

Thesis proposal

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The proposal for my thesis, *Simulation models for predictive ecology*

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Introduction

Within the last several hundred years, human activity has induced rapid changes in Earth's atmosphere, oceans, and surface. Greenhouse gas emissions have caused an increase in the temperature of both Earth's terrain and oceans, and both agricultural and urban development has rapidly reshaped Earth's land cover. The bulk of this change has occurred within the last several hundred years, a geological instant, inducing a sudden shift in conditions to Earth's climate and biosphere. As a result *ecological forecasting*—modeling how ecosystems and their services will change in the future—and then using these forecasts to make decisions to mitigate the negative consequences of this change on ecosystems, their functioning, and the services they provide to humans has emerged as an imperative for ecology and environmental science (Dietze 2017). However, robust prediction of ecological processes is, to say the least, quite difficult (Beckage *et al.* 2011; Petchey *et al.* 2015). This difficulty is compounded by a few factors, the first being that sampling ecosystems is not easy. Ecological data is often biased, noisy, and sparse in both space and time. The current paucity of ecological data has resulted in much interest in developing global systems for *ecosystem monitoring* (Makiola *et al.* 2020), which would systematize the collection of biodiversity data in a manner that makes detecting and predicting change more possible than at the moment (Urban *et al.* 2021).

The second major challenge in ecological forecasting is that the underlying dynamics of ecological processes are unknown and instead must be inferred from this (sparse) data. Much of the history of quantitatively modeling ecosystems have been done in the language of dynamical systems, describing how the value of an observable state of the system, represented by a vector of numbers $[x_1, x_2, \dots, x_n]^T = \vec{x}$ changes over time, yielding models in the form of differential equations in continuous-time settings, $\frac{dx}{dt} = f(x)$, or difference equations in discrete-time settings, $x_t = f(x_{t-1})$, where $f : \mathbb{R}^n \rightarrow \mathbb{R}^n$ is an arbitrary function describing how the system changes on a moment-to-moment basis (e.g. in the context of communities, f could be Lotka-Volterra, Holling-Type-II or DeAngelis-Beddington functional response). The form of this functional response in real systems, and whether it is meaningfully non-zero for a given species interaction, is effectively unknown and must be predicted (Strydom *et al.* 2021b), and some forms of these dynamics are inherently more “forecastable” than others (Beckage *et al.* 2011; Chen *et al.* 2019; Pennekamp *et al.* 2019). The initial success of these forms of models can be traced back to the larger program of ontological reductionism, which became the default approach to modeling in the sciences after its early success in physics, which, by the time ecology was becoming a quantitative science (sometime in the 20th century, depending on who you ask), became the foundation for mathematical models in ecology.

However, we run into many problems when aiming to apply this type of model to empirical ecological data. Ecosystems are perhaps the quintessential example of system that cannot be understood by iterative reduction of its components into constituent parts—ecological phenomena are emergent: the product of different mechanisms operating at different spatial, temporal, and organizational scales (Levin 1992). Further this analytical approach to modeling explicitly ignores known realities: ecological dynamics not deterministic and many analytic models in ecology assume long-run equilibrium. Finally, perhaps the biggest challenge in using these models to describe ecological processes is ecosystems consist of more dimensions than the tools of analytic models are suited for. As the number of variables in

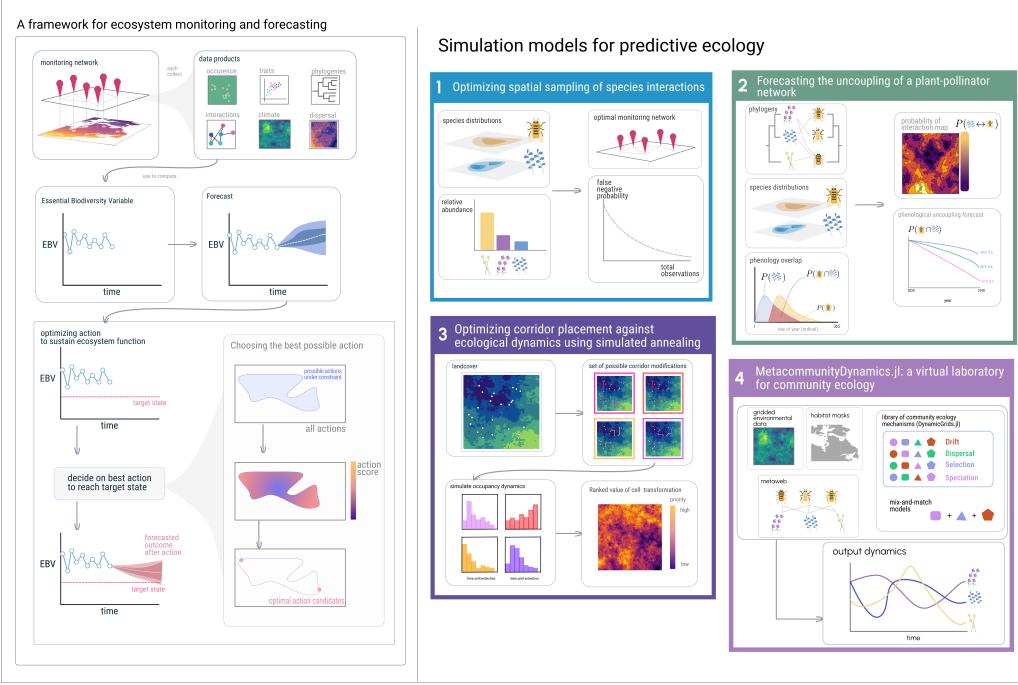


Figure 1 Left: a framework for ecosystem monitoring, forecasting, and mitigation. From the top, a set of biodiversity observatories which form a monitoring network. Each collect various biodiversity data products. From this raw data, we derive essential biodiversity variables (EBVs), and forecast how they change over time. Based on this forecast, we wish to choose the best possible mitigation strategy to maximize the chance the realized future outcomes of the EBV approaches the target state. Right: Each panel represents a chapter of the thesis, which follows the flow of the framework on the left.

a model increases, so does the ability of the scientist to discern clear relationships between them given a fixed amount of data, the so-called “curse” of dimensionality.

But these problems are not solely unique to ecology. The term *ecological forecasting* implicitly creates an analogy with weather forecasting. Although it has become a trite joke to complain about the weather forecast being wrong, over the last 50 years the field of numerical weather prediction (NWP) has dramatically improved our ability to predict weather across the board (Bauer *et al.* 2015). The success of NWP, and the Earth observation systems that support it (Hill *et al.* 2004), should serve as a template for development of a system for monitoring Earth’s biodiversity. Much like ecology, NWP is faced with high-dimensional systems that are governed by different mechanisms at different scales. The success of NWP is that, rather than, say, attempt to forecast the weather in Québec by applying Navier-Stokes to entire province, to instead use simulation models which describe known mechanisms at different scales, and use the availability to increasing computational power to directly simulate many batches of dynamics which directly incorporate stochasticity and uncertainty in parameter estimates via random number generation.

But forecasting is only half the story—if indeed “[ecologists] have hitherto only interpreted the world in various ways; the point is to change it,” then once we have a forecast about how an ecosystem will change in the future, what if this forecast predicts a critical ecosystem service will deteriorate? We are still left with the question, what do we do in the time being to mitigate the potentially negative consequences a forecast predicts? In this framing, mitigating the consequences of anthropogenic change on ecosystems becomes an optimization problem: given a forecast of the future state of the system, and some “goal” state for the future, the problem is then to optimize our intervention into the system to maximize the probability the system approaches our “goal” state. This dissertation aims to provide a framework for ecosystem monitoring and forecasting (fig. 1, left), and each chapter addresses some aspect of this pipeline to data from a monitoring network to forecasts to mitigation strategy (fig. 1, right).

The primary research challenges this thesis addresses are: how do we design ecological samples to detect change? How do we build the software infrastructure to assimilate data from a variety of sources? And how do we propagate uncertainty from data to forecasts? The flow of chapters follows the flow in fig. 1 (left), from data collection via a monitoring network, to forecasting an essential biodiversity variable (EBV), to optimizing mitigation strategy based on constraints. In chapter one, we discuss how simulation can aid in the design of ecological samples and monitoring network design. In chapter two we use data to forecast the uncoupling of a plant-pollinator network. In chapter three, we apply simulation methods in landscape ecology to optimize corridor placement to maximize the time-until-extinction of a metapopulation. The fourth and final chapter is the software (*MetacommunityDynamics.jl*) which enables the rest of the dissertation.

Species A occurs?
Species B occurs?

	Species A observed?		
	true	false	
Species B observed?	true	false	
true	Species A observed? true co-occurrence true-positive Interaction observed? true false interaction true-positive interaction false-negative	Species A observed? false co-occurrence false-negative	co-occurrence true-negative
false	co-occurrence false-negative	occurrence false-negative	occurrence true-negative
false	co-occurrence true-negative		occurrence true-negative

Figure 2 A taxonomy of occurrence, co-occurrence, and interaction false negatives in data

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Chapter One: Optimizing spatial sampling of species interactions

2.1. Context Ecosystems are composed of interactions between species, yet this remains one of the greatest shortfalls of data in biodiversity science (Strydom *et al.* 2021b). This is, in no small part, because species interactions are considerably more difficult to sample than single-species processes. However, understanding and predicting species interactions, and how anthropogenic change is affecting them, is one of the grand challenges faced by modern ecologists (Jordano 2016). Further, co-occurrence is often used as a proxy for species interaction when this is not necessarily always a valid assumption (Blanchet *et al.* 2020).

2.2. Objective The goal of this chapter is to use simulation models to investigate the relationship between species relative abundance, sampling effort, and probability of observing an interaction between species in order to aid in the design of samples of ecological interactions across space, and to provide a null expectation of the false-negative probability for a dataset of a given size. Further, it then proposes a method for optimizing the spatial sampling locations to maximize the probability of detecting an interaction between two species given a fixed number of total observations and the distributions of each species. This addresses the optimization of monitoring network part of the flow from data to mitigation at the top of fig. 1, left.

2.3. Methods We begin by proposing a method to compute a null expectation of the probability of an interaction false-negative as a function number of total observations of individuals of *all species in the species pool*. This is done by simulating the process of observation, where the probability that an observation is of a given species is that species' relative abundance. We show that the realized false-negative

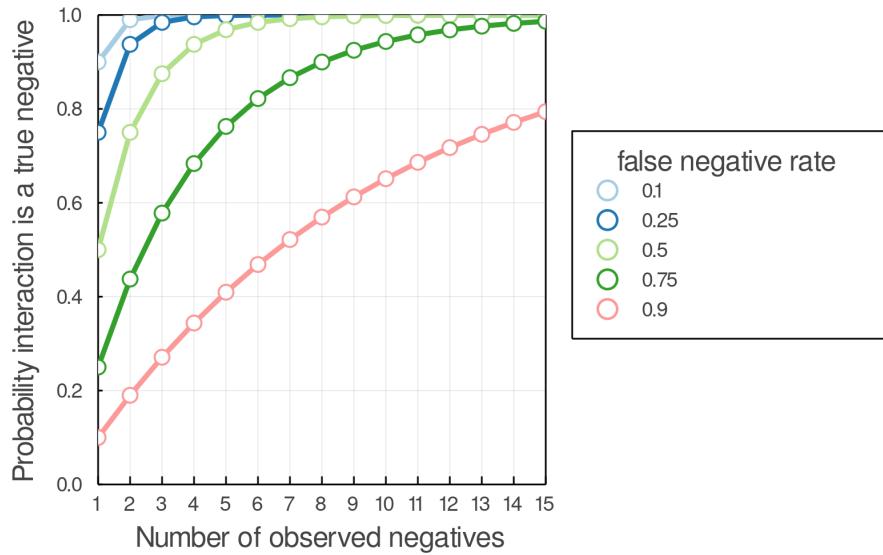


Figure 3 Relationship between total number of observed interactions negatives (x-axis) and the probability that an interaction is a true-negative as a function of different realized false-negative rates (colors), assuming each observed negative is independent—the same as the negative-Bernoulli distribution.

rate can be quite high, simply as a byproduct of the distribution of relative abundance in communities. We use a log-normal distribution of relative abundance (Hubbell 2001) and simulating the process of observation on food-webs generated using the niche model (Williams & Martinez 2000) with connectance parameterized by the flexible-links model (MacDonald *et al.* 2020). An example of this relation for networks with varying species richness is shown in fig. 4.

We then go on to test some assumptions of this neutral model with empirical data. Primarily we analytically show that our neutral model, if anything, underestimates the probability of false-negatives if there are positive associations between species co-occurrence, and we show these positive associations exist in two sets of spatially replicated samples of interaction networks (Thompson & Townsend 2000; Hadfield *et al.* 2014), fig. 5—further I’m planning to add the field data from chapter two into this analysis once available. Finally this chapter proposes a simulated annealing method to optimize the a set of n points in space to maximize the probability of detecting an interaction between two species a and b with known distributions D_a, D_b .

2.4. Results The first major result is using the simulation of the observation process described above to generate expectations of interaction false-negative rate (FNR) as a function of total number of observations, with the goal being for this estimate to be used as correction for detection error when fitting an interaction prediction model. This relationship varies with the total richness of the metaweb (see fig. 4).

The second major result is that we analytically show that this simulated observation model, by assuming that there is no association between observing two species given that they interact, actually under predicts the realized false-negative interaction rate. We then demonstrate that this positive association association exists in two empirical systems fig. 5.

2.5. Progress This chapter is mostly complete. The only remaining work is the implementation of simulated annealing optimization process. This will be done by using a proposal function which takes a set of coordinates in space and proposes a new location for each point based on a distance-decaying kernel.

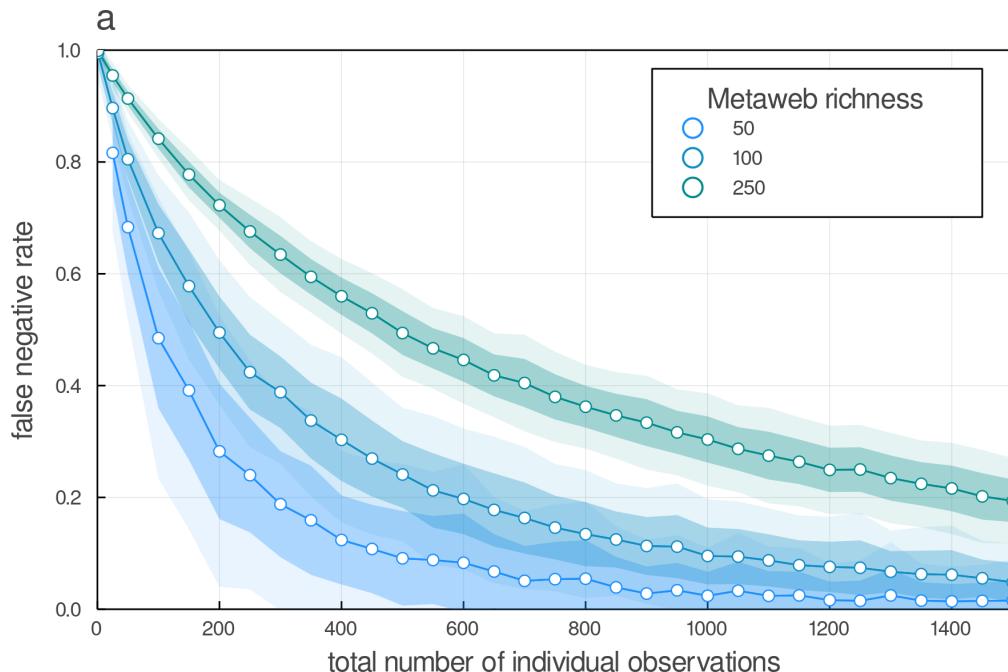


Figure 4 The realized false-negative-rate of interaction detection (y-axis) as a function of the total number of observations of all species in the species pool (different richesses in different colors). Each point is the mean of 50 replicates, with one standard-deviation in the first shade, and two standard deviations in the second shade.

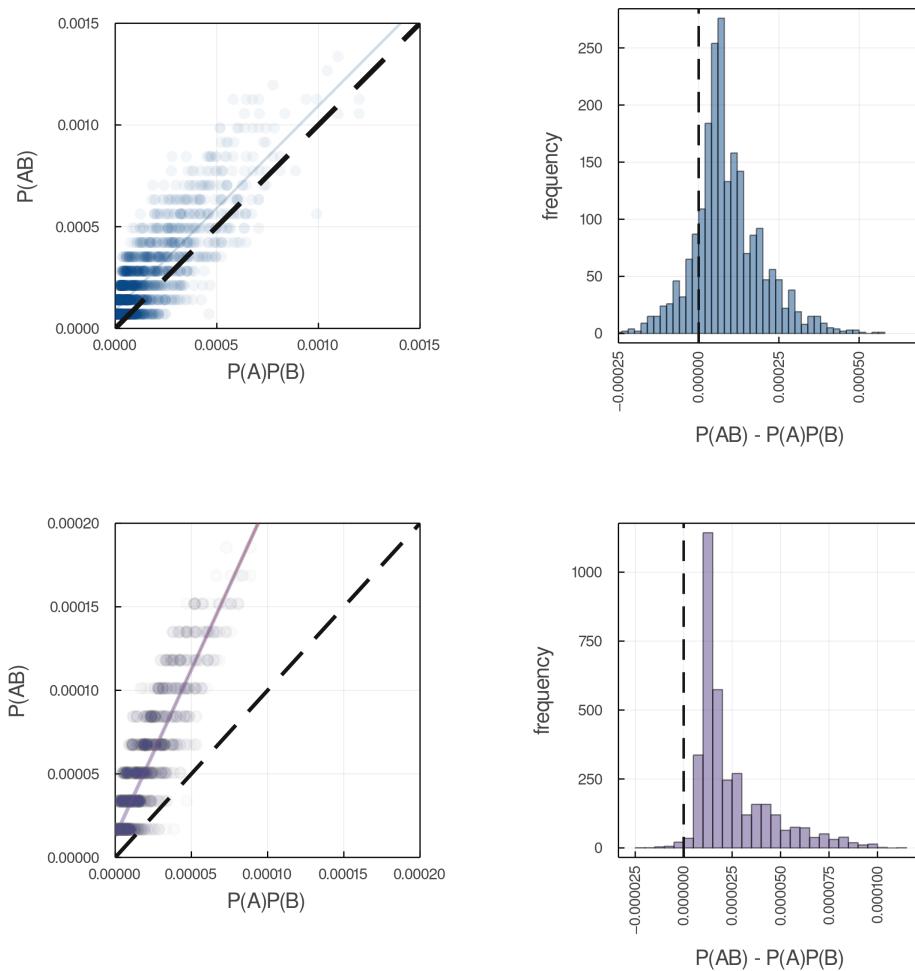


Figure 5 Demonstrates positive associations in co-occurrence. Left: the product of the marginal probability of observing two species (A and B) in a sample (x-axis) against the computed joint probability of observing these species together (y-axis). Dashed line indicates $y = x$, meaning no association between the two. Each point is an observed interaction between two species. Right: the distribution of the difference between these joint and marginal probabilities. Both are non-zero with $p < 10^{-50}$ via a t-test.

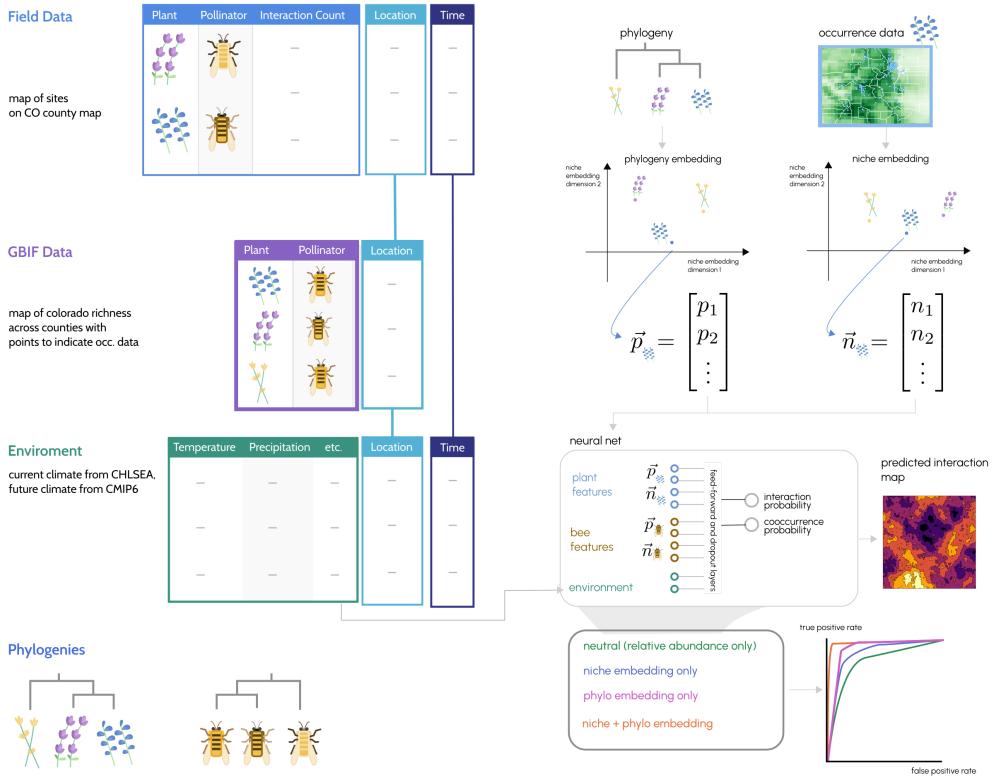


Figure 6 Chapter two conceptual figure. Left: the sources of data and how they can be combined. Right: The flow from data to interaction prediction using a few different interaction prediction models.

Chapter Two: Forecasting the spatial uncoupling of a plant-pollinator network

3.1. Context Interactions between plants and pollinators form networks which together structure the “architecture of biodiversity” (Bascompte & Jordano 2007). The functioning and stability of ecosystems emerge from these interactions, but anthropogenic change threatens to unravel and “rewire” these interaction networks (CaraDonna *et al.* 2017), jeopardizing the persistence of these systems. Plant-pollinator networks face two possible forms of rewiring in response to anthropogenic environmental change: spatial and temporal. Range shifts could cause interacting species to no longer overlap in space, and shifts in phenology could cause interacting species to no longer occur at the same time of year.

3.2. Objective This chapter uses several years of data on bumblebee-flower phenology and interactions across several field sites, each consisting of several plots across an elevational gradient, combined with spatial records of species occurrence via GBIF to forecast the uncoupling of the plant-pollinator metaweb of Colorado.

3.3. Methods The data for this chapter is derived from multiple sources that can be split into four categories. (1) Field data from three different field sites across Colorado, each with multiple plots across an elevational gradient, for seven, seven, and three years respectively. This data was collected by Paul CaraDonna and Jane Oglevie (from the Rocky Mountain Biological Laboratory; RMBL) and Julian Rezasasco (CU Boulder). (2) GBIF spatial occurrence records of each of these species across Colorado, including a metaweb of interactions across all of Colorado taken from GBIF. (3) Remotely sensed data consisting of current and forecasted bioclimatic variables from CHELSA. (4) Phylogenies for both bee and flower species derived from NCBI GenBank barcodes for mitochondrial COI (bumblebees) and chloroplast rbcL (flowers).

As the data we have is spatially sparse and likely to contain many interaction false-negatives, we begin by predicting a metaweb of interactions across Colorado as they exist *in the present*. We do this using a set of candidate interaction prediction models: relative abundance only, phylogenetic embedding only (a la Strydom *et al.* (2021a)), niche embedding only (encompassing both phenology and environmental

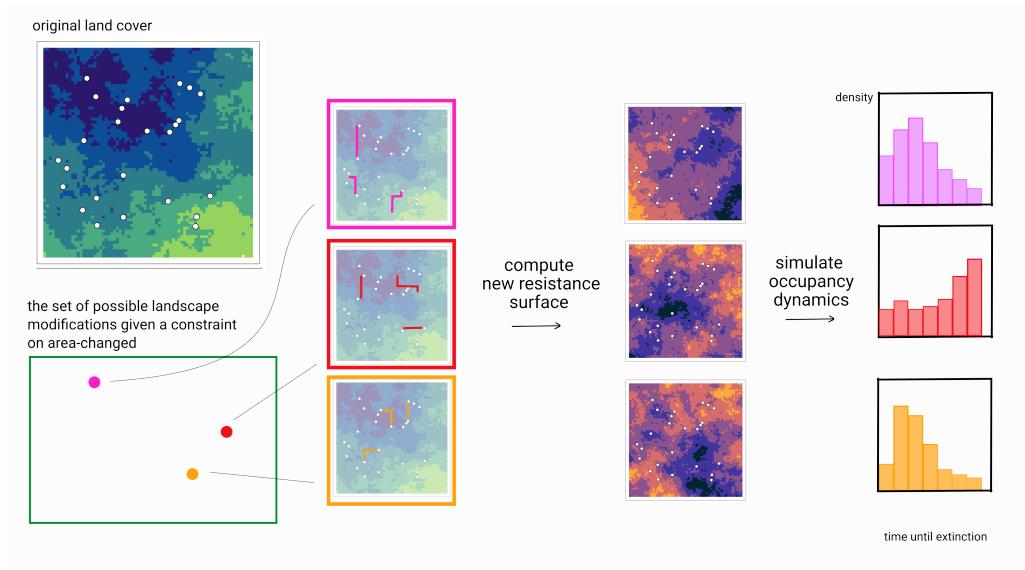


Figure 7 A conceptual example of how we go from a map of landcover with a set of points where occurrence of a species has been recorded (top left), to the set of all possible landscape modifications (green box, where each point in the green box is a unique landscape modification, with three examples shown as pink, red and orange dots), to computing resistance surfaces based on proposed landscape modifications (center) and then simulate the distribution of extinction times for a metapopulation in this new landscape (right).

niche, similar to Gravel *et al.* (2019)), and all pairwise combinations of those constituent models. After validating and selecting the best performing model, we then predict how these distributions of each of these species will change under the CMIP6 consensus climate forecast (Karger *et al.* 2017), and then finally quantify the reduction in spatial overlap between species for which there is a predicted interaction.

3.4. Results The in-progress results are the prerequisites for the analysis outlined above: phylogenies for both plant and bee species (appendix figure one) and species distribution models for all species (an example shown in appendix figure two).

3.5. Progress At the moment, we have derived phylogenies and SDMs for all the species present in the Colorado GBIF metaweb (appendix figures one and two). I've also been exploring the data available from Julian Resasco. The primary constraint on further progress is that we are waiting on the finalization of a data sharing agreement with RMBL.

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Chapter Three: Optimizing corridor placement against ecological dynamics

4.1. Context As land-use change has caused many habitats to become fragmented and patchy, promoting landscape connectivity has become of significant interest to mitigate the effects of this change on Earth's biodiversity (Resasco 2019). However, the practical realities of conservation mean that there is a limitation on how much we can modify landscapes in order to do this.

4.2. Objective What is the best place to put a corridor given a constraint on how much surface-area you can change in a landscape? This is the question this chapter seeks to answer. Models for inferring corridor locations have been developed, but are limited in that are not developed around promoting some element of ecosystem function, but instead by trying to find the path of least resistance in an existing landscape from a derived resistance surface (e.g. Peterman 2018). This chapter proposes a general algorithm for optimizing spatial restoration effort to move a measurement of ecological dynamics toward a target state.

4.3. Methods We propose various landscape modifications that alter the cover of a landscape, represented as a raster. We then compute a new resistance surface based on the proposed landscape modification using Circuitscape (McRae *et al.* 2008), and based on the values of resistance to dispersal between

pair of locations we simulate spatially-explicit metapopulation dynamics (Hanski & Ovaskainen 2000; Ovaskainen *et al.* 2002) to estimate a distribution of time-until-extinction for each landscape modification. The largest challenge in implementing this algorithm is the space of potential modifications grows as $O((nm)!)$ for an n by m raster. For most actual landscapes to which we wish to apply this method, the set of possible modifications becomes uncomputably large, so we use simulated annealing to explore the search space of possible modifications to estimate the modification that maximizes the time-until extinction of simulated metapopulation dynamics under that hypothetical modified landscape.

The biggest challenge in implementing simulated annealing in this context is defining a proposal function for landscape modifications. At the moment this is done by computing the minimum-spanning-tree (MST) of the spatial nodes (locations where occurrence has been observed), and then proposing corridors that only connect nodes that are already connected in the MST. The primary reason for doing this is to cut down the size of the search space to enable quicker convergence, although the final software that implements this algorithm will enable alternative methods of proposing modifications.

The goal output of this chapter is not only to provide a set of discrete corridor options, but also to rank the cells in the raster by priority based on how many times they are included in the distribution of “good” corridors after simulated annealing has converged. Further, the final component of this chapter is measuring the effect of land-use change on the robustness of the optimized corridor by simulating various neutral models of urban and agricultural sprawl, and determining if the proposed modifications still maximize time-until-extinction when the landcover in the landscape is not static.

4.4. Progress Currently I have an algorithm for proposing landscape modifications and a simple implementation of simulated annealing. The only gap left is implementing Circuitscape estimation of resistance surfaces and running benchmarking tests for the resulting chapter.

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Chapter Four: MetacommunityDynamics.jl: a virtual laboratory for community ecology

5.1. Context Building models for ecological forecasting is an imperative (Dietze *et al.* 2018), but before applying forecasting methods to actual data, we need a way to determine the efficacy of different forecasting methods. We need a software library to generate synthetic data from a *known* set of mechanisms and parameters to test our methods for parameter inference and forecasting on a system with *known* ground-truth dynamics to assess the effectiveness of these inference and forecasting methods.

5.2. Objective The final chapter consists of a collection of modules in the Julia language for different aspects of community ecology, including most of the code used for the preceding chapters. Indeed MetacommunityDynamics.jl (MCD.jl) is at the center of this set of tools, but due to the nature of the Julia language, MCD.jl is inter-operable with several existing packages within the EcoJulia organization, including several to which I have contributed.

5.3. Methods A diagram showing the relation between these packages is shown in fig. 8. MetacommunityDynamics.jl is built on DynamicGrids.jl, a library for high-performance gridded simulations in the Julia language, and Dispersal.jl (Maino *et al.* 2021), and extension of DynamicGrids.jl specifically for modeling organism dispersal. It also contains integrations with EcologicalNetworks.jl (Poisot *et al.* 2019) to generate metawebs, or can use empirical networks from Mangal.jl (Banville *et al.* 2021). It implements the general framework for community dynamics proposed by Vellend (2010), where all community processes can be divided into four categories: selection, dispersal, drift, and speciation.

5.4. Results In fig. 9 we see a sample output of simulated food-web dynamics for a metaweb of 100 species generated using the minimum-potential-niche model (Allesina *et al.* 2008) with connectance $C = 0.05$ and forbidden-link probability of 0.5. The dynamics change according to a Lotka-Volterra functional response, dispersal with distance inversely proportional to trophic-level, linear mortality, and logistic growth for any species at the producer trophic-level.

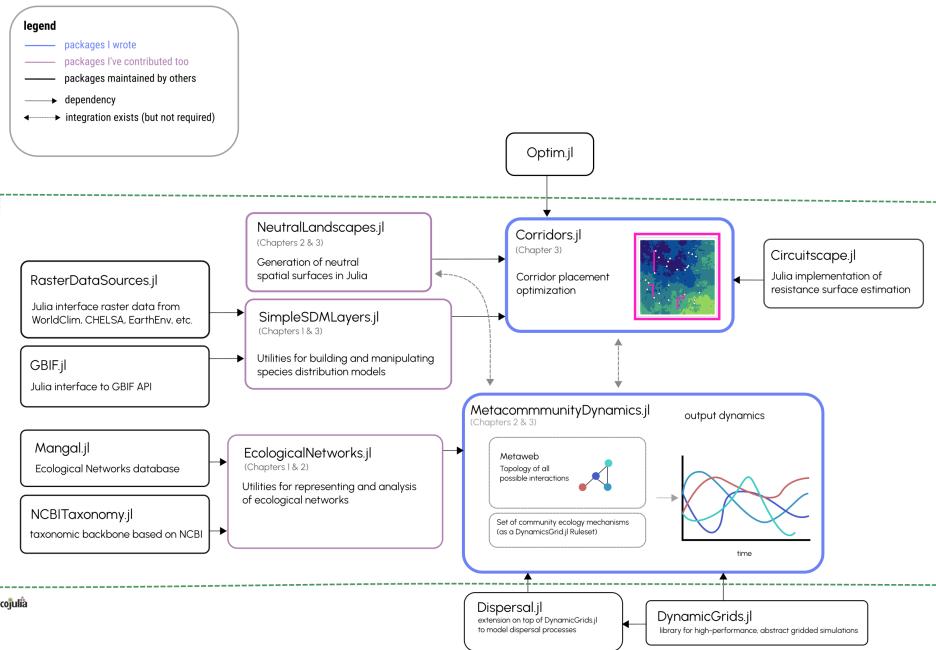


Figure 8 The structure of the software libraries used as part of MCD.jl

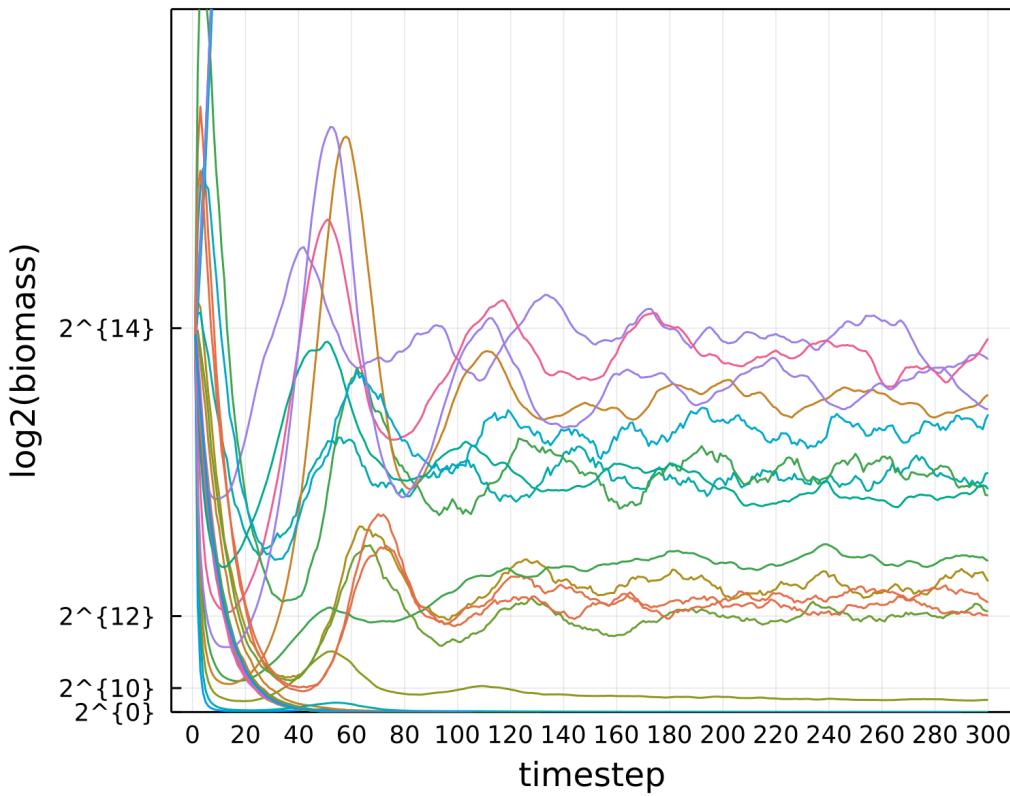


Figure 9 Sample output of simulated food web dynamics from MetacommunityDynamics.jl. Timestep (x-axis), and biomass of each species (y-axis).

5.5. Progress The software as it exists is capable of simulating the biomass dynamics of arbitrarily large food-webs using Lotka-Volterra, Holling Type-II, or Holling Type-III functional responses. It currently has methods to implement Gaussian drift, and various forms of dispersal via `Dispersal.jl`. Also functional are occupancy dynamics for Levins metapopulations (Levins 1969), and spatially explicit Hanski-Ovaskainen metapopulations (Hanski & Ovaskainen 2000; Ovaskainen *et al.* 2002). This is most of what needs to exist for the preceding chapters. In-progress functionality includes selection (which affects growth-rate) on arbitrary environmental variables in progress, as well as traits.

6

Discussion

Developing a system for global biodiversity monitoring is an imperative to mitigate biodiversity loss and its impacts on humanity. In my thesis I hope to provide a template for the digital infrastructure that enables the pipeline from data collection, to forecast, to actionable information, both through software that can be used to solve these problems (chapters one, three, four), and vignettes of how these software can be applied (chapters one, two).

Biodiversity science would be wise to use the success of numerical-weather prediction and the Earth monitoring system that supports it as a template. Further, we should embrace methodological advances in computational statistics that can enable more robust prediction of the dynamics of complex systems than is possible using the tools of analytic models—not just because they can provide more efficacious predictions, but also because they enable a more direct representation of uncertainty, which is crucial for developing ecological forecasting models which provide actionable information to stakeholders, and to find a way for humans to live sustainably on Earth, the only planet on which life has ever been known to occur.

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