

# Thesis proposal

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Last revision: *November 23, 2021*

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*—TK DEFINITION—and then using these forecasts to make decisions to mitigate the negative  
8 consequences of this change on ecosystems, their functioning, and the services they provide to humans  
9 has emerged as an imperative for ecology and environmental science (Dietze 2017). However, robust  
10 prediction of ecological processes is, to say the least, quite difficult (Beckage *et al.* 2011; Petchey *et al.*  
11 2015). This difficultly is compounded by a few factors, the first being that sampling ecosystems is not easy.  
12 Ecological data is often biased, noisy, and sparse in both space and time. The current paucity of  
13 ecological data has resulted in much interest in developing global systems for *ecosystem monitoring*  
14 (Makiola *et al.* 2020), which would systematize the collection of biodiversity data in manner that makes  
15 detecting and predicting change more possible than at the moment (Urban *et al.* 2021).

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

30 you ask), became the foundation for mathematical models in ecology.

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

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

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

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

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

63 [Figure 1 about here.]

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

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

### 75 **Objective**

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

[Figure 2 about here.]

## 87 Methods

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

95 We then go on to testing some assumptions of this neutral model with empirical data. Primarily that we  
 96 analytically show that our neutral model, if anything, underestimates the probability of false-negatives if  
 97 there are positive associations between species co-occurrence, and we show these positive associations  
 98 exist in two sets of spatially replicated samples of interaction networks (Thompson & Townsend 2000;  
 99 Hadfield *et al.* 2014), fig. 4—further I'm planning to add the field data from the previous chapter into this  
 100 analysis once available.

101 Finally this chapter proposes a simulated annealing method to optimize the a set of  $n$  points in space to  
 102 maximize the probability of detecting an interaction between two species  $a$  and  $b$  with *known*  
 103 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 correlation between observing two species given that they interact, actually

112 underpredicts the realized false-negative interaction rate. We then demonstrate that this association exists  
113 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 and SDMs for all the species present in the Colorado GBIF  
157 metaweb. I've also been exploring the data available from Julian Resasco. The primary constraint on  
158 further progress is that we are waiting on the finalization of a data sharing agreement with RMBL.

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

161 **Objective**

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

172 **Methods**

173 [Figure 8 about here.]

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

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

187 **Results**

188 **Progress**

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

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

194 **Objective**

195 The final chapter consists of a collection of modules in the Julia language for different aspects of  
196 community ecology, including most of the code used for the preceding chapters. Indeed  
197 MetacommunityDynamics.jl (MCD.jl) is the epicenter of this set of tools, but due to the nature of the Julia  
198 language, MCD.jl is interoperable with several existing packages within the EcoJulia organization,  
199 including several to which I have contributed. A diagram showing the relation between these packages is  
200 shown in fig. 9.

201 We need tools to generate synthetic data from a *known* set of mechanisms and parameters to test our  
202 methods for parameter inference and forecasting on this *known* system to assess the effectiveness of these  
203 inference and forecasting methods.

204 [Figure 9 about here.]

205 **Methods**

206 Software is structured based on DG.jl (**cite?**) and Dispersal.jl (**cite?**).

- 207 Uses methods from EN.jl to generate metawebs, or can use empirical networks from Mangal.jl (**cite?**).  
208 Framework based on (**Velland2010ConSyn?**), processes divided into four categories: selection, dispersal,  
209 drift, speciation.

210 **Results**

211 Below (fig. 10) is a sample output of simulated food-web dynamics for a metaweb of 100 species generated  
212 using the minimum-potential-niche model with connectance  $C = 0.05$  and forbidden-link probability of  
213 0.5. The dynamics change according to a Lotka-Volterra functional response, dispersal (with dispersal  
214 distance inverse proportional to trophic-level), linear mortality, and logistic growth for any species at the  
215 producer trophic-level.

216 [Figure 10 about here.]

217 **Progress**

218 The software as it exists is capable of simulating the biomass dynamics of arbitrarily large food-webs using  
219 Lotka-Volterra, Holling Type-II, or Holling Type-III functional responses. It currently has methods to  
220 implement Gaussian drift, and various forms of dispersal via Dispersal.jl. Also occupancy dynamics for  
221 Levins metapopulations (**levins1967?**), and spatially explicit Hanski metapopulations (**hanski2001?**).  
222 This is most of what needs to exist for the preceding chapters.  
223 Selection on arbitrary environmental variables in progress, as well as traits.

224 **Discussion**

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

227 **References**

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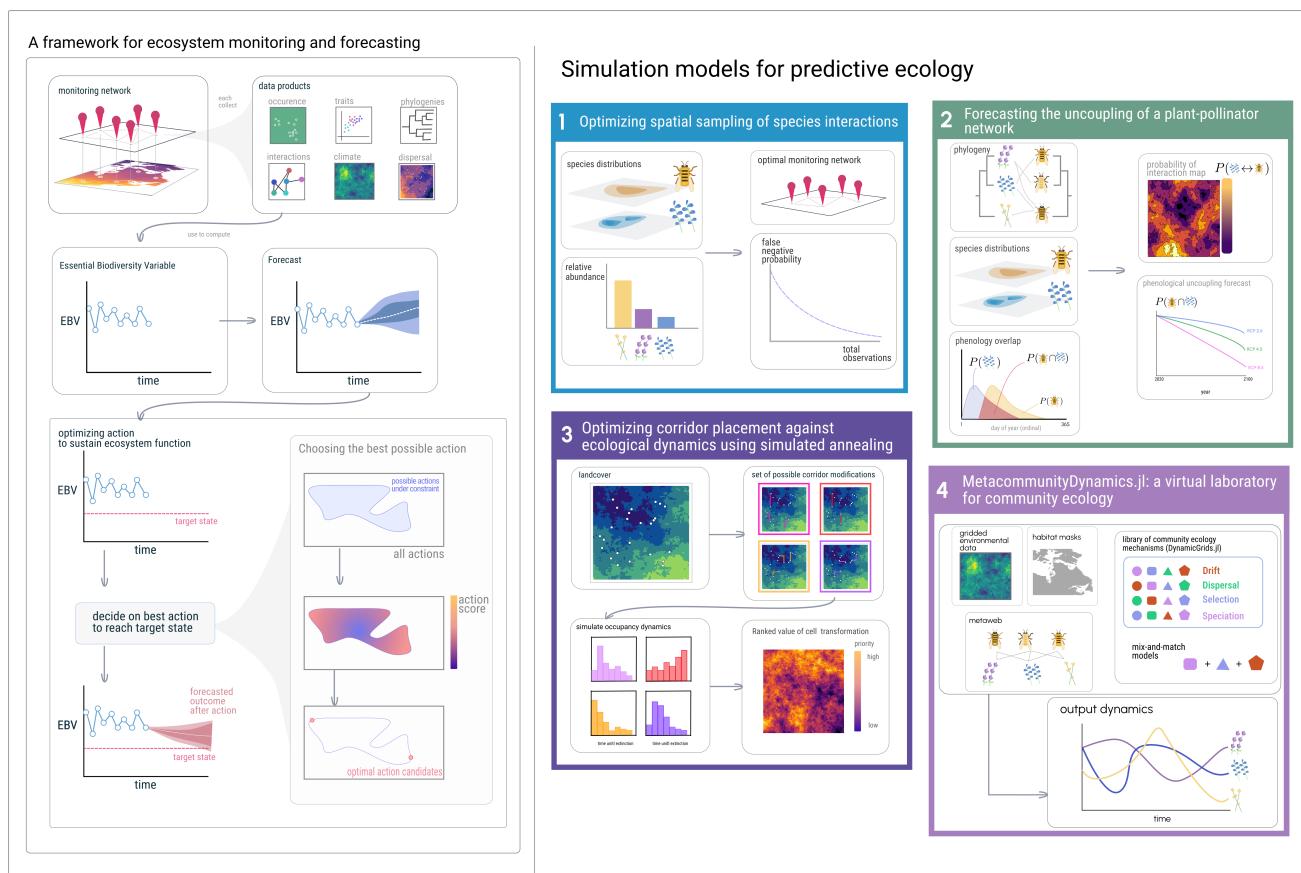


Figure 1: thesis concept

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> <th></th>	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	false											

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

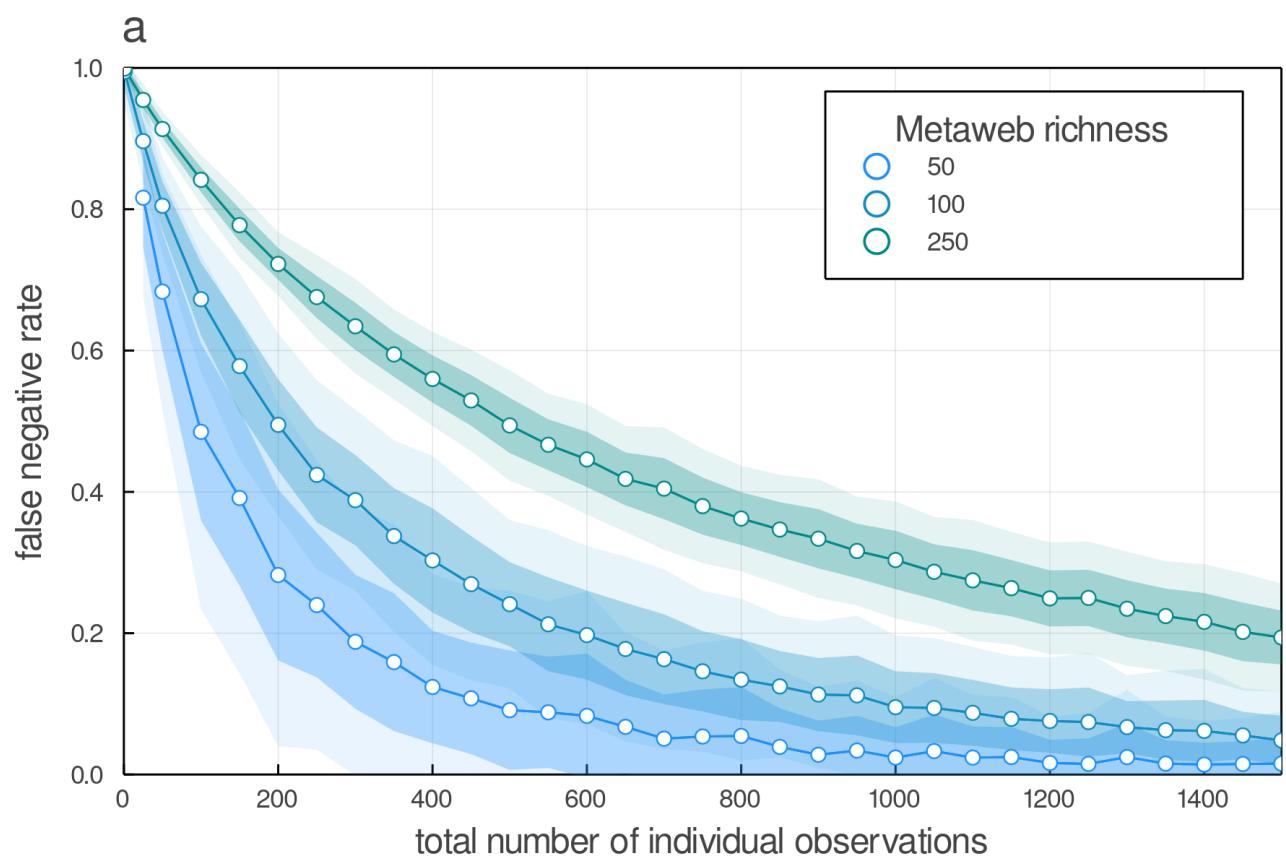


Figure 3: foo

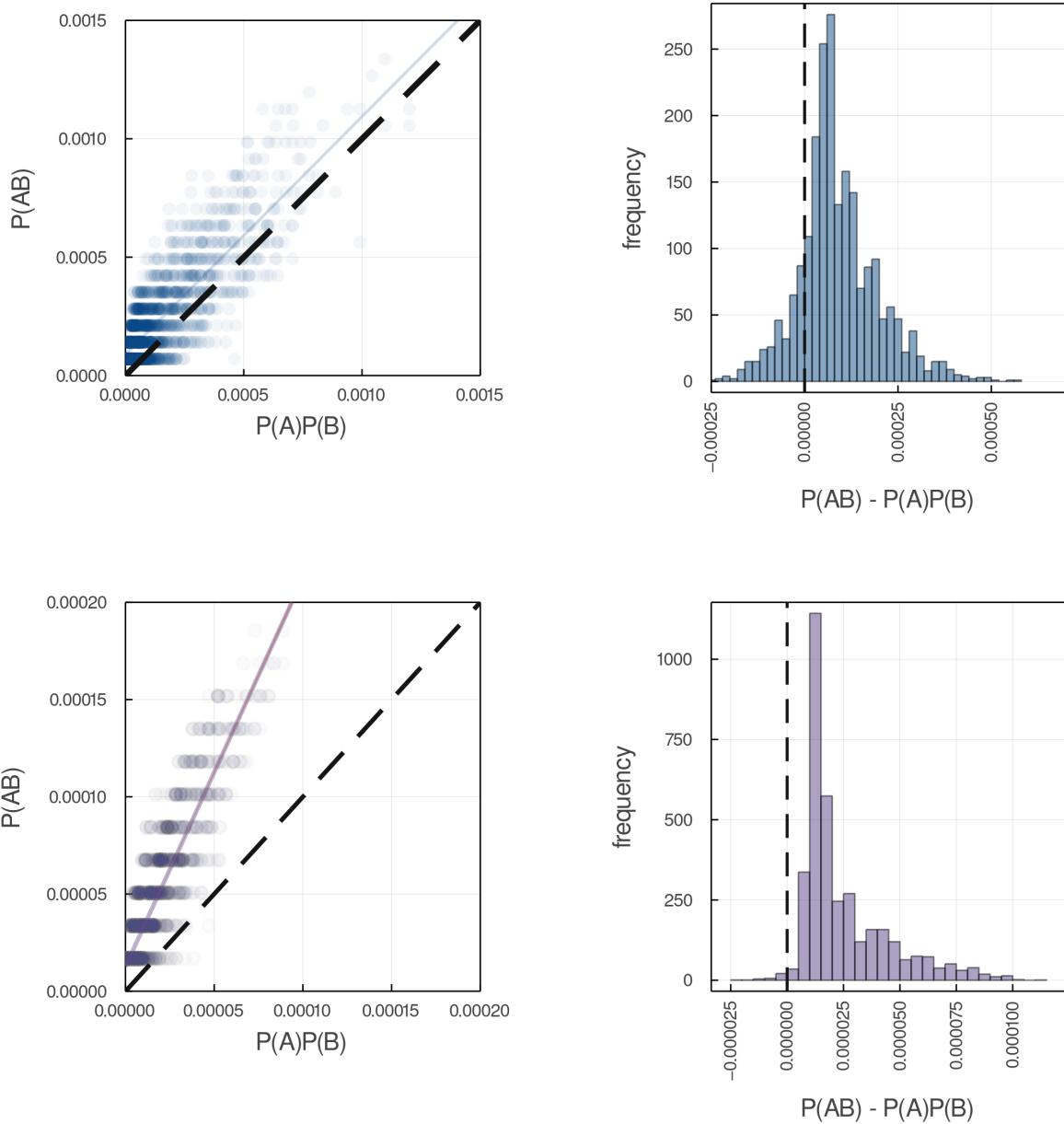


Figure 4: Demonstrates positive associations in co-occurrence

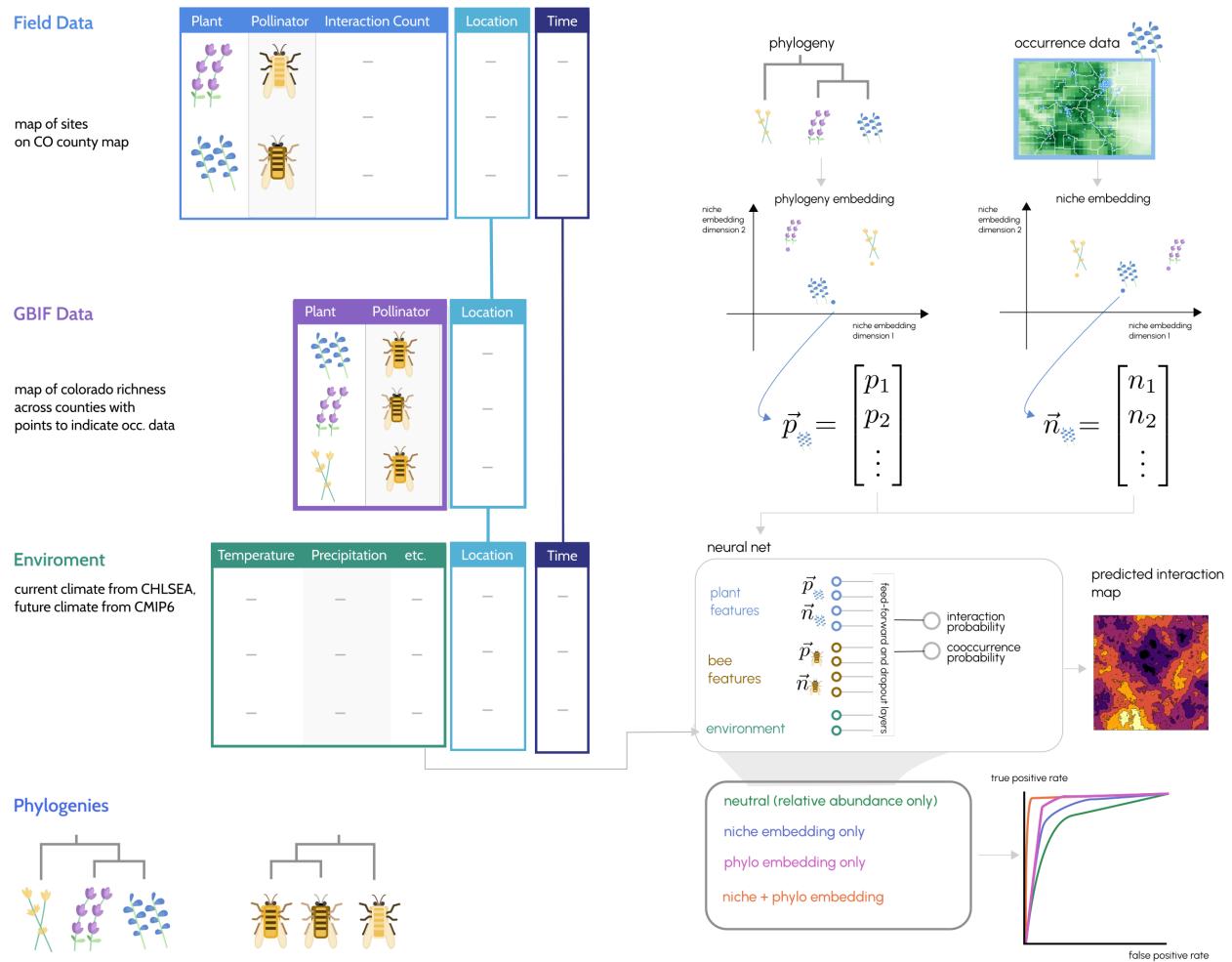


Figure 5: Chapter One conceptual figure. Left: the sources of data and how they can be synthesized. Right: The flow from data to interaction prediction using a few different interaction prediction models.

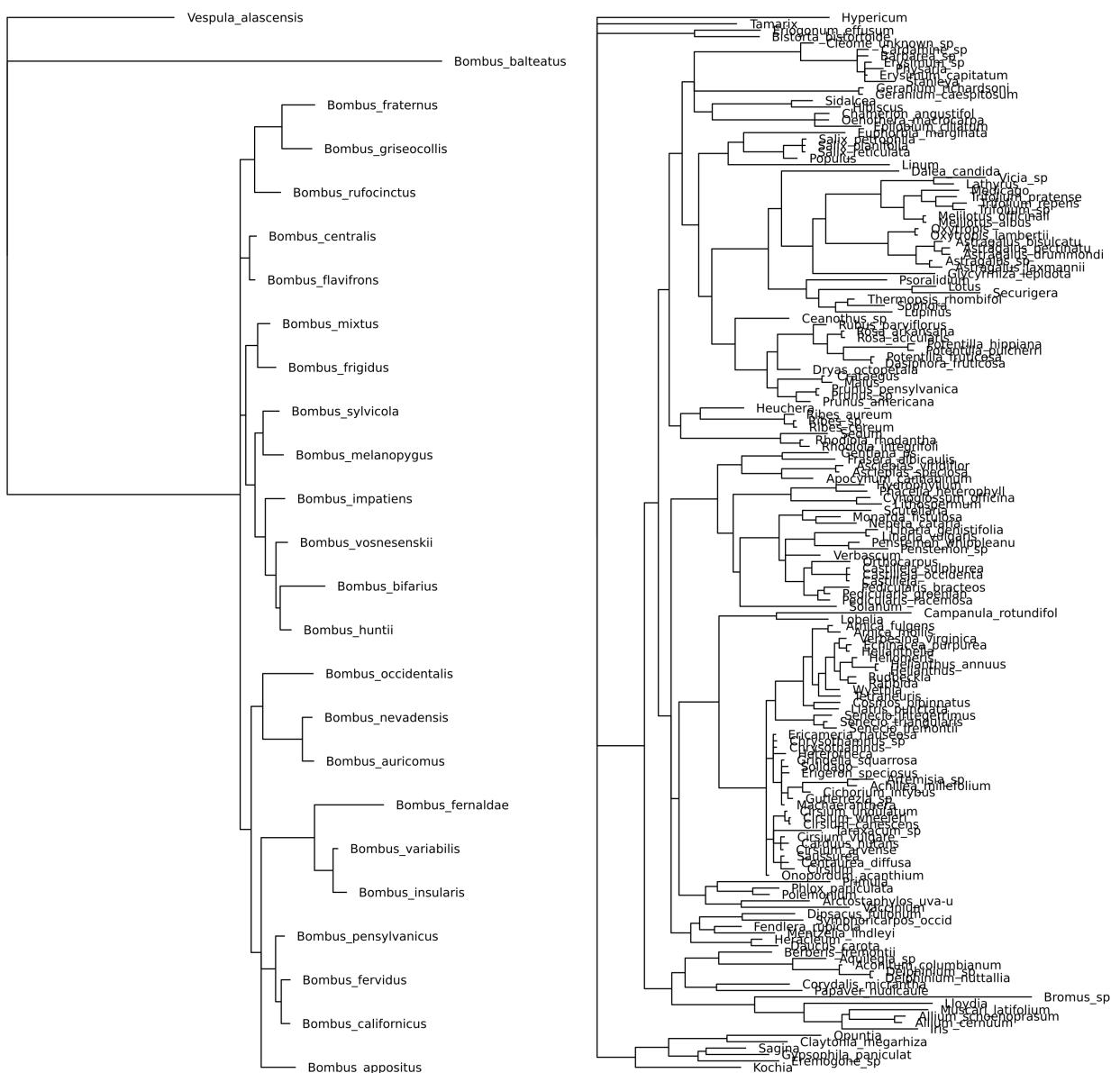


Figure 6: Phylogeny for both bumblebee species (left) and flower species (right)

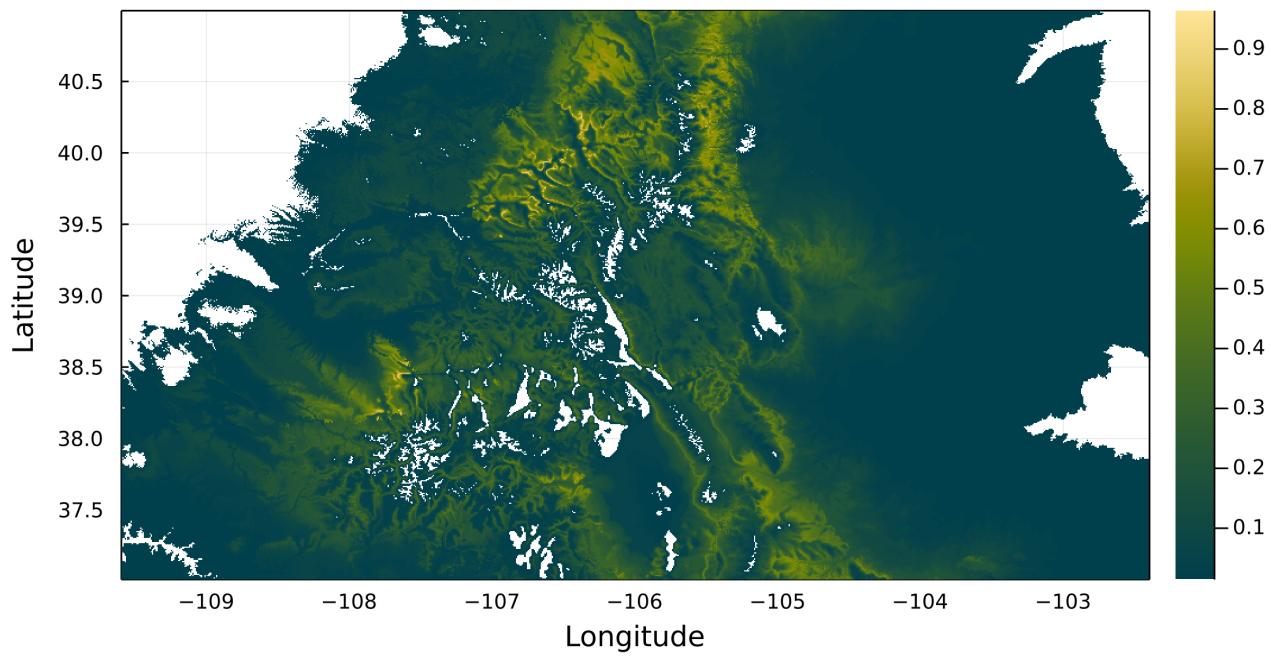


Figure 7: Example SDM for *Achillea millefolium*

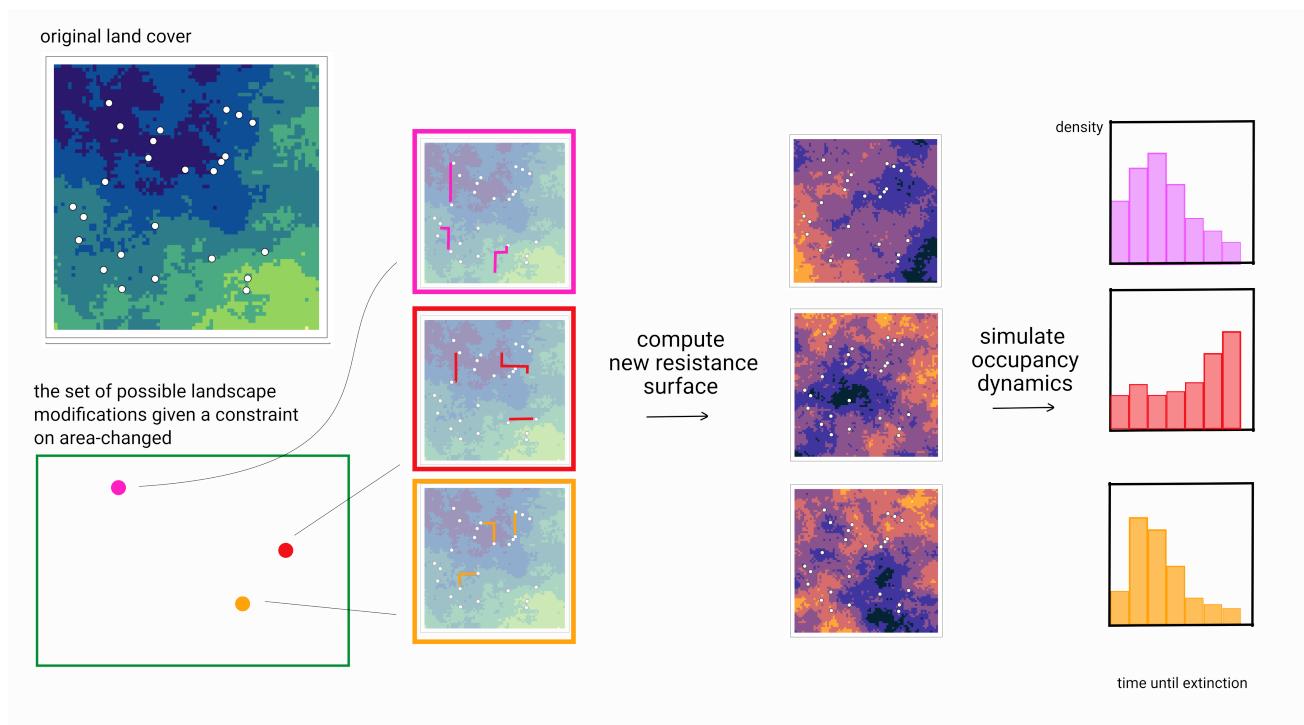


Figure 8: foo

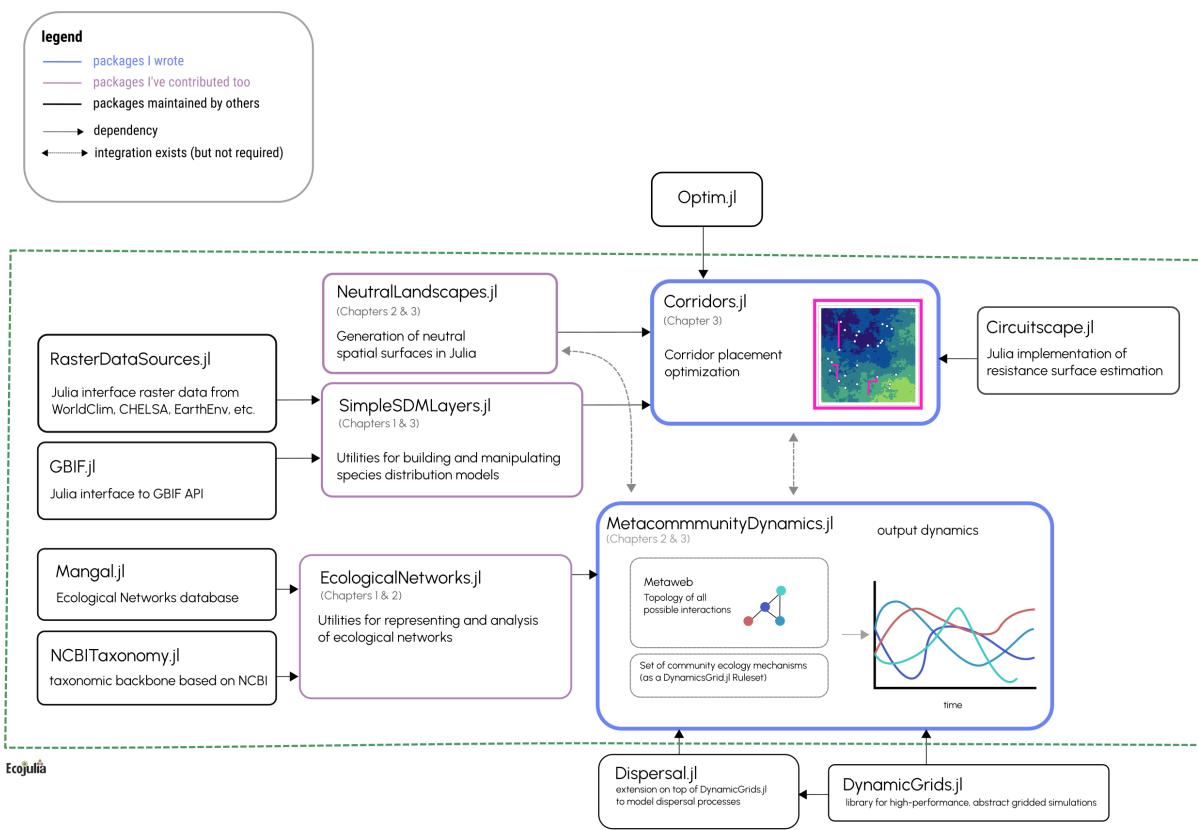


Figure 9: The structure of the software libraries used as part of MCD.jl

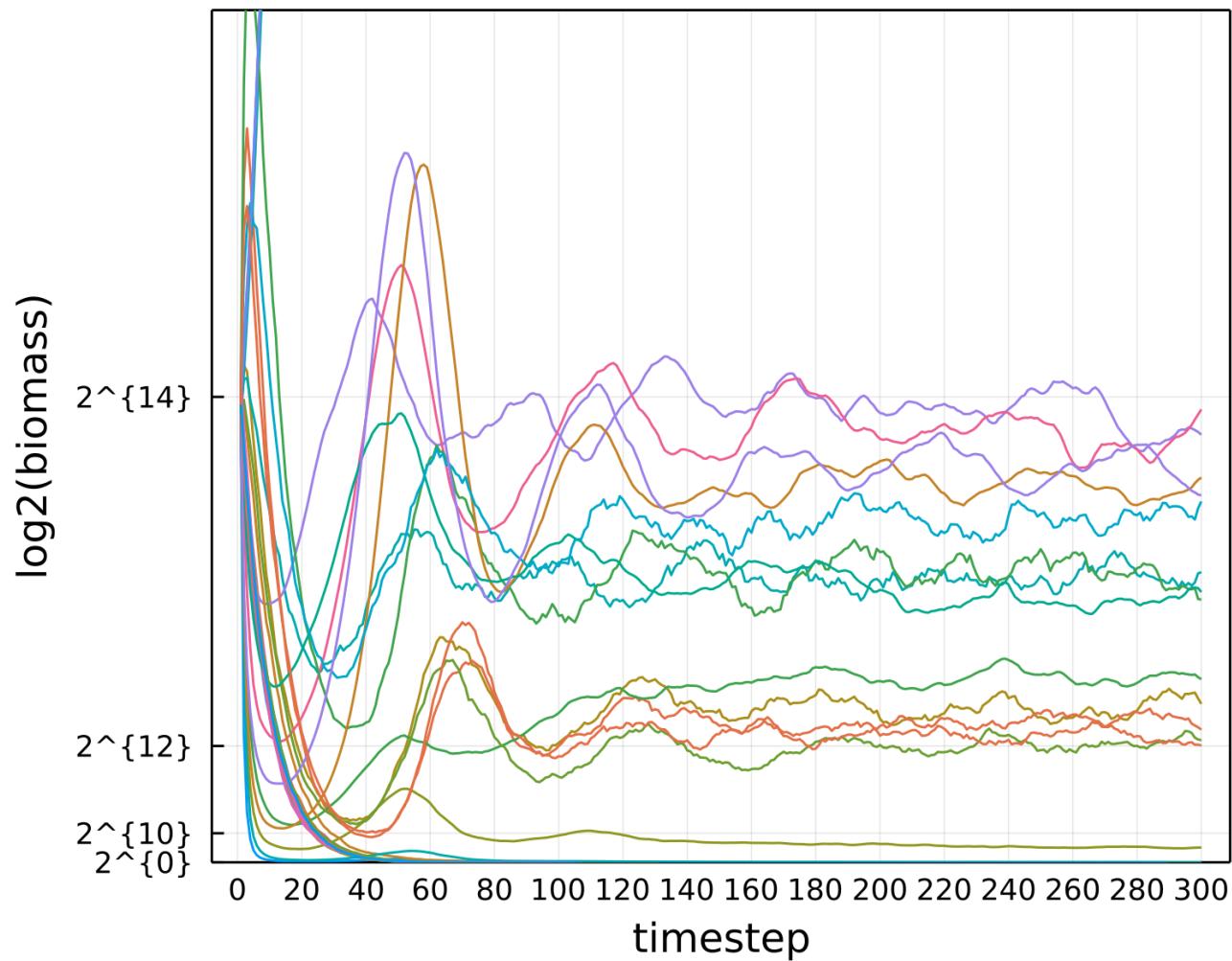


Figure 10: Sample output of simulated food web dynamics from MetacommunityDynamics.jl