), UK, and the Northwest Florida Water Management District (NWF), USA. For YWT, siting an additional office effectively could save $43,000 in annual travel costs. Optimally siting NWF’s four existing offices could save $95,000 annually. These savings are sufficient for each organization to acquire 171-360 additional hectares of protected area or to hire an additional protected area manager. I also calculated the reduction in greenhouse gas emissions made possible by optimizing office locations.

Introduction

Faced with limited funding, conservation organizations must aim to allocate what resources are available to conserve species and ecosystems as effectively as possible. Framing choices between different conservation strategies as optimization problems can enable conservation organizations to identify those choices that will provide the greatest conservation benefit per dollar invested (Groves 2003, Murdoch *et al.* 2007 Moilanen *et al.* 2009, Wilson *et al.* 2009, Cullen 2012). Recently, there have been calls for conservation groups to consider other organizational aspects, such as how they structure their operations, through a similarly strategic lens (Kark *et al.* 2009, Sutherland *et al*. 2009, Armsworth *et al*. 2012). While many authors have focused on where

conservation groups should allocate funding for land acquisition or management (e.g. Meyers *et al.* 2000, Underwood *et al.* 2008), allocating available human resources to support conservation actions is also important. Here I focus on a particular version of this question-- namely, where should a conservation organization locate its staff relative to its protected areas, in order to carry out conservation actions cost effectively?

Spatial prioritization studies in conservation planning have tended to focus on the efficient selection of protected areas (Cullen 2012). In addition to the spatial distribution of biodiversity, recent examples account for factors such as heterogeneous land costs (Ando *et al.* 1998, Armsworth 2014), heterogeneous threats (Strange *et al*. 2006, Pressey *et al.* 2007, Wilson *et al*. 2007, Wade *et al*. 2011), the use of different types of conservation activity in different locations (Murdoch *et al*. 2007, Wilson *et al.* 2007) and the optimal sequencing of land protection efforts (Costello & Polasky 2004, Strange *et al.* 2006). Some authors have explicitly considered distances between candidate locations for protected areas and their proximity to other features on the landscape (e.g. Önal & Briers 2002, Williams 2008, Bauer *et al.* 2009). For example, when choosing protected areas intended to support recreation as well as biodiversity goals, distance to population centers is important (Önal & Yanprechaset 2007). In addition, proximity between protected areas can influence the likelihood that protected species actually persist (Williams 2008, Bauer *et al.* 2009).

In this paper, I take a spatial approach to siting human resources to reduce management-necessitated travel costs. Conservation organizations that are active in land protection commonly maintain a small number of administrative offices where staff are based, and employ a team of site managers who travel from these offices to visit protected areas to conduct management, monitoring and maintenance activities. With this organizational structure, office-to-site travel is necessary but costly in terms of manager time, as well as fuel and maintenance of organization-owned vehicles. While by no means the biggest cost component involved in protecting land, travel costs can nonetheless sum to meaningful amounts when totaled across a protected area network, as I show below. Locating offices and staff to reduce these travel costs would allow some of the funds used for travel to instead be used directly for conservation action (e.g. land acquisition, hiring additional staff).

Like other spatial prioritization studies in conservation planning, I draw on techniques from location science, an active area of operations research (Hale &

Moberg 2003, ReVelle & Eiselt 2005, Daskin 2008). Reserve site selection has adapted covering problems from the field of discrete location science to maximize species representation in protected area networks (ReVelle *et al.* 2002). Similarly, I find the *p*-median problem to be a well-studied analogue to the efficient siting of conservation staff (Reese 2006, Daskin 2008). The *p*-median problem places *p* supply points (e.g. warehouses) into a network to serve *n* demand nodes (e.g. retail outlets) in a way that minimizes the total distance between each demand node and its nearest supplier (Hakimi 1965, Daskin 2008). Here, conservation offices represent supply points of the management effort demanded by the organization's protected areas.

A full accounting of the travel costs involved in protected area management should also include the resulting greenhouse gas (GHG) emissions. Many conservation organizations involved in managing protected areas are also involved in policy and advocacy campaigns seeking to persuade other sectors of society to reduce their greenhouse gas emissions. It is imperative therefore that conservation organizations are seen to be taking whatever steps possible to reduce their own emissions (National Park Service, http://www.nps.gov/climatefriendlyparks/, accessed on June 6th, 2013). What studies are available to date suggest that many conservation organizations do not have a climate mitigation plan (Lemieux *et al.* 2011a), but that changes to their operations can reduce GHG emissions substantially. For example, Parks Canada reduced emissions from its operations by 10.5% within a decade (Lemieux *et al.* 2011b).

To explore the savings made possible by reducing management-related travel, I apply a heuristic office-siting algorithm to two real-world case studies. For each, I find travel-minimizing locations for their existing offices, and for an additional office, given the existing configuration. I compare the resulting annual travel savings with the cost of (*a*) land acquisition and (*b*) hiring additional managers. I also calculate the differences in travel-related GHG emissions produced in each case, and estimate their social cost.

Methods

Case Studies

To demonstrate the benefit of using optimization approaches in conservation office siting, I analyzed two case studies. These differ in organizational structure,

regional extent and shape, road density and settlement patterns. For each case study, I explored the advantages of (a) optimally re-siting all existing offices and (b) optimally siting an additional office with the current configuration. For both formulations, I assume that the protected areas and their management burdens are already established.

Yorkshire Wildlife Trust

The Yorkshire Wildlife Trust (YWT) is a regional conservation nonprofit with a land trust like business model. YWT manages 84 small protected areas covering 2067 Ha distributed across the county of Yorkshire (UK) (Figure 3.1a). Staff involved in site management are based out of 2 offices, one in York and one located onsite at Potteric Carr, their most intensively managed protected area. Levels of management effort applied to each site were obtained using a questionnaire survey of site managers (see Armsworth *et al.* 2011).The median annual management cost per protected area is $3,204 in 2008 equivalent US dollars (Armsworth *et al.* 2011).

NorthWest Florida Water Management District

The Northwest Florida Water Management District (NWF) is one of five districts covering the state of Florida (US), which enact water-quality projects, water-use permitting, and the acquisition and management of wetlands, floodplains and uplands for water resource protection. NWF (Figure 3.2a) manages 12 protected areas and 19 conservation easements totaling 89,396 Ha. Properties managed by NWF are larger, more distant from each other and more elongated than those managed by YWT. NWF is subdivided into three management regions, each served by a regional office. Conservation easements are monitored once a year, from the NWF headquarters. Management effort is determined from time sheets spanning January 2008 to May 2012.

Solution Method

I based my approach to minimizing total annual travel between management offices and protected areas on the *p*-median problem (Hakimi 1965, Daskin 2008). In my formulation, management offices ‘supply’ conservation effort to a set of protected areas that each demands some level of management. I use the number of manager-days spent annually at each protected area as a measure of demand. Because the spatial distribution of management effort may not always be known, I explore the consequences of simpler weighting schemes in the supporting information (Appendix 3).

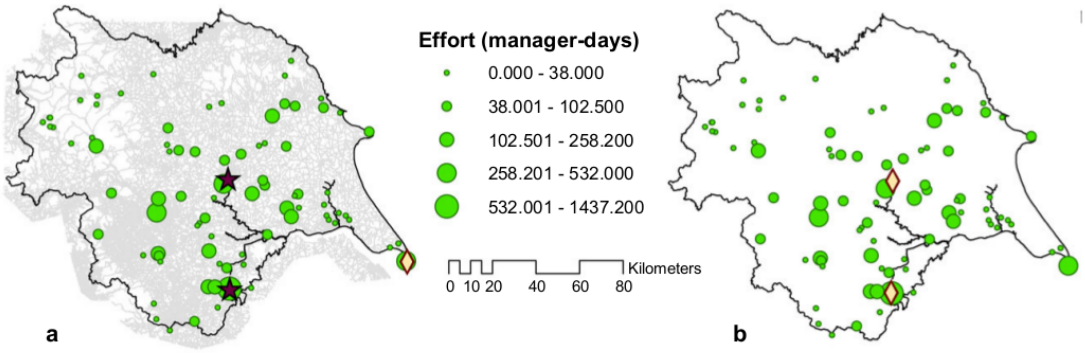


Figure 3.1. (a) Yorkshire roads (gray lines), and YWT's protected areas (circles) and offices (stars). The size of each circle denotes the number of manager-days are spent annually at that site. A travel-minimizing third office (diamond) would be placed at Spurn, the largest and second most intensively managed protected area. (b) The travel-minimizing configuration of two offices (diamonds) is similar to their existing locations.

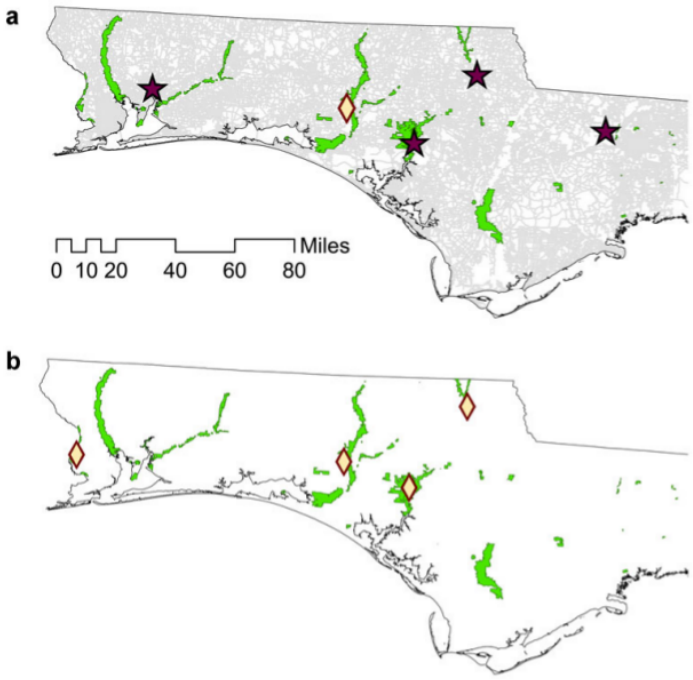


Figure 3.2. (a) NWF's road network (gray lines) and managed lands. Four offices carry out NWF's management and monitoring activities (stars). A travel-minimizing fifth management office (diamond) would be located in the middle of the region. (b) The travel-minimizing locations of four offices (diamonds).

To simplify the optimization problem, I restrict the search for office locations to road junctions and endpoints. Similarly, I assume that conservation demand occurs at the centroid of each protected area rather than across its spatial extent (but see Appendix 3 for sensitivity tests on the number and location of centroids). This discretized problem always has at least one optimal solution (Hakimi 1965). Discretizing the solution space reduces the number of possible office locations to 670,543 in YWT and 150,634 in NWF. To find travel-minimizing sets of office locations, I used ArcGIS 10 (ESRI) to calculate the road distance between the centroid of each protected area and every possible office location. I then imported these distances to MATLAB 2011a (Mathworks), and applied an interchange algorithm (Teitz & Bart 1968) to find an optimal office placement (see Appendix 3). This algorithm is a commonly used heuristic for solving *p*-median problems (Reese 2006). When choosing multiple office locations, I ran the algorithm 100 times with a random initial solution set.

The office siting algorithm generates a set of travel-minimizing office locations, as well as the total annual distance that managers would travel from those offices to maintain all protected areas at present effort levels. In both cases, I assume that each protected area is managed by its nearest office. Distance is a natural metric to express travel savings, but because I am interested in how those savings compare to the magnitude of other conservation costs (e.g. land acquisition, cost of employing site managers), I convert the results into monetary values. To calculate a time cost, I use average speed data (USDOT 2009, Wang *et al*. 2009) and staff pay rates (provided by YWT and NWF). I use government reimbursement rates to estimate the costs of fuel and vehicle wear. In calculating costs, I accounted for the average number of managers per vehicle (see Appendix 1 for details). All monetary amounts are presented in 2008 equivalent US dollars.

I also estimated GHG emissions that would result from travel. I converted annual travel distances to tonnes of CO_2e emissions using The Nature Conservancy's carbon footprint calculator (http://www.nature.org/greenliving/carboncalculator/index.htm, accessed on March 14th, 2013) for mid-size (20-30 mpg) and large (<20 mpg) vehicles. I convert the CO_2e estimates to dollar values using $12, the mean value of social cost estimates collected by the IPCC 4th Assessment (IPCC 2007), as well as the more conservative estimate of $85 suggested in the Stern Review on the Economics of Climate Change (Stern 2007). Converted to 2008 equivalent dollars, these values are $12.46 and $88.26, respectively.

Results

Office Placement

Table 3.1 details my estimates of management-related travel costs in terms of monetary value (Table 3.1, first column) and associated GHG emissions (second column). Costs are shown for (a) the current office configuration of YWT and NWF, (b) for an optimized placement of existing offices, and (c) the optimized placement of an additional office.

These results are underpinned by my use of existing management effort data to estimate conservation demand at each protected area. Other weighting schemes based on more easily obtained data, such as the size of each protected area, are possible. However, using the size of protected areas as a proxy for management effort can result in inefficient recommendations because effort scales differently with area for different conservation networks (see Appendix 3 for a comparison between YWT and NWF).

Yorkshire Wildlife Trust

For YWT, my analysis identified travel-cost minimizing office locations very close to the organization's existing offices. These are located near protected areas whose management demands are heavily weighted (Figure 3.1b). The optimized office configuration offers a slight reduction in travel costs, of about $2000 annually, and would also prevent the emission of about 1 tonne of CO_2e.

Both existing offices are located within the main cluster of protected areas, but both are relatively far from the site with the second-highest management demands. A third office, optimally sited in or near this protected area, would save $43,000 in travel costs and 19-21 tonnes of CO_2e annually. This reduction in emissions from adding a third office to YWT could reduce the social cost of its operations by $237-262 annually when using the IPCC's estimate of social cost of CO_2e emissions, or $1677-1853 when using the Stern Review's estimate.

NorthWest Florida Water Management District

Optimizing the locations of all four management offices across NWF results in a configuration (Figure 3.2b) in which three of the offices are near their current locations and the fourth is quite different. This revised configuration could reduce annual management-related travel cost by $95,000. Expansion of the existing office configuration by adding an optimally-placed fifth office (Figure 3.2a) would save $60,000 per year.

Table 3.1. Estimate of annual cost of management-related travel (2008 dollars) and annual GHG output from management trips (CO2e) for both YWT and NWF. Numbers are given for the current configuration of offices in the region (first row), a travel-minimizing configuration with the same number of offices (second row), and for a configuration of existing offices with a travel-minimizing additional office.

	YWT		NWF	
	Travel Cost (2008 dollars)	**GHG Emissions (tonnes CO_2e)**	**Travel Cost (2008 dollars)**	**GHG Emissions (tonnes CO_2e)**
Current	$128,000	54 (mid-size car*) 62 (large car†)	$199,000	74 (mid-size car*) 86 (large car†)
Optimized (all offices)	$126,000	53 (mid-size car*) 61 (large car †)	$104,000	39 (mid-size car*) 45 (large car†)
Optimized (additional office)	$85,000	35 (mid-size car*) 41 (large car †)	$139,000	52 (mid-size car*) 61 (large car†)

** 20-30 miles per gallon (47-71 km/L)*
† less than 20 miles per gallon (47 km/L)

In terms of GHG emissions, optimally locating four offices would save 35-41 metric tonnes of CO_2e emissions per year with an estimated social cost of $436-511 using the IPCC estimate and $3089-3619 using the Stern review's estimate. Taking the current office locations as given but expanding by adding a fifth optimally sited office would reduce travel-related emissions by 22-25 tonnes of CO_2e per year with a social cost savings of $274-312 (IPCC estimate) or $1942-2207 (Stern Review estimate).

Discussion

Organizations active in conservation management necessarily face travel costs in managing their protected areas. I examine how organizations can reduce these costs by allocating their staff resources effectively. My case studies reveal that some conservation organizations may have arrived near a travel-minimizing configuration without ever having relied on a formal algorithm and careful travel cost accounting, while others may not. My approach can also be used to estimate where the greater savings lie - whether in a reconfiguration of existing offices or in the addition of a new office.

Here I seek to put the magnitude of the possible savings in better context for conservation. The savings from a travel-minimizing additional YWT office is 13 times the annual median cost of managing one of its protected areas. These savings are also more than enough to employ an additional site officer at current salary rates. Reorganizing the offices of NWF into a travel-minimizing configuration also saves nearly twice the salary of a management officer. Alternately, travel savings could be used to acquire new protected areas. The addition of a travel-minimizing third office to YWT yields savings with a net present value (5% discount rate) of $860,000. This would be enough to acquire 360 hectares of comparable protected land in Yorkshire using the median of past acquisition costs paid by YWT. Similarly, the savings resulting from a reconfiguration of NWF's four existing offices have a net present value of $1,900,000, enough to acquire 171 hectares in Northwest Florida at a median price of $11,085 per Ha (USDA 2007). The savings that I detail here are increased slightly (by 0.5-4.5% annually) by including the estimated social costs of carbon, although there is no means for these externalized costs to be recovered by the organizations.

I have developed this analysis from the perspective of expanding conservation networks, but organizations facing budget shortages may also consider closing offices. In these cases, this analysis could identify which office closure affects travel cost the least. As a hypothetical example, an office closure would increase

NWF's annual travel costs by $11,000-$229,000. Similarly, were YWT to close an office, its travel costs would increase by $56,000-$72,000 annually. Although office closures reduce other operating expenses, the increase in travel costs may be substantial.

My results illustrate the importance of considering office-to-site distance when choosing office locations. In practice, travel cost would be included alongside many other considerations. The cost of opening and closing offices varies spatially, affected by land values, zoning, and whether the new office must be rented, bought or built. Quality-of-life considerations also figure in to many business relocation decisions (Love & Crompton 1999), because factors like housing availability, commuting time and school quality affect organizations' ability to attract and retain employees. My model can be extended to address such concerns, for example by restricting candidate sites to those within a specified driving distance of the nearest population center. A related consideration is that longer home-to-work commutes could increase GHG emissions from employees' vehicles, potentially offsetting some of the carbon savings associated with an office location that only minimizes management-related travel. Moreover, regional offices have other benefits and costs that should be considered in actual siting decisions, such as providing conservation organizations with an on-the-ground presence through which to connect to local communities.

Introducing greater detail into the analysis clearly improves its applicability. At the same time, the cost of data collection and the human effort needed to conduct an analysis increases as detail is added. Because conservation planning is itself costly (Groves 2003, Bottrill & Pressey 2012), one important extension of my work would be an evaluation of just how much detail is needed in different aspects of office location decisions in order to offer a reasonable level of efficiency gain. For example, the assumptions I make about the distribution of management effort across protected areas affect the cost of the solutions. In my illustrative examples, I started from the current protected area networks and had detailed information on the allocation of recent management effort across these protected areas. For some applications, such information may be costly to collate. In order to test the importance of management effort to travel cost, I re-created two simple approaches to data-poor scenarios (assuming that all reserves receive equal management effort, or that management effort scales linearly with protected area size) and calculated their travel cost under current management regimes (Appendix 3). In YWT, optimizing office locations under the assumption that all areas require equal management effort gives an office configuration that would increase annual travel costs by $20,000 compared to the current office locations when the actual distribution of management effort is

applied. In NWF, using the size of protected areas instead as a proxy for management demand increases annual travel cost by $100,000 compared to the existing office configuration. This suggests that realistic management effort data may play an important role in this type of analysis. It is also possible that travel costs already affect how management effort is distributed across sites, in which case changing the office configuration could also change the amount of effort directed at each site. Organizations may even prioritize areas for protection differently, something I will examine in future work.

Conservation organizations, like other businesses, stand to benefit from increasing the efficiency of their operations. Much could be gained by broadening application of techniques from the field of operations research, beyond their customary application to reserve site selection problems to other decisions that conservation organizations take. This is something I have sought to illustrate here by considering where conservation organizations should locate the human resources they have available for management.

Acknowledgements

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Appendix 3

Optimization Workflow

In order to find office placements, I developed a workflow that integrates ArcGIS 10 and MATLAB (2011a). I used ArcGIS for data processing and preparation, and MATLAB (2011a) for finding travel-minimizing office locations (Figure A3.1).

I found the centroid of each protected area, and calculated the over-road distance between each centroid and every road junction or endpoint using ARCGIS's Network Analyst toolbox. These distances were stored in an origin-destination (OD) cost matrix, which I imported to MATLAB to find travel-minimizing office locations.

Because each site's management demand affects the number of trips that staff make to that site, I weighted each protected area by management effort before optimizing for office location. Specifically, I multiplied each protected area's distances in the OD cost matrix by the management effort devoted to that protected area (in manager-days per year). Higher effort levels translate to longer weighted distances, which serve to 'pull' the optimal office locations closer to heavily-managed areas than to less intensively managed ones.

To find travel-minimizing office locations, I implemented the interchange algorithm (Teitz & Bart 1968). The interchange algorithm is a standard heuristic for solving p-median problems (Reese 2006). It takes an initial solution set of p nodes, then replaces solution nodes one by one with others not in the solution set. Swaps that decrease the total travel distance are kept, and the process continues on the new solution set either until it is improved, or all swaps with non-solution nodes have been tried. I ran the optimization 100 times for each case study, with random initial office placements.

Cost Conversion

The output of the office siting algorithm includes the total distance that managers travel annually to serve all protected areas at the present effort levels. Because I am interested in how that savings compares to other conservation costs (e.g. land acquisition, cost of employing managers), I convert it to a monetary value.

Total annual travel cost depends on the cost of employee time and the cost of operating vehicles, including fuel and wear and tear. Although the two are

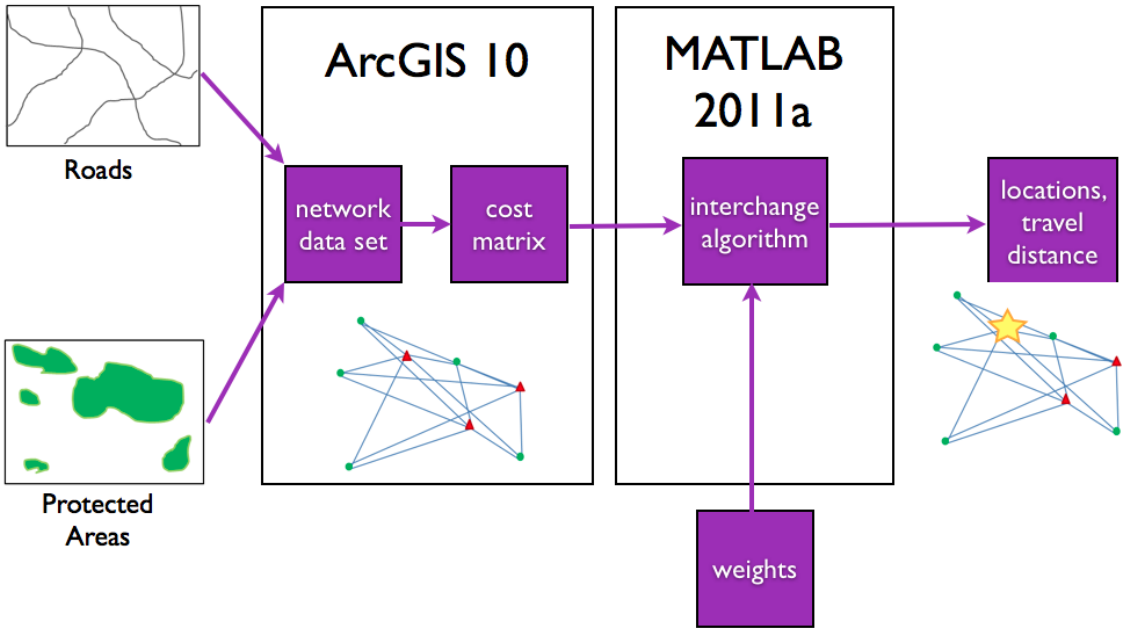


Figure A3.1. Workflow to find travel-minimizing office locations, given data on existing protected areas and roads. All data are in the form of ArcGIS layers. Data processing, including the calculation of an origin-destination cost matrix, takes place in ArcGIS 10. MATLAB is used to find travel-minimizing office locations.

related, employee costs increase with travel time, whereas vehicular costs increase with travel distance:

$$c = 2d\left(\frac{hm}{s} + r\right) \qquad \text{(A3.1)}$$

where *d* is the total weighted annual trip distance. The solver returns this value along with the travel-minimizing office locations. I assume that managers return to the office after each site visit, doubling the annual distance driven. Manager travel costs accrue with hourly pay rate h, number of managers per vehicle m (here, I assume that *m* is 1.5), and the inverse of average vehicle speed s. Vehicle-related costs depend only on the travel distance, and I represent them using the governmental reimbursement rate, *r*.

I calculated the cost of employee travel time by multiplying the average hourly pay rate by the duration spent in the vehicle, i.e. the reciprocal of average vehicle speed. For YWT, I used an hourly rate of £10/hr ($18.52/hr), and for NWF, I used $24 per hour (calculated from time sheet data provided by NWF).

The average traffic speed in England in 2009 was 49.2 km per hour (Wang *et al*. 2009). To find the average traffic speed in Florida over the same period, I used the 2009 National Household Travel Survey (NHTS 2009). The travel day trip data set contains durations and distances of all trips made by a survey respondent on an assigned day. For all over-road trips taking place in Florida on weekdays, I divided the trip distance by its duration to find the average vehicle speed per trip. The average speed over these trips was 45.2 km per hour.

I used governmental reimbursement rates as an estimate for vehicle-related costs. The UK government reimburses at a rate of 40p/mile (46¢ per km), and the US government reimbursed at a rate of 34¢ per km for 2009 (http://www.irs.gov/uac/IRS-Announces-2009-Standard-Mileage-Rates, accessed on March 15th, 2013).

Greenhouse Gas Emissions Estimates

I estimated each organization's yearly output of greenhouse gases (CO_2 equivalent) using a carbon footprint calculator provided by The Nature Conservancy (http://www.nature.org/greenliving/carboncalculator/index.htm, accessed on March 14th, 2013). The calculator takes an annual distance driven (in this case, the output of the office location algorithm) and calculates greenhouse gas emissions based on fuel efficiency. I calculated emissions for two sizes of vehicles (Table 3.1).

Importance of Weighting by Management Effort

Minimizing office-to-site travel requires information on the locations of protected areas and of potential office sites. The amount of management demanded by each protected area is also an important factor, because frequently-visited protected areas comprise a disproportionate share of travel. In the main text, I used management effort (number of manager-days spent at each protected area annually) as a measure of conservation demand.

In the illustrative examples, I took the current protected area networks and had detailed information on the allocation of recent management effort across thes protected areas. The spatial distribution of management effort is not necessarily fixed over time. For example, management effort was heavily allocated to NWF's westernmost protected area during the time period covered by the dataset. This concentration of effort reflects a pulse of startup work on that property, which NWF had recently acquired. Changes in management effort over time affect how closely the estimated and actual management distributions, and therefore affect the ability of my analyses to identify cost-minimizing solutions.

To show the importance of using realistic management effort data, I re-create two simple approaches to data-poor scenarios and calculated their travel cost under current management regimes. First, I explore the inefficiencies that would result if seeking to minimize office-to-site travel when only accounting for the locations of protected areas. I illustrate this using data for YWT. Next, I use NWF to illustrate that weighting by area instead of actual management effort also is problematic. Finally, I compare area and management effort for both YWT and NWF to show that the allocation of management effort among protected areas can be organization-specific.

Ignoring management demand altogether when choosing office locations is equivalent to siting offices to minimize total over-road distance between offices and protected areas. To compare the usefulness of weighted and unweighted solutions, I ran the optimization for 2 offices in the YWT case study with all weights set to 1. I then calculated travel cost under the current management regime.

The office configuration resulting from the unweighted problem (Figure A3.2, left) incurs an annual travel cost of $148,850, which is $20,549 greater than YWT's current travel cost. Not only does the unweighted solution fail to reduce travel under the current distribution of management effort, this result emphasizes that optimizing with respect to the wrong criteria can actually increase costs.

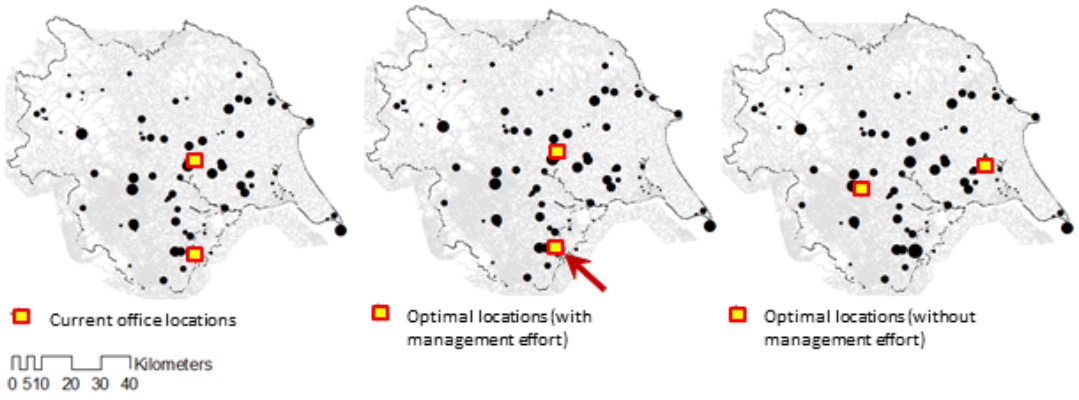


Figure A3.2. Left: Current office locations. Center: Optimal office locations, when travel is weighted by the number of days spent at each protected area over the course of a year. The arrow points to the protected area with the most management (1437 manager-days), which has almost three times more than the next most managed site (532 manager-days). Right: Optimal office locations, when sites are not weighted.

For both case studies, I collected management effort data not included in the GIS layer that contains the sizes and locations of protected areas. If management effort scales with area in a consistent way across different sets of protected areas, then future applications of the office placement problem could perhaps generate good solutions without needing effort surveys or time sheet data. I also explored the usefulness of weighting by area in the NWF case study. As with the unweighted problem, travel costs are calculated under the existing distribution of management effort.

Weighting by management effort and area can give dramatically different results (Figure A3.3). The annual travel cost of the management-weighted solution is $103,530. When the optimization is weighted by area, the annual travel cost of the solution is $133,688.

Finally, linear regression of management against site area shows that, for different organizations, effort scales differently with protected area size (Figure A3.4). I performed the regression against each organization's recorded or estimated distribution of management effort. All sites in NWF had at least one manager-day of effort (left), and I removed non-managed sites from the analysis for YWT (right).

For YWT, management effort scaled with area with a slope of 0.45 (s.e. 0.06, p = 8.943x10 -12 , r 2 = 0.4736). This slope is substantially lower than NWF's 0.94 (s.e. 0.13, p = 1.166x10 -7 , r 2 = 0.626). Despite having many conservation easements that get 1163 manager-day of effort annually regardless of their size, the management demands of NWF's sites grow much more rapidly with area than do those of YWT.

Additionally, management effort scales approximately linearly with area for NWF but at something closer to the square root of site area for YWT, as can be seen by back-transforming the data in Figure A3.4. It appears based on these two case studies therefore that the management effort-area relationship may not generalizable across conservation organizations.

Sensitivity Tests on Selected WMAs in NorthWest Florida

Many of the protected areas in NWF, particularly those along rivers, are large and elongated compared to their counterparts in YWT. In the main text, I treat the centroids of all protected areas as destinations for management-related travel. For large and/or elongated areas, centroids may be a poor representation of the spatial distribution of management effort. The presence of a river through a

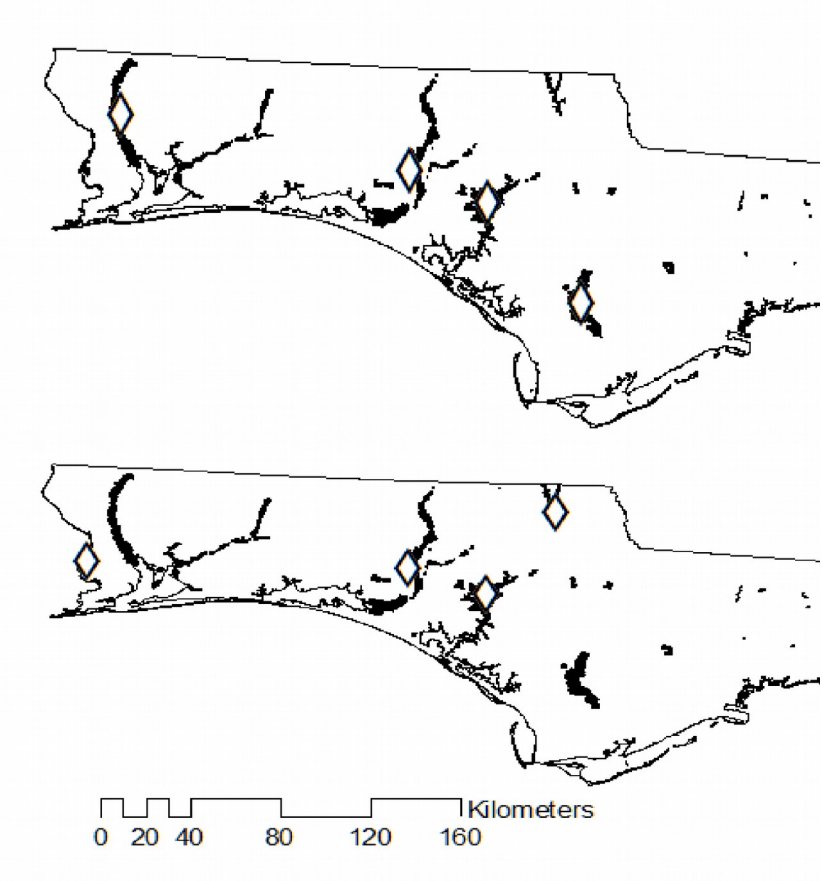


Figure A3.3. Top: Four travel-minimizing office locations, when the solution is weighted by the area of each site. Bottom: Four travel-minimizing offices when travel is weighted by management effort (the number of manager-days spent at each protected area, annually).

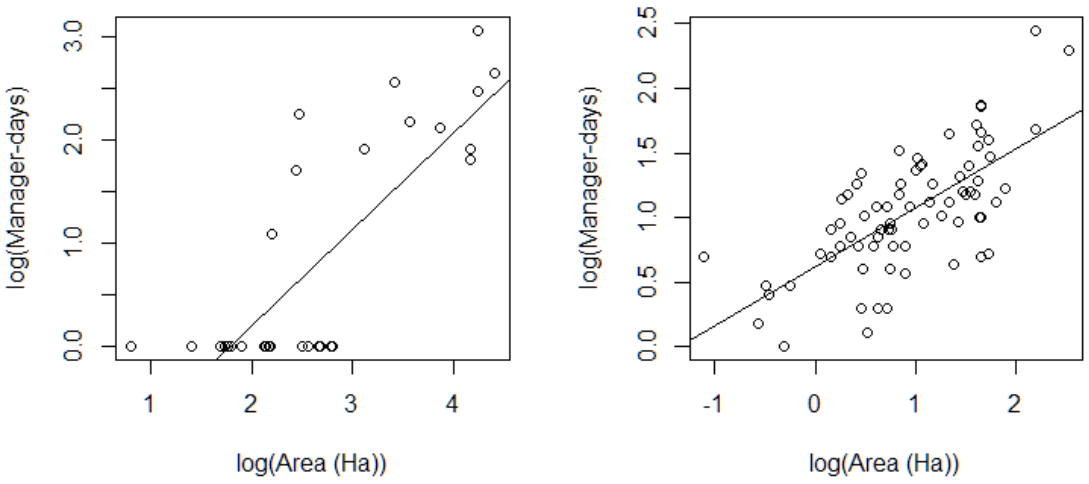


Figure A3.4. For the NWF regression of management effort against site area (left), n = 31, p = 1.166x10 -7 , r 2 = 0.626 and the slope is 0.94 with a standard error of 0.13. For the YWT regression (right), n = 74, p = 8.943x10 -12 , r 2 = 0.4736, and the slope is 0.45 with a standard error of 0.06.

protected area may exacerbate these situations if crossings are few and the centroid falls on the opposite side of the river from the nearest office.

To test the effect of assigning management effort to centroids, I split the Escambia River, Yellow River and Choctawhatchee River water management areas of NWF in two ways (Figure A3.5) and compared the optimal office locations to those reported in the main text. I first split these areas along their respective rivers (Figure A3.5, left), in order to explore how the need for river crossings affects travel distances. By splitting them into shorter segments (Figure A3.5, right), I create areas that are better described by their centroids. In each case, I allocated management effort to the new areas based on their size compared to the original area (e.g. if the river split the management area evenly in half, each part would be allocated half of the management effort put into the original site). This was necessary because data on the spatial allocation of management effort within sites is unavailable.

I ran optimizations for each scenario with all other management areas included and left intact. As in the main text, I found both the optimal location of an additional office given the four existing offices, and the optimal locations of those four offices.

In both sensitivity test cases, offices in optimal locations would decrease the annual cost of management-related travel (Table A3.1). Although these costs differ somewhat (due to differences in the spatial allocation of management effort between the divided areas and the number of trips made), the travel-minimizing office locations are the same (Table A3.1, Figure A3.6).

Additionally, the travel-minimizing configurations for the test cases are similar to those reported in the main text (Figure A3.6). All travel-minimizing office locations in the sensitivity test cases are less than 13 km from their corresponding locations in the main text. Were this optimization to be used in an office-siting process, it would be important to represent more accurately the spatial distribution of management effort, and how it changes over time. But because management travel is not the only consideration when siting offices, I believe that these sensitivity tests show results that are robust for illustrative purposes.

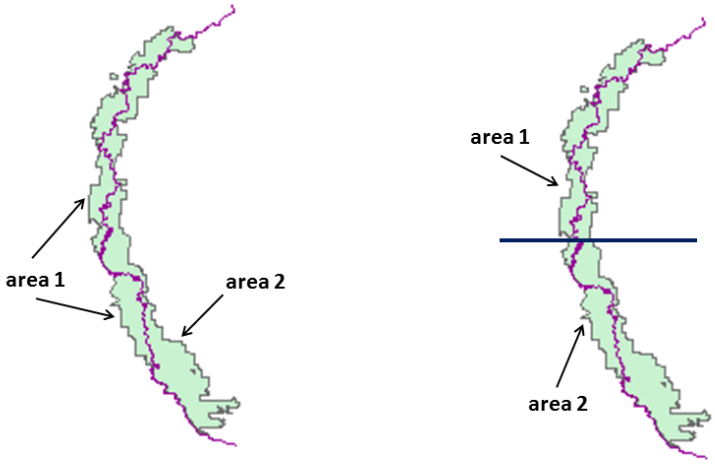


Figure A3.5. Escambia River Water Management Area, split along the river (left) and into shorter segments (right).

Table A3.1. Estimated annual travel costs for both sensitivity test cases, with the current office locations, a travel-minimizing fifth office, and a travel-minimizing configuration of four offices. The 'Office Locations' column denotes the ID of the road junctions where offices are located.

NWF	River split		Segment split	
	Travel Cost (2008 dollars)	Office Locations	Travel Cost (2008 dollars)	Office Locations
Current	$210,000	26006 83203 99478 123417	$211,000	26006 83202 99478 123417
Optimized (all offices)	$116,000	2408 60612 81104 94995	$126,000	2408 60612 81104 94995
Optimized (additional office)	$159,000	60612	$169,000	60612

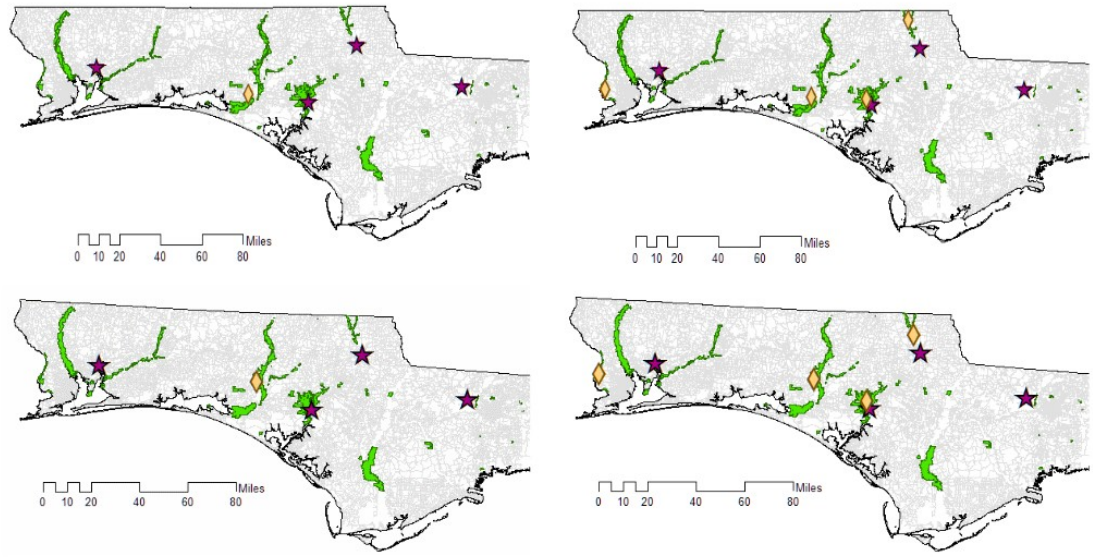


Figure A3.6. Current office locations (stars) and travel-minimizing locations (diamonds) in NWF. Top row: Travel-minimizing locations for an additional office (left) and four offices (right), for both sensitivity tests. Splitting management areas along the river or cross-sectionally produced the same optimal office configurations. Bottom row: Travel-minimizing office locations as reported in the main text.

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CONCLUSION

Human activity has elevated extinction rates far above background levels. Conservation practice seeks to prevent biodiversity losses, but the scope of the problem is such that the resources currently available are insufficient to remedy declines in all taxonomic groups. Due to this shortfall, conservation science not only addresses the biology but the business of conservation. For example, conservation biology seeks to clarify the relationship between different threats and the persistence of species or sets of species. Conservation planning integrates this understanding with information about land use, availability, and cost to guide decisions about how to allocate spending and effort among species.

In this dissertation, I identify leading-edge questions in both the biological and operational aspects of conservation. I first examine how patterns of extinction risk in mutualist communities are driven by community dynamics, interaction structure and environmental variability. I then develop a technique to aid in the siting of conservation offices, in order to reduce the costs that conservation organizations incur when managing networks of protected areas. Although these topics are taken from very different sides of conservation science, they are both embedded in a multi-scale context with directional drivers of change, and are amenable to computational and network approaches. Moreover, both have implications for conservation decision-making.

Although the extinction risk patterns that I discuss in Part 1 may seem far removed from practical considerations, they speak to the conditions under which poorly-connected obligate mutualists may be of concern. Under the protected area model of conservation, species-level priorities necessarily translate to the habitat level, thus contributing to land protection choices. Similarly, if conservation organizations make decisions that reduce their operating costs, they are able to devote more resources to land protection and management, thus affecting species persistence.

Comparing Scales

The work that I undertake in the two parts of this dissertation takes place at different but interacting scales. The community-dynamic model I develop in Part 1 assumes the scale of a single habitat, whereas the cost calculations and decision algorithm in Part 2 take place across a landscape containing numerous protected areas and the space in between. In this sense, both organizations discussed in this section have a regionally-defined focus. For the sake of this

discussion, I refer to the scale of focus in Part 1 as ‘local’, and the scale of decision-making in Part 2 as ‘regional’. Both parts, however, make assumptions about and/or have implications at both scales.

The pollination networks used in Part 1 are based on empirical studies conducted at the scale of a field site. Even those studies that address plant-pollinator interactions across a larger spatial extent (Arroyo *et al*. 1982, Medan *et al.* 2002, Vazquez & Simberloff 2002, Kaiser-Bunbury *et al.* 2009) divide their data into multiple local interaction networks. Consequently, any extinctions generated by the community-dynamic model occur at this same scale. The communities that these networks are based on, however, exist in a larger context of regional-scale environments and metapopulations. Although I do not model metapopulations here, local extinctions in a metapopulation context potentially reduce the influx of individuals to nearby populations. Additionally, if extinctions are driven by a regional-scale process (e.g. a constant level of environmental variability across sites), then extinction risk at one site could convey information about risk at other sites.

In Part 2, the decision of where to base management staff occurs at a regional level. Office locations are recommended based on travel cost, which depends on the distance between each office and the protected areas that it is responsible for, as well as the number of times each site is visited. Protected areas may be acquired based on considerations at the regional (e.g. habitat representation, spatial patterns of threat, complementarity) or local (e.g endemic species, features, or habitats, adjacency to existing protected areas) scale (Groves 2003). Decisions about management approach and intensity are made at the local level, but also prioritized across the region (Wilson *et al.* 2007). As I show in the Appendix to Chapter 3, the spatial distribution of management effort strongly influences which potential office locations are travel-minimizing. Thus, local-scale decisions influence the cost-efficiency of the activities of regional-scale organizations.

Both systems discussed in this dissertation can be used to highlight the consequences of ignoring processes at a particular scale. For example, an organization tasked with conserving pollinator biodiversity in a specified area may fail to protect specialists if community interactions are not taken into account. More broadly, changing abundances of a species may have cascading effects within interaction networks of all types, with unexpected consequences (e.g. invasions; trophic cascades; mesopredator release) (Terborgh & Estes 2013). Ignoring patterns at the regional scale, on the other hand, could lead to overinvestment in high-threat areas where the chances of successful conservation are low, or in low-threat areas where species of concern are likely

to persist without conservation action. A regional-scale outlook is also needed if organizations are to take advantage of complementarity.

Although I illustrate cross-scale dynamics as a simplified local/regional dichotomy in this discussion, similar arguments can be made across (a) different disparities in spatial scale, (b) temporal scales, and (c) scales of organization.

Relationship to Environmental Change

Anthropogenic changes to biodiversity patterns motivate conservation science and practice. While human impacts can be direct (e.g. overexploitation), human activities largely affect biodiversity via changes to species' habitat and climate (Groom 2005). Environmental change is implicit in both parts of this dissertation, albeit in different ways. In Part 1, stochastically changing conditions at each time step affect the persistence of modeled species, with population dynamic consequences for their mutualists and the network as a whole. Part 2 focuses on improving the efficiency of conservation by land protection, a paradigm that responds to environmental changes driven by the conversion of land to agricultural and urban uses. Management and monitoring actions, an important component of both case studies in Part 2, respond not only to past changes in land use, but also to other drivers of habitat change, for example the establishment of invasive species.

Despite the central role of environmental change in motivating this dissertation, neither part incorporates it in a directional sense. Part 1 tracks community dynamics and extinctions over time, but all parameters, including the variance of introduced stochasticity, remain constant throughout each replicate. The occurrence of extinctions in these models reiterates, at the community level, the potential of non-directional environmental change to produce directional results (something commonly shown in single-species models). Part 2 seeks to improve the efficiency of conservation organizations' responses to directional change into the future. Its recommendations, however, are based on static assumptions--namely, that the set of protected areas, the allocation of management effort, and the structure of the road network, are fixed.

It is realistic to expect, however, that the systems in both sections of this dissertation are subject to directional change through time. The communities in Part 1 require a certain amount of suitable habitat, which may be lost through land use change or as a consequence of alterations to temperature and precipitation regimes by climate change. From a life-history parameter perspective, habitat alteration and loss may lead to reductions in carrying

capacity and increased mortality rates. Additionally, environmental variability is itself expected to increase as climate change progresses (Christensen *et al*. 2013)-- a scenario that Part 1 indicates will lead to elevated extinction rates. Conservation organizations like those in Part 2 also change over time. Many organizations acquire land for protection as part of their mission, altering the spatial pattern of their holdings. The distribution of management effort between protected areas also changes as old projects are completed and new ones begin. In the NWF case study, the pulse of effort applied to a single newly-acquired area was sufficiently intense to affect office location recommendations (Appendix 3). Additionally, land acquisition choices respond to broad patterns of threat that follow from directional changes to land use and climate.

The inevitability of directional change suggests that both parts of this dissertation could be extended by the explicit inclusion of directional drivers of environmental change. I describe possible future directions in more detail below.

Comparing Network Approaches

Both parts of this dissertation rely heavily on network representations of their study systems. In Part 1, I represent plant and pollinator species as nodes in a bipartite network; pollination interactions constitute the links. In Part 2, I base my work on data from two conservation organizations that rely on over-road travel to move staff between their home offices and the protected areas where they carry out management actions. I represent this road system as a single-mode network of intersections connected by roads; all management-necessitated travel takes a path through these networks.

Network structure informs the outcomes of these chapters in different ways. Part 1 emphasizes the interplay between network structure and species loss. Structure affects extinction risk on both the species level via specialization, and at the network level though connectance and nestedness. Similarly, species losses change the structure of the interaction network on both of these levels. Because I am interested in relative extinction risk, I treat the links in a simplified way. In the four-species network in Chapter 1 and the empirical networks in Chapter 2, I assume that each species relies on all of its mutualists equally.

In contrast, Part 2 relies on static networks with a more detailed representation of link properties. Nodes are only important to the extent that they offer a plausible location for a conservation office or protected area. The cost of traveling between an office and a protected area depends on both distance and time. The length of the shortest path between any office and protected area depends upon the

structure of the network. This length is characterized by the sum of the distances between all intersections along that path. Since staff time is taken into account, speed limits also contribute to the total cost. Ignoring these link attributes would distort cost estimates, and consequently change locations that are considered travel-minimizing.

Sequences of extinctions in Part 1 can also be thought of as pathways, although that is beyond the scope of the current work. Because all simulations begin with a deterministically stable model with identical equilibrium population sizes across species, the first extinction is a consequence of stochastic dynamics. The deterministic consequences of partner loss (e.g. reduced population size; complete loss of mutualist benefits) then play a role in subsequent extinctions, but their relative contributions to risk depend upon both species identity and prior losses.

Multi-scale dynamics, directional environmental change, and choices in network representation are three cross-cutting issues that apply to both parts of this dissertation. Although modeling stochastic community dynamics and finding travel-minimizing locations for conservation offices take different perspectives on conservation science, these considerations are common to both. Scale issues act as a reminder that ecology and conservation do not occur in self-contained systems; directional environmental change is abstracted out of both models but is present in the systems they represent; and both models rely on network assumptions that could be relaxed. Below, I elaborate on three logical extensions for research arising from the latter two syntheses.

Future Directions

The above discussions of directional environmental change and network approaches suggest possible extensions of the work that I present in this dissertation. Although both parts assume that directional environmental change is occurring, neither incorporates it explicitly. Part 1 focuses on directional outcomes (i.e. species losses) of non-directional change, while Part 2 makes recommendations based on a snapshot of protected area and road locations, as well as the spatial distribution of management effort. Due to expected increases in environmental variability, and the conversion of land for human use, a natural extension for both Parts 1 and 2 would be to include directional environmental change.

Parts 1 and 2 also both rely on network approaches, but I use different sets of assumptions about how the underlying networks function. These differences

highlight possible next steps for each. The choice of pathway through a road network affect conclusions about which potential office locations are travel-minimizing, and how much they save; similarly, the pathway of realized extinctions through an interaction network influences the remaining species' extinction risk. Likewise, my representation of species interactions is dynamic, but road networks and protected area portfolios also change through time.

Directional Change: Extinction Risk in Pollination Networks

The community-dynamic model that I develop in Part 1 of this dissertation incorporates information about the environment through its parameterization. Consequently, directionally changing environments can be represented through directional changes in parameter values over the course of simulation replicates. In contrast to a parameter sweep, where parameter values vary between replicates, changing parameter values within replicates allows for exploration of historical effects and community responses at different rates of change.

Different types of environmental change may enter on different parameters. As noted above, environmental variability is expected to increase through time, and this could be modeled with increasing variance of stochasticity within each replicate, rather than the parameter sweep approach that I took in Chapter 1. Changes that lead to habitat loss (e.g. land conversion, increasing temperature in montane environments) may be well-represented as changes to species' carrying capacity through time. Similarly, changes that affect population growth (e.g. thermal stress, drought) could be applied to mortality rates. Changes that affect community interactions (namely, interaction strength and pollination efficiency) would necessarily enter into the birth function, since community structure only affects reproduction in this model.

Applications of directional change to model parameters could be used to answer a range of questions about how such change affects plant-pollinator communities in stochastic environments:

- How does the rate of change of parameters affect extinction times?
- What is the relative importance of directional change in different parameters?
- How does directional parameter change in one species propagate through the community?

Travel cost in dynamic conservation networks

Road networks, protected area holdings, and the distribution of management effort change through time. Consequently, an office location that is travel-minimizing now may not be in the future. Conducting a similar analysis on networks that are expected to change in a predictable way (e.g. where land acquisition priorities are known; where management effort is expected to shift predictably with a changing climate) may be useful in projecting which locations will be travel-minimizing in the future, even if those offices are built at the outset of a regional conservation initiative. Such an analysis could also be used to predict how long current location is expected to be more travel-efficient than a future choice, and aid decision-making in when and whether a move should be made.

As in Part 1, Land use and climate are also major sources of directional change for the types of conservation organizations that I address in Part 2. Development pressure and sea level rise will affect the spatial distribution of threats to biodiversity in both Yorkshire and Northwest Florida. Development also implies changes to the regional road network. Although new roads increase fragmentation and disturbance by traffic, they may also reduce the cost of travel between conservation offices and protected areas. The protection of land for conservation purposes is also a form of directional change. As new areas are protected, the spatial pattern of management demand changes, and previously travel-minimizing office locations may thereby become less efficient over time.

In order to anticipate whether an office location remains travel-minimizing into the future, Part 2 of this dissertation could be expanded to incorporate projected future scenarios. Scenarios based on human population growth projections and the severity of climate change can inform current decision-makers about which sites and management strategies are likely to be prioritized in the future. These factors affect the distribution of management demand across the region where each organization operates. Economic projections that estimate the future cost of fuel and labor could also inform current decision-makers about changes in the importance of operating a travel-efficient office. For example, if the fuel and labor costs both increase through time, the benefit to choosing an efficient office location will also grow.

Climate and development scenarios could be incorporated into the office location algorithm that I describe in Part 2 to answer questions such as:

- On what time scale would it make sense to relocate a conservation office?
- How do travel-minimizing locations move over time?

- Do the likely scenarios have any travel-minimizing office locations in common?

Extinction Pathways

In natural environments of high conservation concern, extirpations may have already occurred. In these cases, changes to the community interaction structure caused by prior losses could influence which remaining species are the most vulnerable. This raises the question of whether certain extinction sequences are more probable than others. If this is the case, it may be possible to make predictions about future losses based on past ones.

The model I describe in Chapter 1 is capable of recording the order in which species are lost, by extracting extinction times from the population trajectories of the species in the network. I have done this for the 4-species model, and the preliminary results suggest that environmental variance and relative differences in equilibrium population size contribute to the likelihood that a given sequence will be realized. Since increased environmental variability leads to greater numbers of extinctions (Chapter 1), the mean length of extinction sequences also increases. When the 4-species model is simulated with asymmetry on the *c* parameter (Appendix 1), the equilibrium population size is smaller for pollinators than it is for plants. Under these conditions, pollinator-initiated sequences were realized almost exclusively: of 200,000 replicates, only 7 sequences began with the loss of a plant.

Given the elevated vulnerability of specialists relative to generalists, I expect that interaction structure will also affect the frequency with which different sequences are realized. The four-species results could speak to the role of specialists and generalists, but larger networks would be needed to investigate whether and how network-level properties affect sequence likelihood. These networks have a much larger space of possible sequences, but it is possible to gain some insight with data mining techniques and enough computational time.

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VITA

Christine Dumoulin grew up in upstate New York. She earned a Bachelor's of Science in physics from McGill University in 2005. While there, she developed an interest in computational modeling and dynamical systems, which turned out to be surprisingly compatible with her long-standing interest in conservation. She earned a Master's of Science in plant biology and conservation at Northwestern University and the Chicago Botanic Garden in 2011. Christine continued on to earn a PhD in ecology and evolutionary biology at the University of Tennessee.