

# Thesis proposal

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

## 1 Introduction

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

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

30 becoming a quantitative science (sometime in the 20th century, depending on who you ask), became the  
31 foundation for mathematical models in ecology.

32 However, we run into many problems when aiming to apply this type of model to empirical ecological  
33 data. Ecosystems are perhaps the quintessential example of system that cannot be understood by iterative  
34 reduction of its components into constituent parts—ecological phenomena are emergent: the product of  
35 different mechanisms operating at different spatial, temporal, and organizational scales (Levin 1992).

36 Further this analytical approach to modeling explicitly ignores known realities: ecological dynamics not  
37 deterministic and many analytic models in ecology assume long-run equilibrium. Finally, perhaps the  
38 biggest challenge in using these models to describe ecological processes is ecosystems consist of more  
39 dimensions than the tools of analytic models are suited for. As the number of variables in an analytic  
40 model increases, so does the ability of the scientist to discern clear relationships between them given a  
41 fixed amount of data, the so-called “curse” of dimensionality.

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

54 But forecasting is only half the story—if indeed “[ecologists] have hitherto only interpreted the world in  
55 various ways; the point is to change it,” then once we have a forecast about how an ecosystem will change  
56 in the future, what if this forecast predicts a critical ecosystem service will deteriorate? We are still left  
57 with the question, what do we in the time being to mitigate the potentially negative consequences a  
58 forecast predicts? In this framing, mitigating the consequences of anthropogenic change on ecosystems  
59 becomes an optimization problem: given a forecast of the future state of the system, and some “goal” state

60 for the future, the problem is then to optimize our intervention into the system to maximize the  
61 probability the system approaches our “goal” state. This dissertation aims to this framework for ecosystem  
62 monitoring and forecasting (fig. 1, left), and each chapter address some aspect of this pipeline to data from  
63 a monitoring network to forecasts to mitigation strategy (fig. 1, right).

64 [Figure 1 about here.]

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

## 75 **Chapter One: Optimizing spatial sampling of species interactions**

### 76 **Objective**

77 This chapter uses simulation models to investigate the relationship between species relative abundance,  
78 sampling effort, and probability of observing an interaction between species in order to aid in the design of  
79 samples of ecological interactions, and to provide a null expectation of false-negative probability for a  
80 dataset of a given size. Further it then proposes a method for optimizing the spatial sampling locations to  
81 maximize the probability of detecting an interaction between two species given a fixed number of total of  
82 observations, and the distributions of each species. This addresses the optimization of monitoring  
83 network part of the flow from data to mitigation at the top of fig. 1, left. As explored in the previous  
84 chapter, there are false-negatives in interaction data. However, there is more than one way to observe a  
85 false-negative when sampling interactions. fig. 2 shows a taxonomy of false-negatives in occurrence,  
86 co-occurrence, and interaction data.

87

[Figure 2 about here.]

## 88 Methods

89 The first result is to compute a null expectation of the probability of an interaction false-negative as a  
 90 function number of total observations of individuals of *any species*. This is done by simulating the process  
 91 of observation, where the probability of observing a given species is its relative abundance. We use a  
 92 log-normal distribution of relative abundance (Hubbell 2001) and simulating the process of observation on  
 93 food-webs generated using the niche model (Williams & Martinez 2000) with connectance parameterized  
 94 by the flexible-links model (MacDonald *et al.* 2020). An example of this relation for networks with varying  
 95 species richness is shown in fig. 3.

96 We then go on to testing some assumptions of this neutral model with empirical data. Primarily that we  
 97 analytically show that our neutral model, if anything, underestimates the probability of false-negatives if  
 98 there are positive associations between species co-occurrence, and we show these positive associations  
 99 exist in two sets of spatially replicated samples of interaction networks (Thompson & Townsend 2000;  
 100 Hadfield *et al.* 2014), fig. 4—further I'm planning to add the field data from the previous chapter into this  
 101 analysis once available. Finally this chapter proposes a simulated annealing method to optimize the a set  
 102 of  $n$  points in space to maximize the probability of detecting an interaction between two species  $a$  and  $b$   
 103 with *known* distributions  $D_a, D_b$ .

## 104 Results

105 The first major result is using the simulation of the observation process described above to generate  
 106 expectations of interaction false-negative rate (FNR) as a function of total number of observations, with  
 107 the goal being for this estimate to be used as correction for detection error when fitting an interaction  
 108 prediction model. This relationship varies with the total richness of the metaweb fig. 3.

109

[Figure 3 about here.]

110 The second major result is that we analytically show that the this simulated observation model, by  
 111 assuming that there is no association between observing two species given that they interact, actually

112 under predicts the realized false-negative interaction rate. We then demonstrate that this positive  
113 association association exists in two empirical systems fig. 4.

114 [Figure 4 about here.]

## 115 **Progress**

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

## 119 **Chapter Two: Forecasting the spatial uncoupling of a plant-pollinator 120 network**

121 Interactions between plants and pollinators form networks which together structure the “architecture of  
122 biodiversity” (Bascompte & Jordano 2007). The functioning and stability of ecosystems emerge from these  
123 interactions, but anthropogenic change threatens to unravel and “rewire” these interaction networks  
124 (CaraDonna *et al.* 2017), jeopardizing the persistence of these systems. Plant-pollinator networks face two  
125 possible forms of rewiring in response to anthropogenic environmental change: spatial and temporal.  
126 Range shifts could cause interacting species to no longer overlap in space, and shifts in phenology could  
127 cause interacting species to no longer occur at the same time of year. This chapter uses several years of  
128 data on bumblebee-flower phenology and interactions across several field sites, each consisting of several  
129 plots across an elevational gradient, combined with spatial records of species occurrence via GBIF to  
130 forecast the uncoupling of the plant-pollinator metaweb of Colorado.

131 [Figure 5 about here.]

## 132 **Methods**

133 The data for this chapter is derived from multiple sources that can be split into four categories. (1) Field  
134 data from three different field sites across Colorado, each with multiple plots across an elevational

135 gradient, for seven, seven, and three years respectively. This data was collected by Paul CaraDonna and  
136 Jane Oglevie (from the Rocky Mountain Biological Laboratory; RMBL) and Julian Resasco (CU Boulder).  
137 (2) GBIF spatial occurrence records of each of these species across Colorado, including a metaweb of  
138 interactions across all of Colorado taken from GBIF. (3) Remotely sensed data consisting of current and  
139 forecasting bioclimatic variables from CHELSA. (4) Phylogenies for both bee and flower species derived  
140 from NCBI GenBank barcodes for mitochondrial COI (bumblebees) and chloroplast rbcL (flowers).

141 As the data we have is spatially sparse and likely to contain many interaction “false-negatives” (Strydom *et*  
142 *al.* 2021b), we begin by predicting a metaweb of interactions across Colorado as they exist *in the present*.  
143 We do this using a set of candidate interaction prediction models: relative abundance only, phylogenetic  
144 embedding only (a la Strydom *et al.* (2021a)), niche embedding only (Gravel *et al.* 2019), and all pairwise  
145 combinations of those constituent models. After validating and selecting the best performing model, we  
146 then predict how these distributions of each of these species will change under the CMIP6 consensus  
147 climate forecast (Karger *et al.* 2017), and then finally quantify the reduction in spatial between species for  
148 which there is a predicted interaction.

## 149 **Results**

150 Here we show the in-progress results, which are the prerequisites for the analysis outlined above:  
151 phylogenies for both plant and bee species (fig. 6) and species distribution models for all species (an  
152 example shown in fig. 7).

153 [Figure 6 about here.]

154 [Figure 7 about here.]

## 155 **Progress**

156 At the moment, we have derived phylogenies (fig. 6) and SDMs (fig. 7) for all the species present in the  
157 Colorado GBIF metaweb. I’ve also been exploring the data available from Julian Resasco. The primary  
158 constraint on further progress is that we are waiting on the finalization of a data sharing agreement with  
159 RMBL.

160 **Chapter Three: Optimizing corridor placement against ecological**  
161 **dynamics**

162 **Objective**

163 As land-use change has caused many habitats to become fragmented and patchy, promoting landscape  
164 connectivity has become of significant interest to mitigate the effects of this change on Earth's biodiversity.  
165 However, the practical realities of conservation mean that there is a limitation on how much we can  
166 modify landscapes in order to do this. So what is the best place to put a corridor given a constraint on how  
167 much surface-area you can change in a landscape? This is the question this chapter seeks to answer.  
168 Models for inferring corridor locations have been developed, but are limited in that they are not developed  
169 around promoting some element of ecosystem function, but instead by trying to find the path of least  
170 resistance in an existing landscape from a derived resistance surface (Peterman 2018). This chapter  
171 proposes a general algorithm for choosing corridor placement to optimize a measurement of ecosystem  
172 functioning derived from simulations run on each proposed landscape modification.

173 **Methods**

174 [Figure 8 about here.]

175 We propose various landscape modifications which alter the cover of a landscape, represented as a raster.  
176 We then compute a new resistance surface based on the proposed landscape modification using  
177 Circuitscape (McRae *et al.* 2008), and based on the values of resistance to dispersal between pairs of  
178 locations we simulate spatially-explicit metapopulation dynamics model (Hanski & Ovaskainen 2000;  
179 Ovaskainen *et al.* 2002) to estimate a distribution of time until extinction for each landscape modification.  
180 The largest challenge in implementing this algorithm is the space of potential modifications grows as  
181  $O((nm)!)$  for an  $n$  by  $m$  raster. For most actual landscapes to which we wish to apply this method, the set  
182 of possible modifications becomes uncomputably large, so we use simulated annealing to explore the  
183 search space of possible modifications to estimate the modification that maximizes the time-until  
184 extinction of simulated metapopulation dynamics under that hypothetical modified landscape.  
185 The biggest challenge in implementing simulated annealing in this context is defining a proposal function

186 for landscape modifications. At the moment this is done by computing the minimum-spanning-tree  
187 (MST) of the spatial nodes, and then proposing corridors that connect nodes that are already connected in  
188 the MST.

189 The final component of this chapter is measuring the effect of land-use change on the robustness of the  
190 optimized corridor.

## 191 **Progress**

192 The current progress is that I have an algorithm for proposing landscape modifications and a simple  
193 implementation of simulated annealing. The only gap left is implementing Circuitscape estimation of  
194 resistance surfaces.

## 195 **Chapter Four: MetacommunityDynamics.jl: a virtual laboratory for 196 community ecology**

### 197 **Objective**

198 The final chapter consists of a collection of modules in the Julia language for different aspects of  
199 community ecology, including most of the code used for the preceding chapters. Indeed  
200 MetacommunityDynamics.jl (MCD.jl) is the epicenter of this set of tools, but due to the nature of the Julia  
201 language, MCD.jl is interoperable with several existing packages within the EcoJulia organization,  
202 including several to which I have contributed. We need a software library like this to generate synthetic  
203 data from a *known* set of mechanisms and parameters to test our methods for parameter inference and  
204 forecasting on this *known* system to assess the effectiveness of these inference and forecasting methods.

205 [Figure 9 about here.]

### 206 **Methods**

207 A diagram showing the relation between these packages is shown in fig. 9. MetacommunityDynamics.jl is  
208 built on DynamicGrids.jl, a library for high-performance gridded simulations in the Julia language, and

209 Dispersal.jl (Maino *et al.* 2021), and extension of DynamicGrids.jl specifically for modeling organism  
210 dispersal. It also contains integrations with EcologicalNetworks.jl (Poisot *et al.* 2019) to generate  
211 metawebs, or can use empirical networks from Mangal.jl (Banville *et al.* 2021). It implements the general  
212 framework for community dynamics proposed by Vellend (2010), where all community processes can  
213 divided into four categories: selection, dispersal, drift, and speciation.

## 214 **Results**

215 Below (fig. 10) is a sample output of simulated food-web dynamics for a metaweb of 100 species generated  
216 using the minimum-potential-niche model with connectance  $C = 0.05$  and forbidden-link probability of  
217 0.5. The dynamics change according to a Lotka-Volterra functional response, dispersal (with dispersal  
218 distance inverse proportional to trophic-level), linear mortality, and logistic growth for any species at the  
219 producer trophic-level.

220 [Figure 10 about here.]

## 221 **Progress**

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

## 229 **Discussion**

230 Describing expected/anticipated contributions of the thesis. Very important for QE. This  
231 should be at least half a page.

232 **References**

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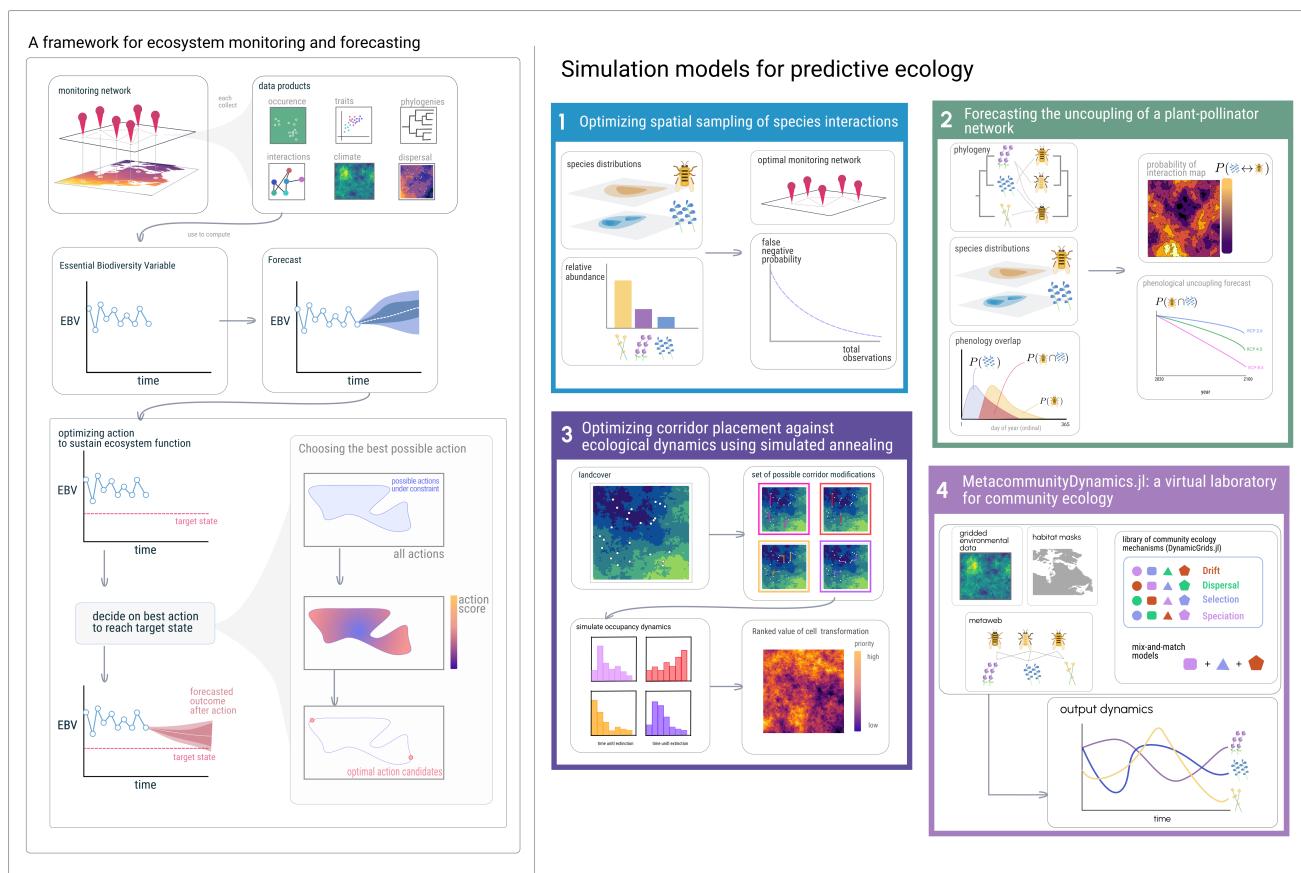


Figure 1: thesis concept

Species A occurs?

		true		false								
		true	Species A observed?									
		true	Species B observed? <table border="1"> <tr> <td>true</td><td>co-occurrence <b>true-positive</b></td><td>Interaction observed? true      false</td><td>co-occurrence <b>false-negative</b></td></tr> <tr> <td>false</td><td>co-occurrence <b>false-negative</b></td><td>interaction <b>true-positive</b>      interaction <b>false-negative</b></td><td>occurrence <b>false-negative</b></td></tr> </table>	true	co-occurrence <b>true-positive</b>	Interaction observed? true      false	co-occurrence <b>false-negative</b>	false	co-occurrence <b>false-negative</b>	interaction <b>true-positive</b> interaction <b>false-negative</b>	occurrence <b>false-negative</b>	
true	co-occurrence <b>true-positive</b>	Interaction observed? true      false	co-occurrence <b>false-negative</b>									
false	co-occurrence <b>false-negative</b>	interaction <b>true-positive</b> interaction <b>false-negative</b>	occurrence <b>false-negative</b>									
Species B occurs?	true	co-occurrence <b>true-negative</b>		occurrence <b>true-negative</b>								
false												

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

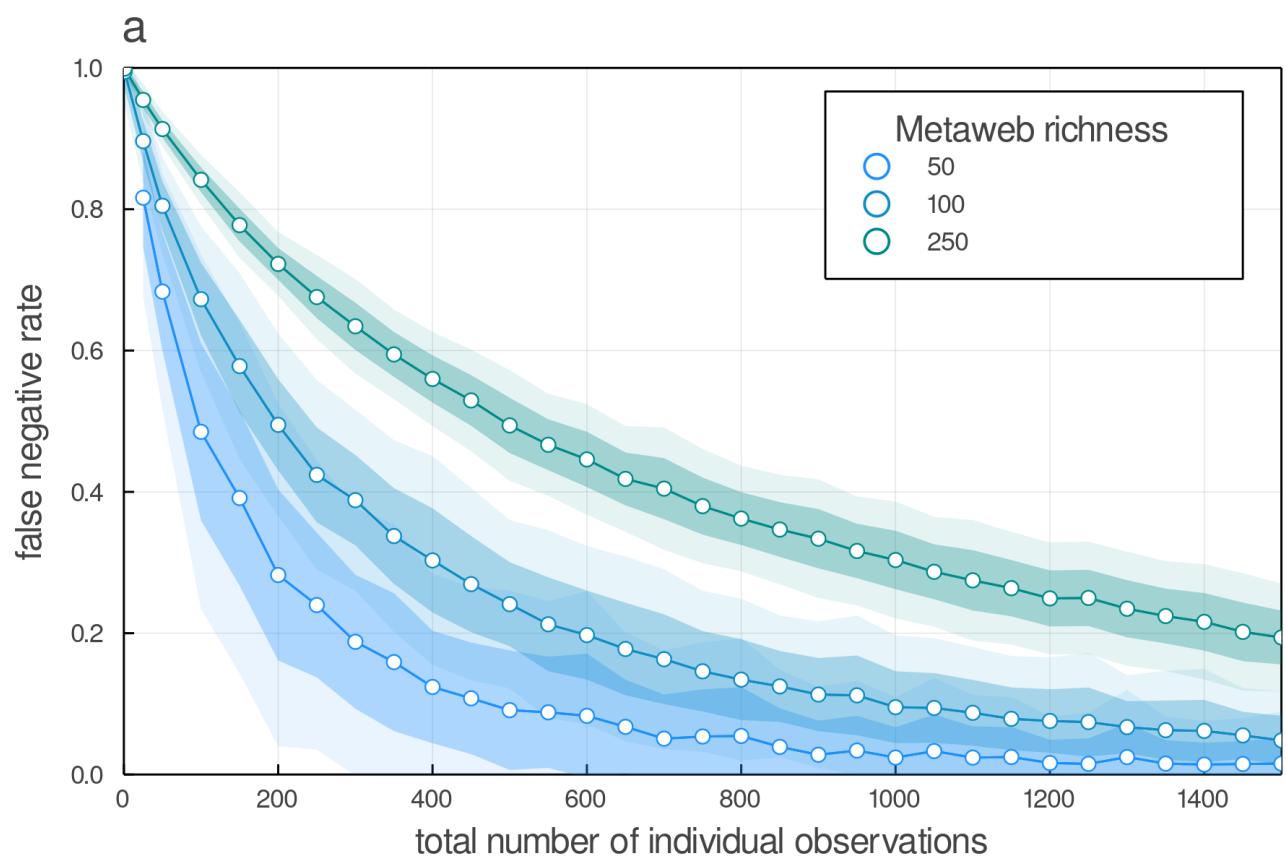


Figure 3: foo

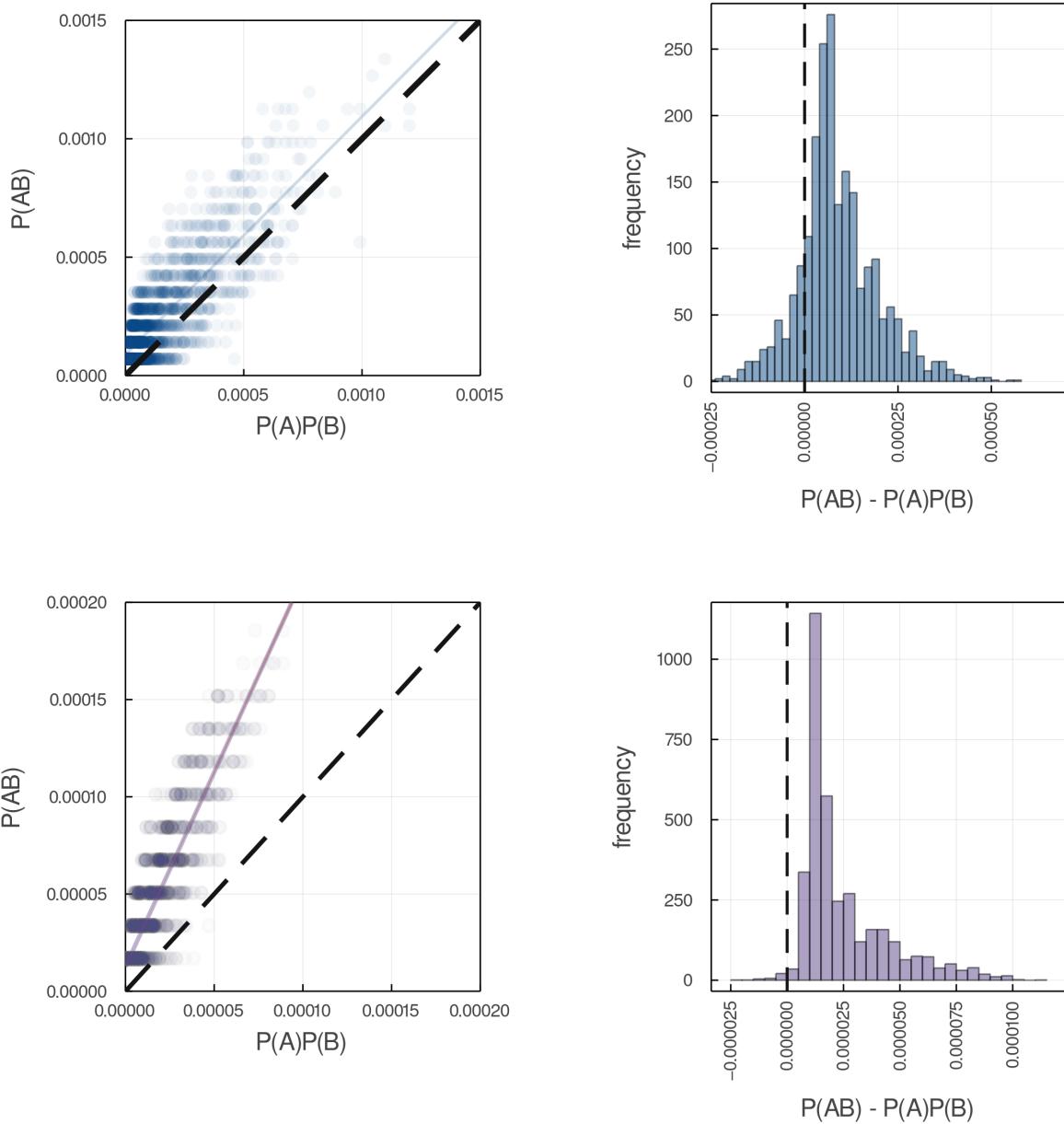


Figure 4: Demonstrates positive associations in co-occurrence

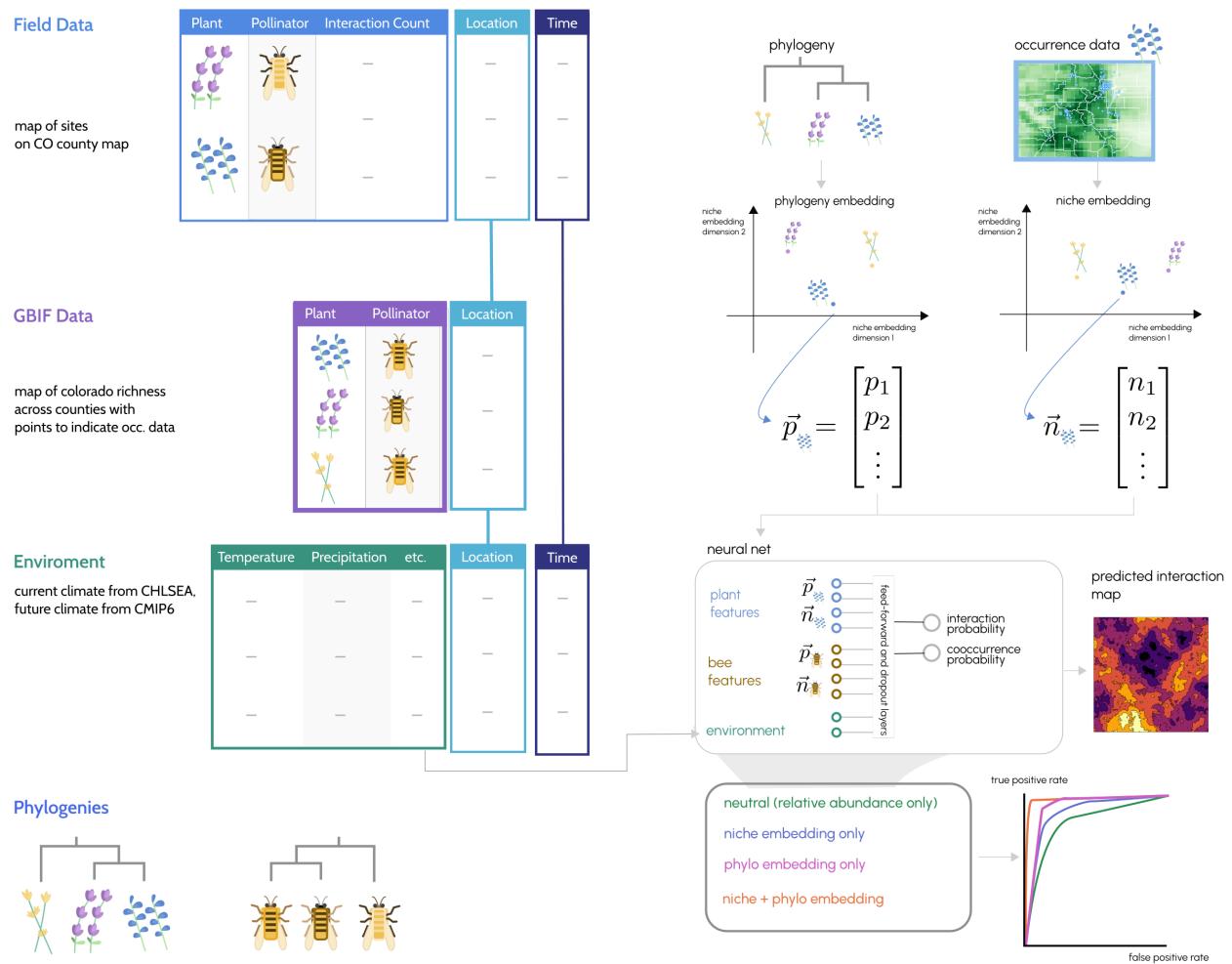


Figure 5: Chapter One conceptual figure. Left: the sources of data and how they can be synthesized. Right: The flow from data to interaction prediction using a few different interaction prediction models.

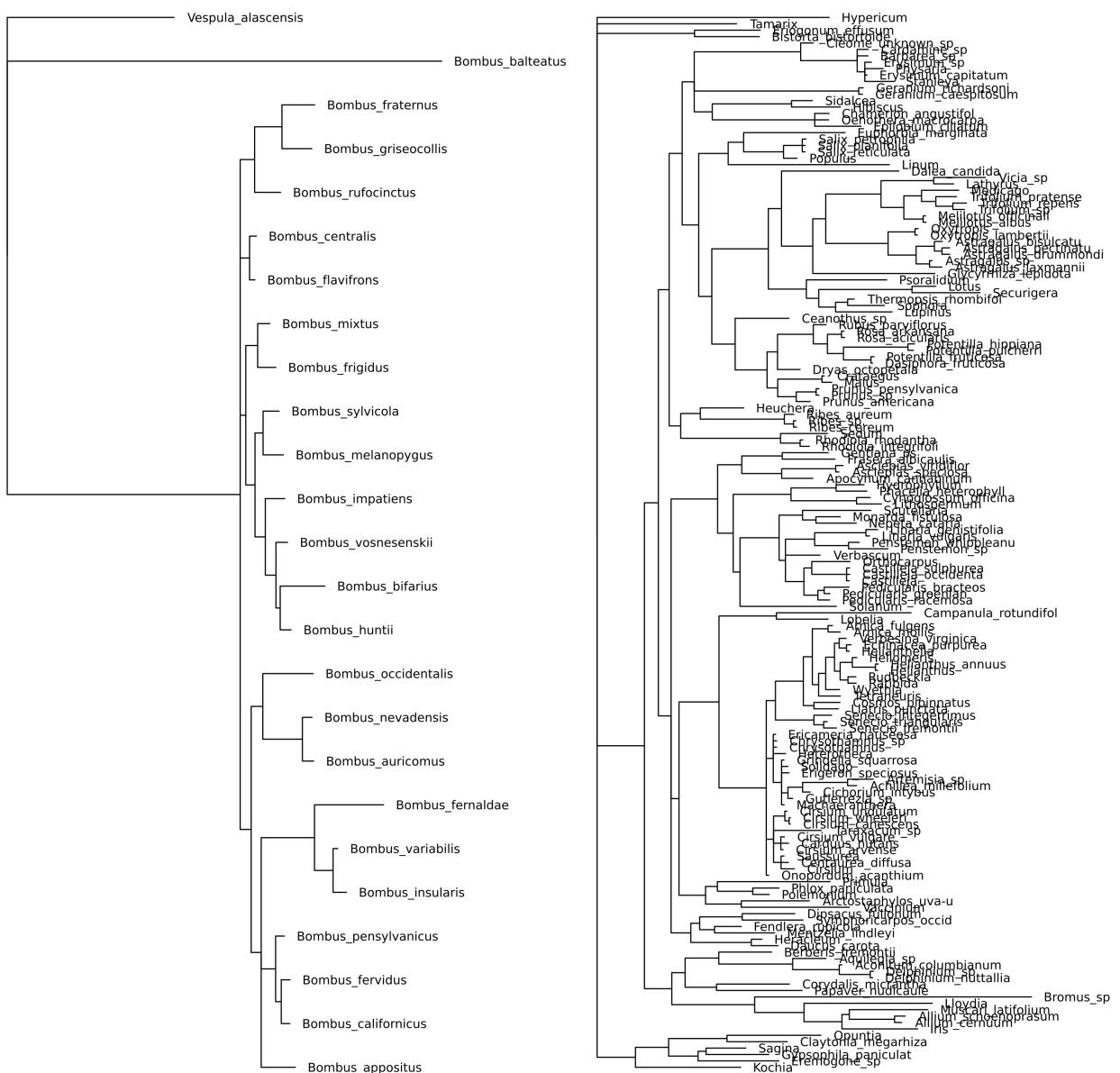


Figure 6: Phylogeny for both bumblebee species (left) and flower species (right)

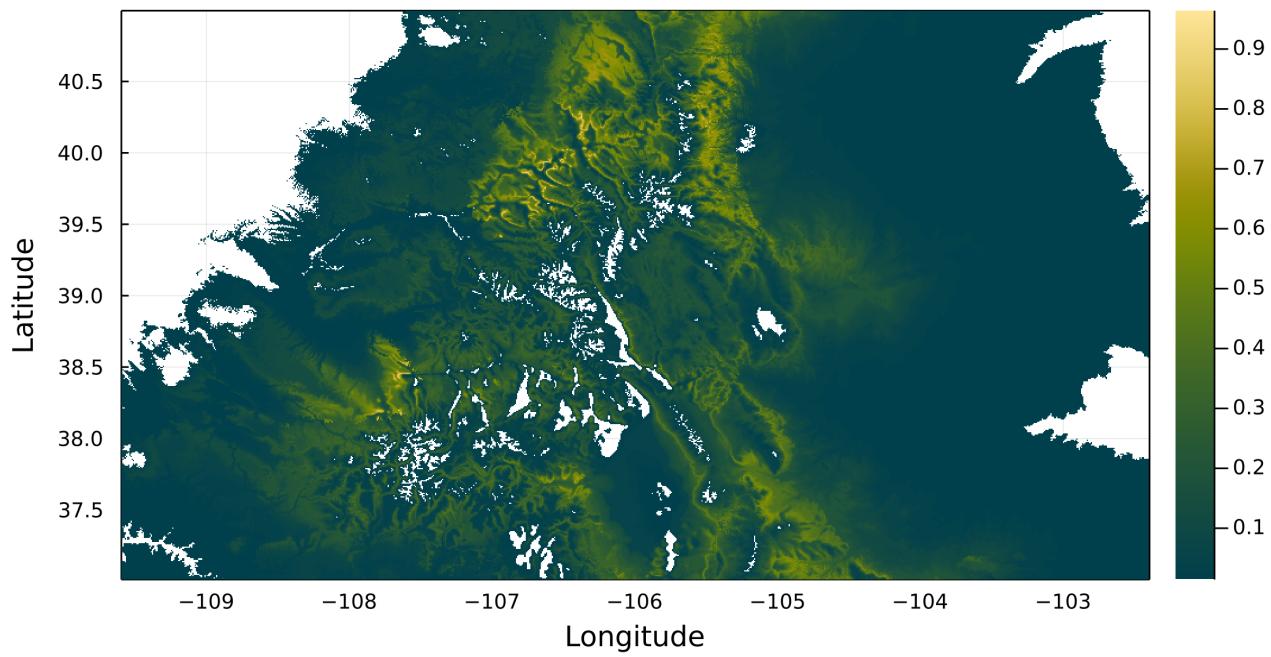


Figure 7: Example SDM for *Achillea millefolium*

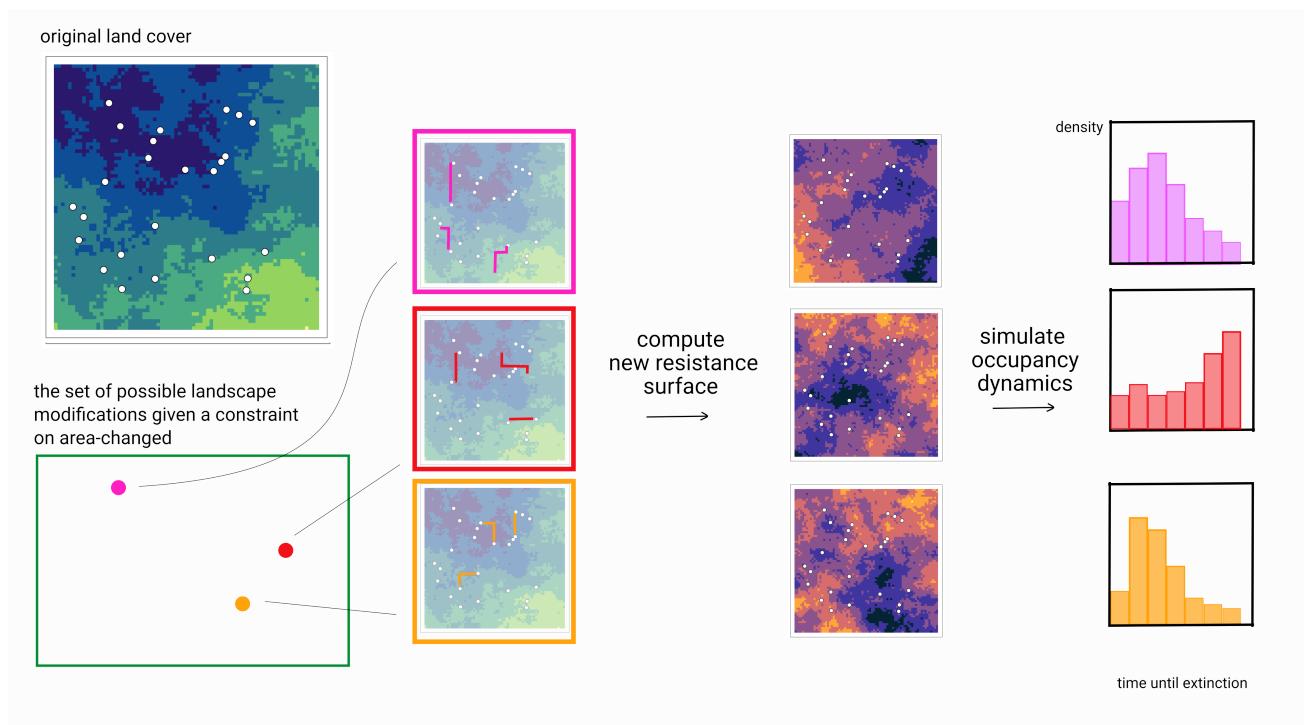


Figure 8: foo

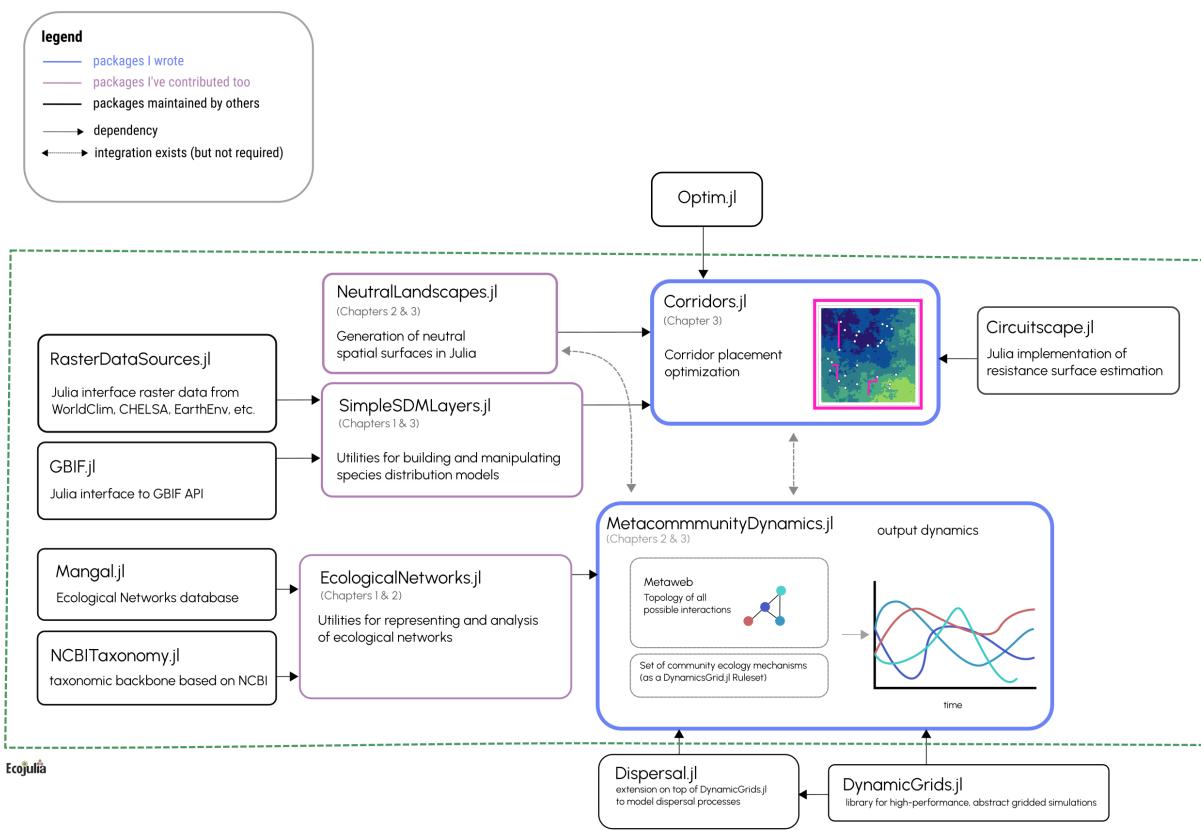


Figure 9: The structure of the software libraries used as part of MCD.jl

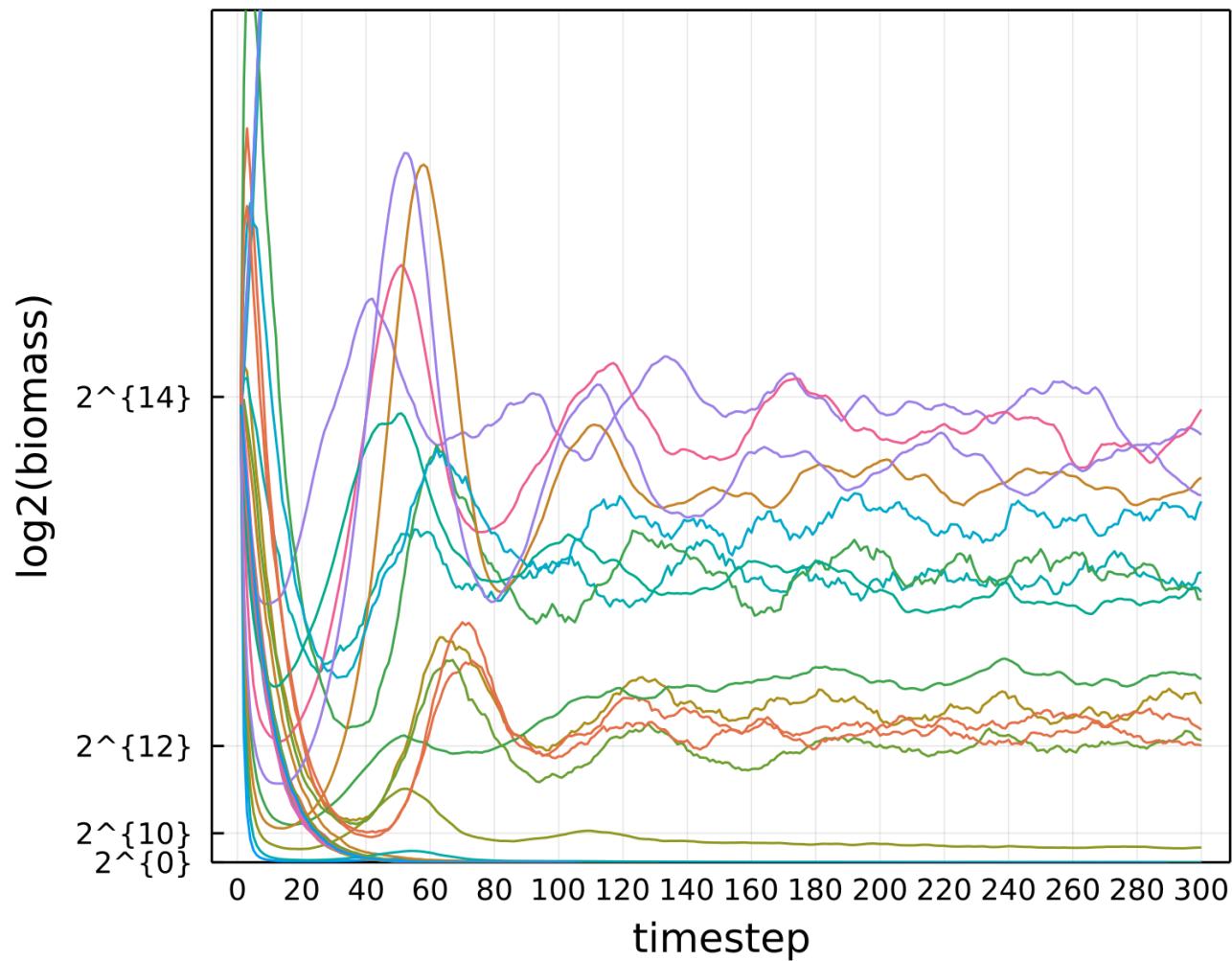


Figure 10: Sample output of simulated food web dynamics from MetacommunityDynamics.jl