

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

16 The second major challenge in ecological forecasting is that the underlying dynamics of most ecological
17 processes are unknown and instead must be inferred from this (sparse) data. Much of the history of
18 quantitatively modeling ecosystems have been done in the language of dynamical systems, describing how
19 the value of an observable state of the system, represented by a vector of numbers $[x_1, x_2, \dots, x_n]^T = \vec{x}$
20 changes as over time, yielding models in the form of differential equations in continuous-time
21 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
22 an arbitrary function describing how the system changes on a moment-to-moment basis (e.g. in the
23 context of communities, f could be Lotka-Volterra, Holling-Type-III or DeAngelis-Beddington functional
24 response). The initial success of these forms of models can be traced back to the larger program of
25 ontological reductionism, which became the default approach to modeling in the sciences after its early
26 success in physics, which, by the time ecology was becoming a quantitative science (sometime in the 20th
27 century, depending on who you ask), became the foundation for early quantitative models in ecology.

28 However, we run into many problems when aiming to apply this type of model to empirical data in
29 ecology. Ecosystems are perhaps the quintessential example of system that cannot be understood by

30 iterative reduction of its components into constituent parts—ecological phenomena are emergent are the
31 product of different mechanisms operating a different spatial, temporal, and organizational scales (Levin
32 1992). Further, the form of this functional response in real systems is effectively unknown, and some
33 forms are inherently more “forecastable” than others (Beckage *et al.* 2011; Chen *et al.* 2019; Pennekamp *et*
34 *al.* 2019). Further this analytical approach to modeling explicitly ignores known realities: ecological
35 dynamics not deterministic, many analytic models in ecology assume long-run equilibrium. Finally,
36 perhaps the biggest challenge in using these models to describe ecological processes is ecosystems vary
37 across more variables than the tools of analytic models are suited for. As the number of variables in an
38 analytic model increases, so does the ability of the scientist to discern clear relationships between them
39 given a fixed amount of data, the so-called “curse” of dimensionality.

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

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

60 monitoring and forecasting (fig. 1, left), and each chapter address some aspect of this pipeline to data from
61 a monitoring network to forecasts to mitigation strategy (fig. 1, right).

62 [Figure 1 about here.]

63 **Chapter One: Forecasting the spatial uncoupling of a plant-pollinator 64 network**

65 Interactions between plants and pollinators create networks of interactions, which together form the
66 “architecture of biodiversity” (Bascompte & Jordano 2007). The functioning and stability of ecosystems
67 emerge from these interactions, but anthropogenic change threatens to unravel and “rewire” these
68 interaction networks (CaraDonna *et al.* 2017), threatening the persistence of these systems.

69 Plant-pollinator networks face two possible forms of rewiring in response to anthropogenic environmental
70 change: spatial and temporal. Spatially, range shifts could cause interacting species to no longer overlap in
71 space, and shifts in phenology could cause interacting species to no longer occur at the same time of year.
72 This chapter uses several years of data on bumblebee-flower phenology and interactions across several
73 field sites, each consisting of several plots across an elevational gradient, combined with spatial records of
74 species occurrence via GBIF to forecast this uncoupling. This addresses the EBV to forecast element of the
75 flow from data to mitigation in fig. 1 (left).

76 [Figure 2 about here.]

77 **Data**

78 The data for this chapter is derived from multiple sources that can be split into four categories. (1) Field
79 data from three different field sites across Colorado, each with multiple plots across an elevational
80 gradient, for seven, seven, and three years respectively. This data was collected by Paul CaraDonna and
81 Jane Oglevie (from the Rocky Mountain Biological Laboratory; RMBL) and Julian Resasco (CU Boulder).
82 (2) GBIF spatial occurrence records of each of these species across Colorado, including a metaweb of
83 interactions across all of Colorado taken from GBIF. (3) Remotely sensed data consisting of current and

84 forecasting bioclimatic variables from CHELSA. (4) Phylogenies for both bee and flower species derived
85 from NCBI GenBank barcodes for mitochondrial COI (bumblebees) and chloroplast rbcL (flowers).

86 **Methods**

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

95 **Preliminary Results**

96 Here we show the in-progress work on the prerequisites for the analysis outlined above: phylogenies for
97 both plant and bee species (fig. 3) and species distribution models for all species (an example shown in
98 fig. 4).

99 [Figure 3 about here.]

100 [Figure 4 about here.]

101 **Chapter Two: Optimizing spatial sampling of species interactions**

102 This chapter uses simulation models to investigate the relationship between species relative abundance,
103 sampling effort, and probability of accurately detecting an interaction between species, and further
104 proposes a method for optimizing the spatial sampling locations to maximize the probability of detecting
105 an interaction between two species given their distributions. This addresses the optimization of
106 monitoring network part of the flow from data to mitigation at the top of fig. 1, left. As explored in the
107 previous chapter, there are false-negatives in interaction data. However, there is more than one way to

108 observe a false-negative when sampling interactions. fig. 5 shows a taxonomy of false-negatives in
109 occurrence, co-occurrence, and interaction data.

110 Co-occurrence is not the same thing as interaction (Blanchet *et al.* 2020), but often is used as a proxy.

111 [Figure 5 about here.]

112 The first result is using a log-normal distribution of relative abundance (Hubbell 2001) to compute a null
113 expectation of the number of total observations of individuals of *any species* by simulating the process of
114 observation on food-webs generated using the niche model (Williams & Martinez 2000) with connectance
115 parameterized by the flexible-links model (MacDonald *et al.* 2020). An example of this relation for
116 networks with varying species richness is shown in fig. 6.

117 [Figure 6 about here.]

118 We then go on to testing some assumptions of this neutral model with empirical data. Primarily that we
119 analytically show that our neutral model, if anything, underestimates the probability of false-negatives if
120 there are positive associations between species co-occurrence, which we show exist in two sets of spatially
121 replicated samples of interaction networks (Thompson & Townsend 2000; Hadfield *et al.* 2014),
122 fig. 7—further I'm planning to add the field data from the previous chapter into this analysis once
123 available.

124 [Figure 7 about here.]

125 Finally this chapter proposes a simulated annealing method to optimize the efficacy of interaction
126 detection given a set of observation locations for a pair of species *known* distributions D_a, D_b .

127 **Chapter Three: Optimizing corridor placement against ecological
128 dynamics**

129 As land-use change has caused many habitats to become fragmented and patchy, promoting landscape
130 connectivity has become of significant interest to mitigate the effects of this change on Earth's biodiversity.

131 However, the practical realities of conservation mean that there is a limitation on how much we can
132 modify landscapes in order to do this. So what is the best place to put a corridor given a constraint on how
133 much surface-area you can change in a landscape? This is the question this chapter seeks to answer.
134 Models for inferring corridor locations have been developed, but are limited in that they are not developed
135 around promoting some element of ecosystem function, but instead by trying to find the path of least
136 resistance in an existing landscape from a derived resistance surface (Peterman 2018). This chapter
137 proposes a general algorithm for choosing corridor placement to optimize a measurement of ecosystem
138 functioning derived from simulations run on each proposed landscape modification.

139 [Figure 8 about here.]

140 Methods

141 We propose various landscape modifications which alter the cover of a landscape, represented as a raster.
142 We then compute a new resistance surface based on the proposed landscape modification, and based on
143 the values of resistance to dispersal between each location we simulate spatially-explicit metapopulation
144 dynamics model (Hanski & Ovaskainen 2000; Ovaskainen *et al.* 2002) to estimate a distribution of time
145 until extinction for each landscape modification.
146 We then use simulated annealing to explore the search space of possible modifications to estimate the
147 modification that maximizes the time-until extinction of simulated metapopulation dynamics under that
148 hypothetical modified landscape.

- 149 • brief overview of simulated annealing describe how you build the
150 • proposal function optimize landscape optimization

151 Chapter Four: MetacommunityDynamics.jl: a virtual laboratory for 152 community ecology

153 This chapter consists of a collection of modules in the Julia language for different aspects of community
154 ecology, including most of the code used for the preceding chapters. Indeed MetacommunityDynamics.jl
155 (MCD.jl) is the epicenter of this set of tools, but due to the nature of the Julia language, MCD.jl is

156 interoperable with several existing packages within the EcoJulia organization, including several to
157 which I have contributed. A diagram showing the relation between these packages is shown in fig. 9.

158 [Figure 9 about here.]

159 **Conclusion**

160 **References**

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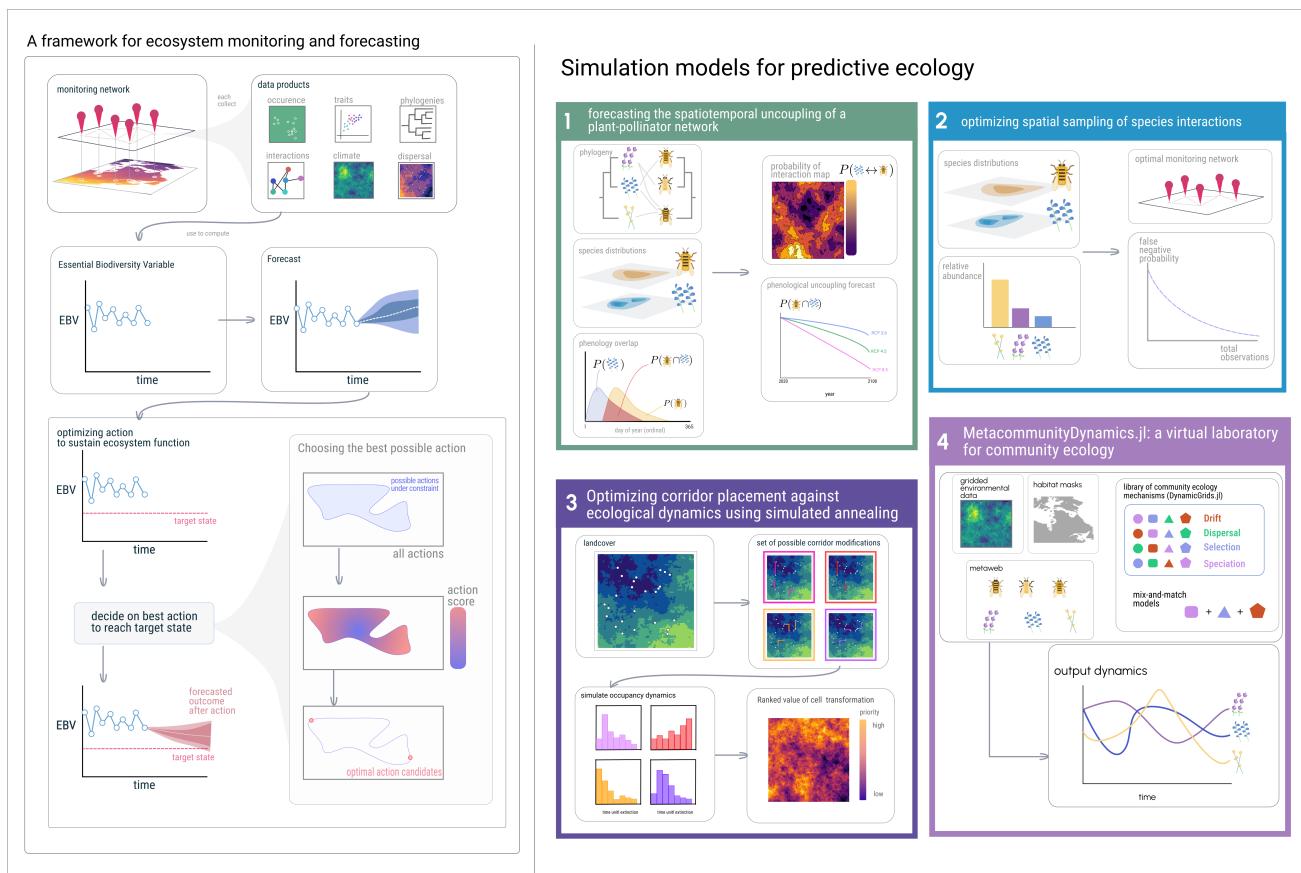


Figure 1: thesis concept

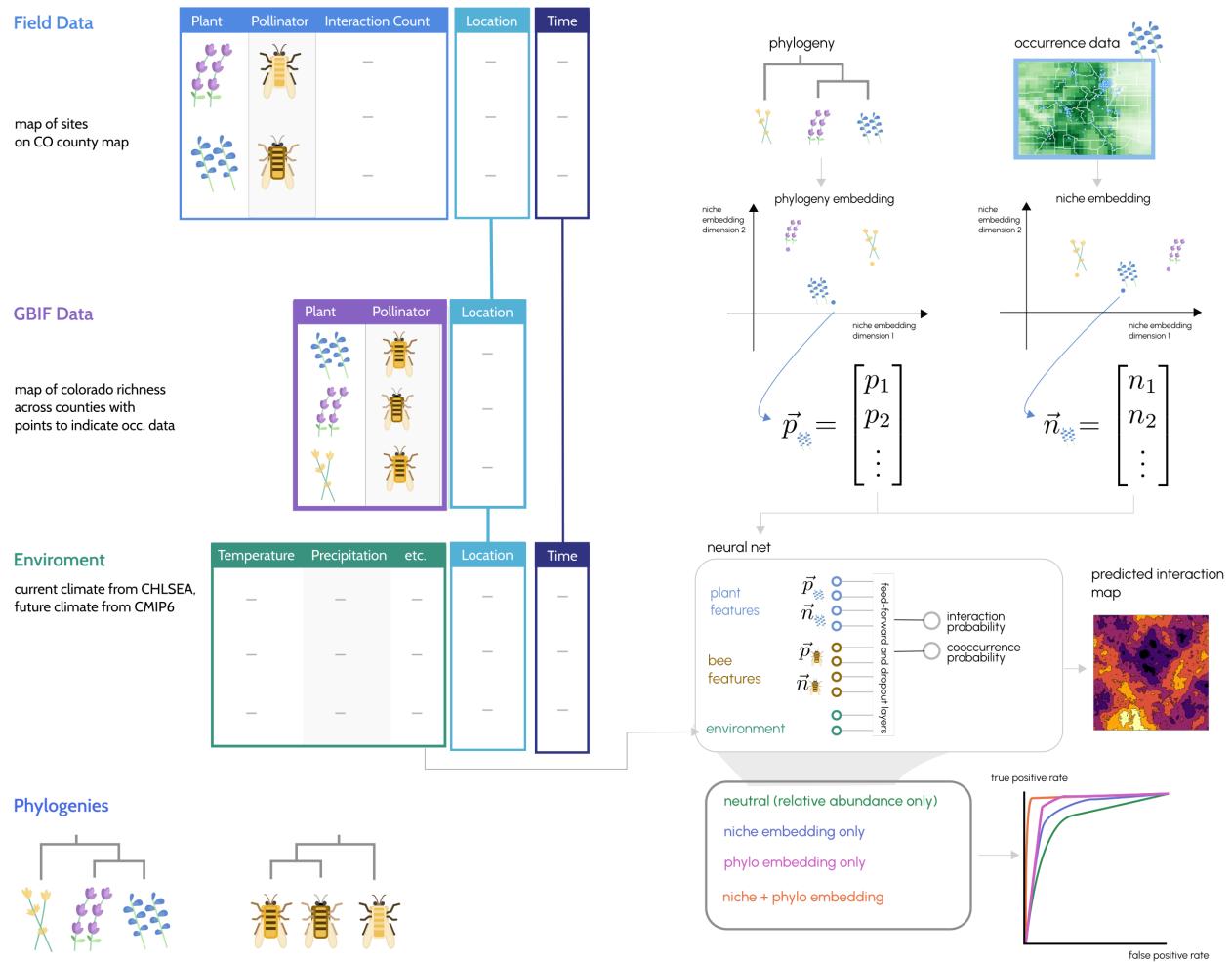


Figure 2: Chapter One conceptual figure. Left: the sources of data and how they can be synthesized. Right: The flow from data to interaction prediction using a few different interaction prediction models.

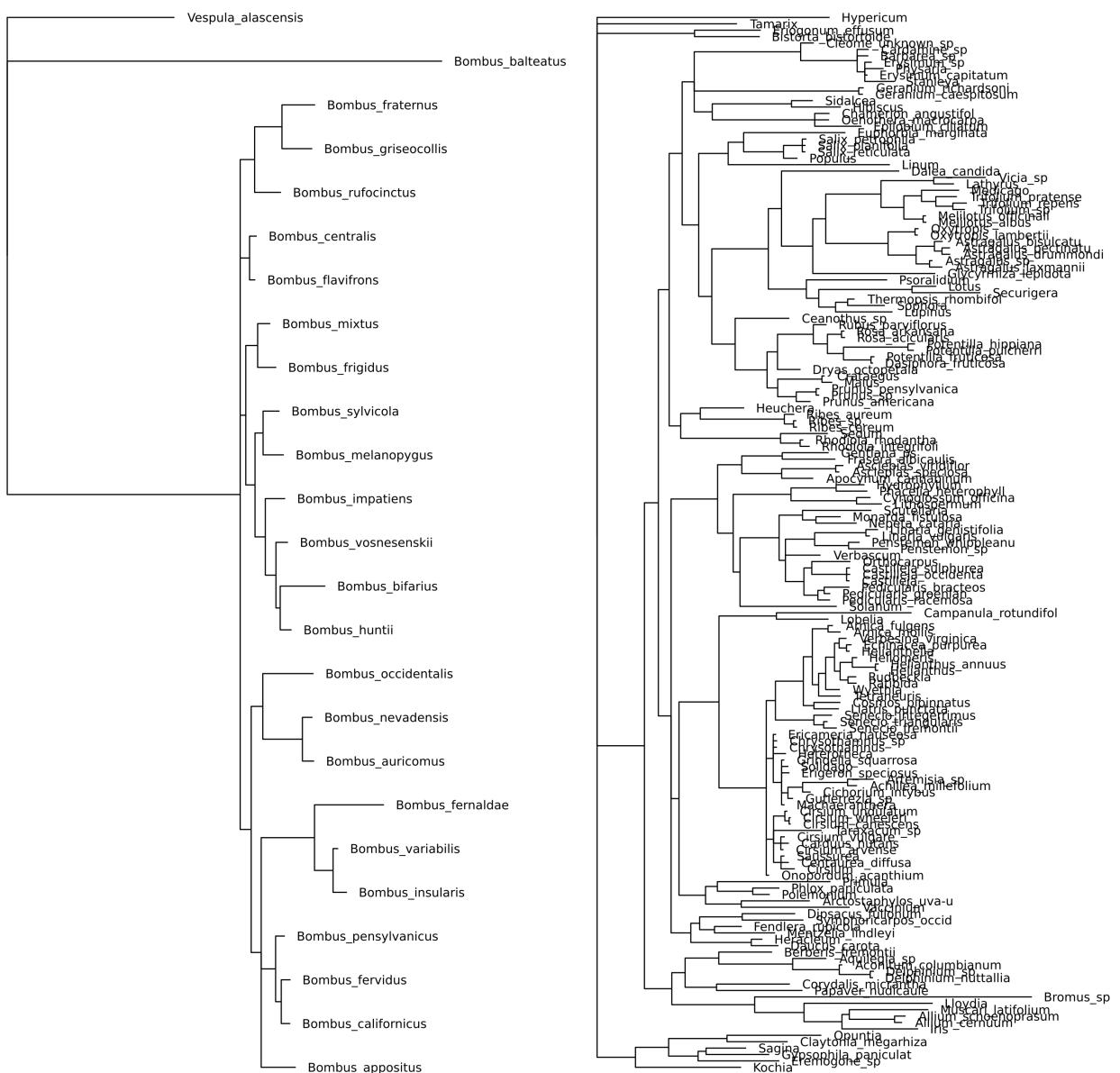


Figure 3: Phylogeny for both bumblebee species (left) and flower species (right)

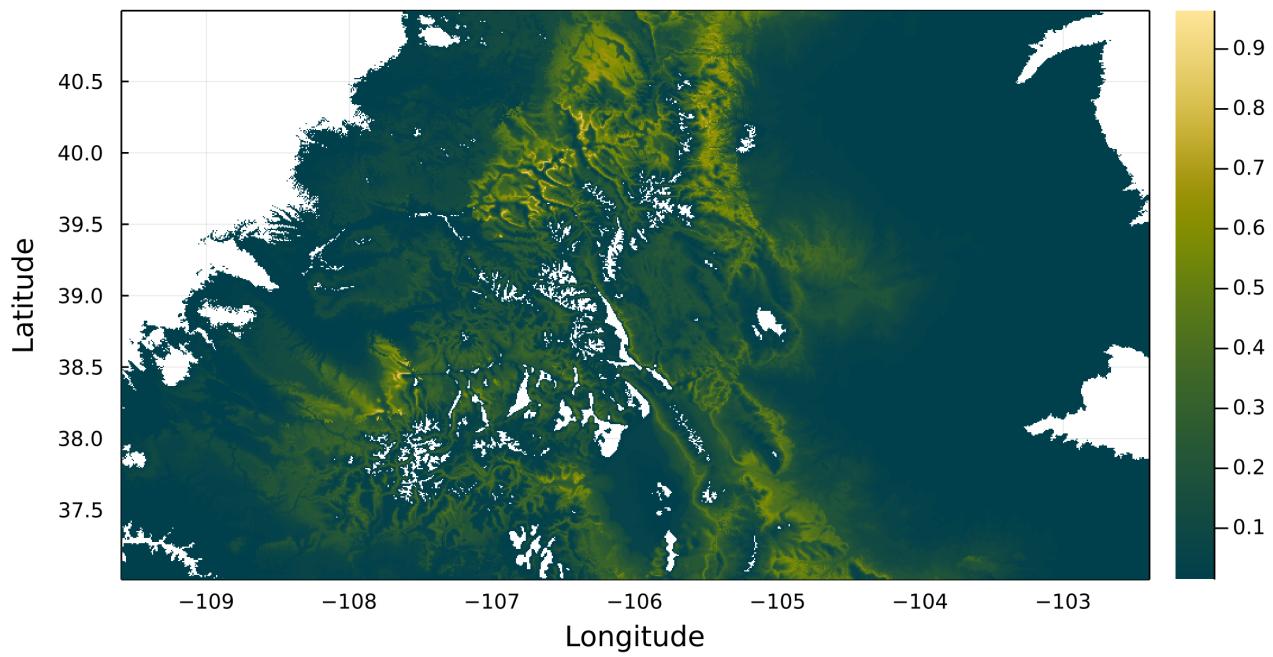


Figure 4: Example SDM for *Achillea millefolium*

Species A occurs?

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

Figure 5: A taxonomy of occurrence, co-occurrence, and interaction false negatives in data

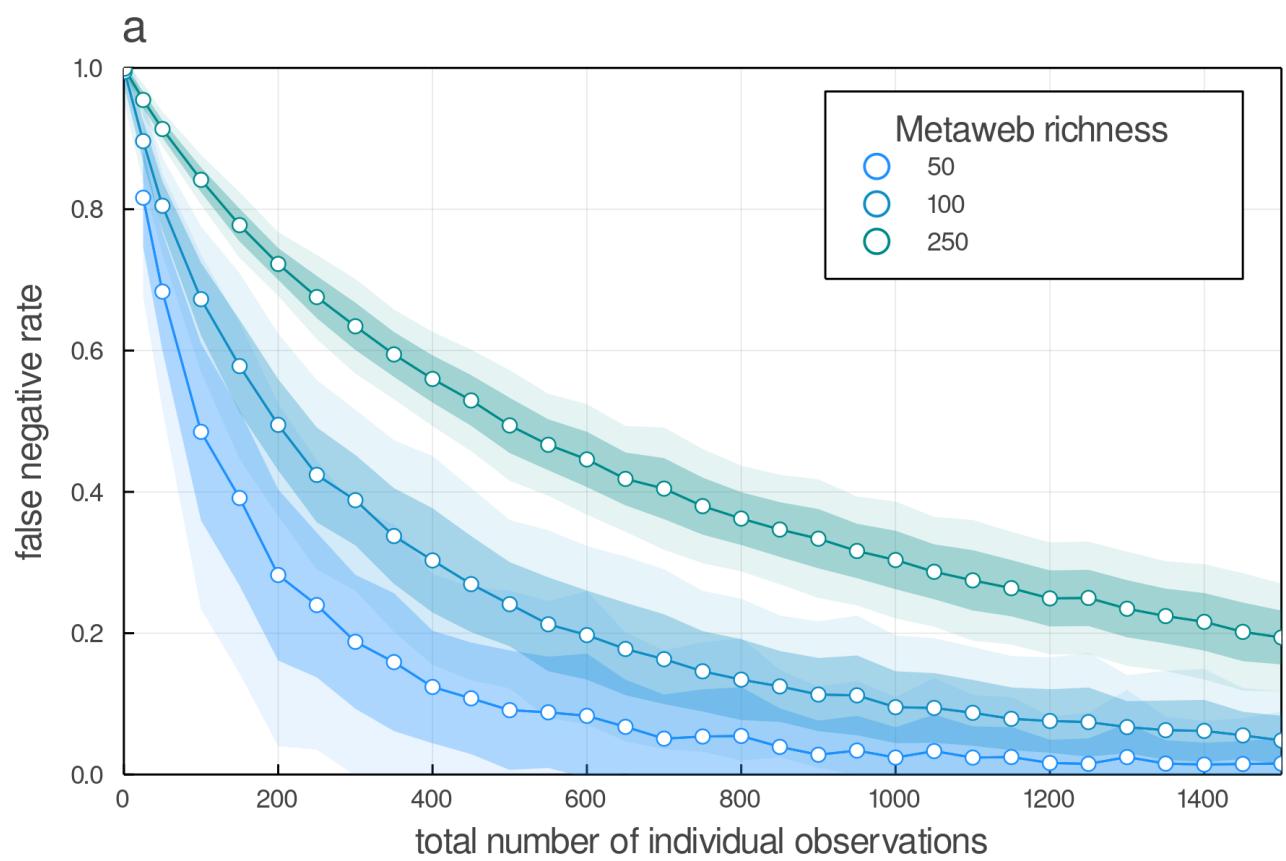


Figure 6: foo

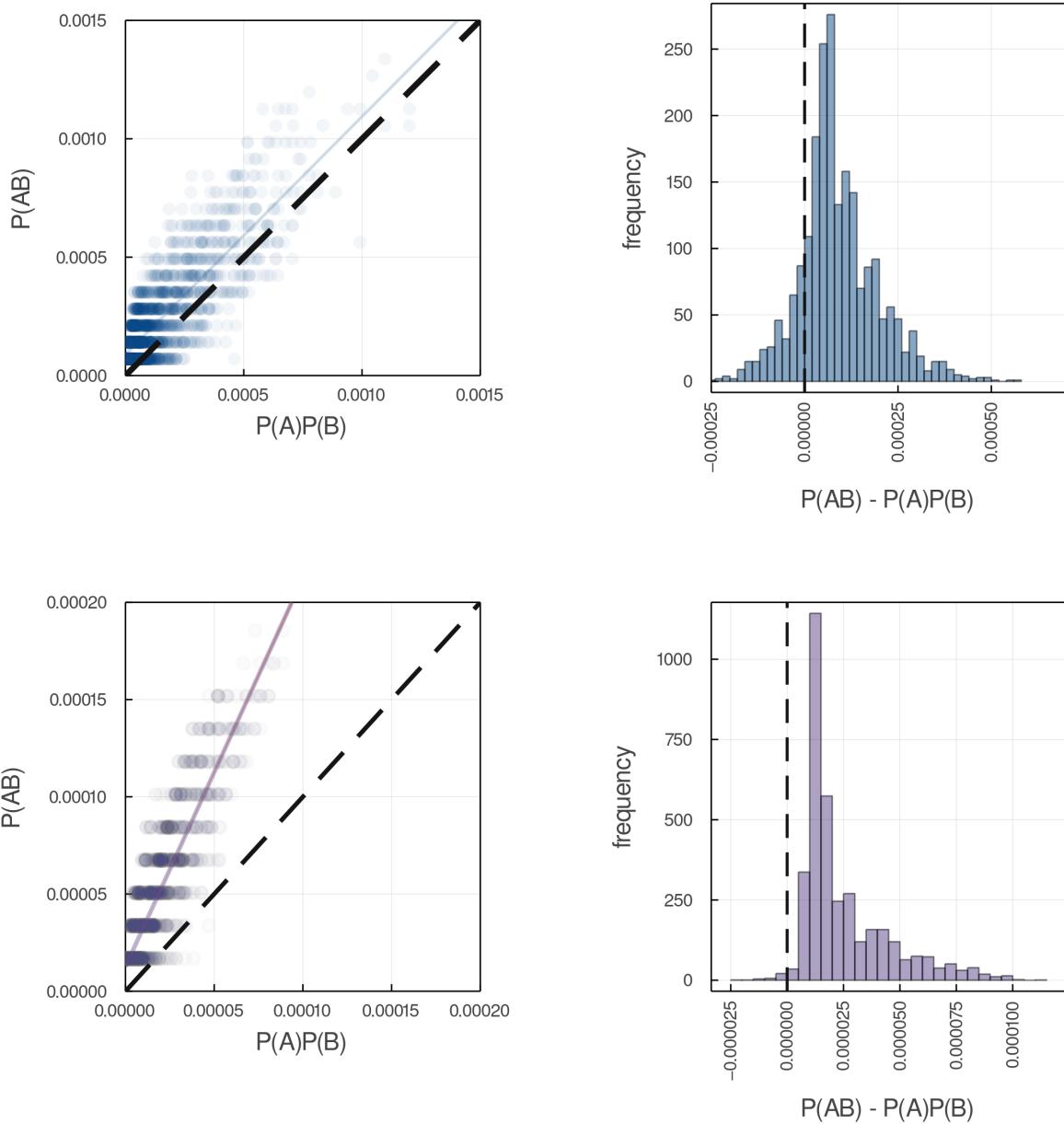


Figure 7: Demonstrates positive associations in co-occurrence

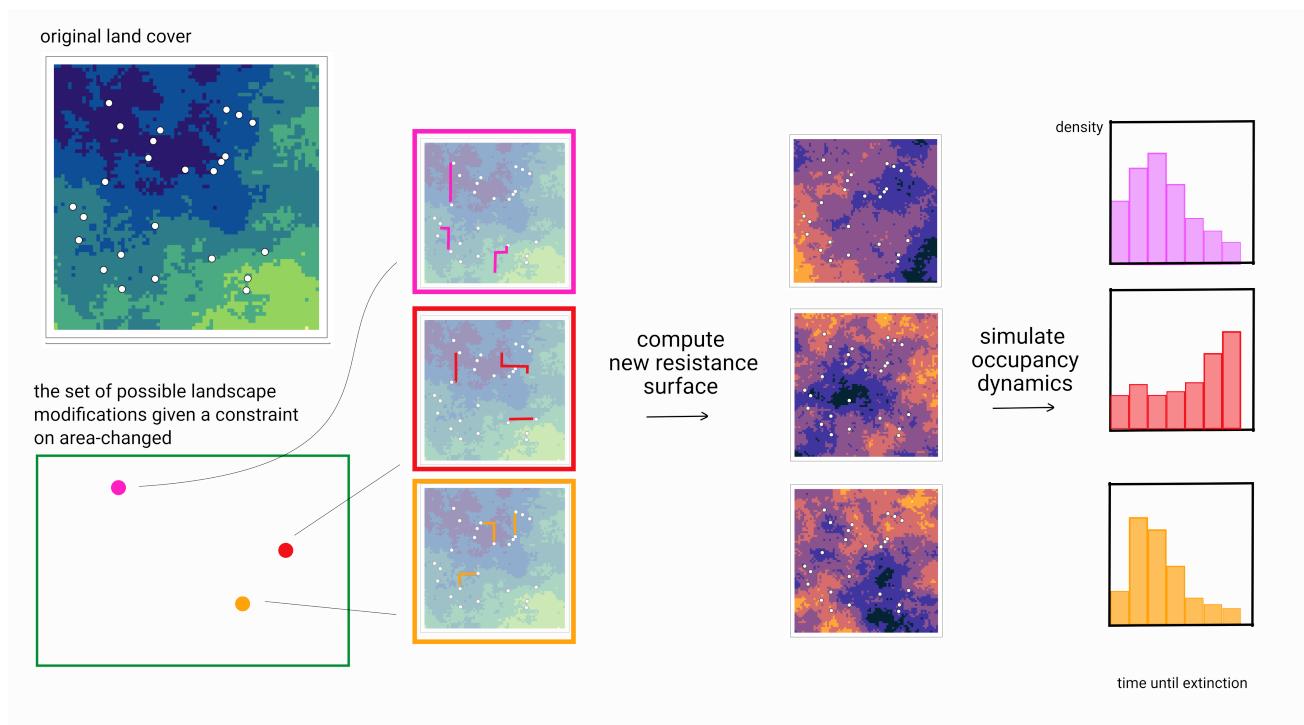


Figure 8: fig

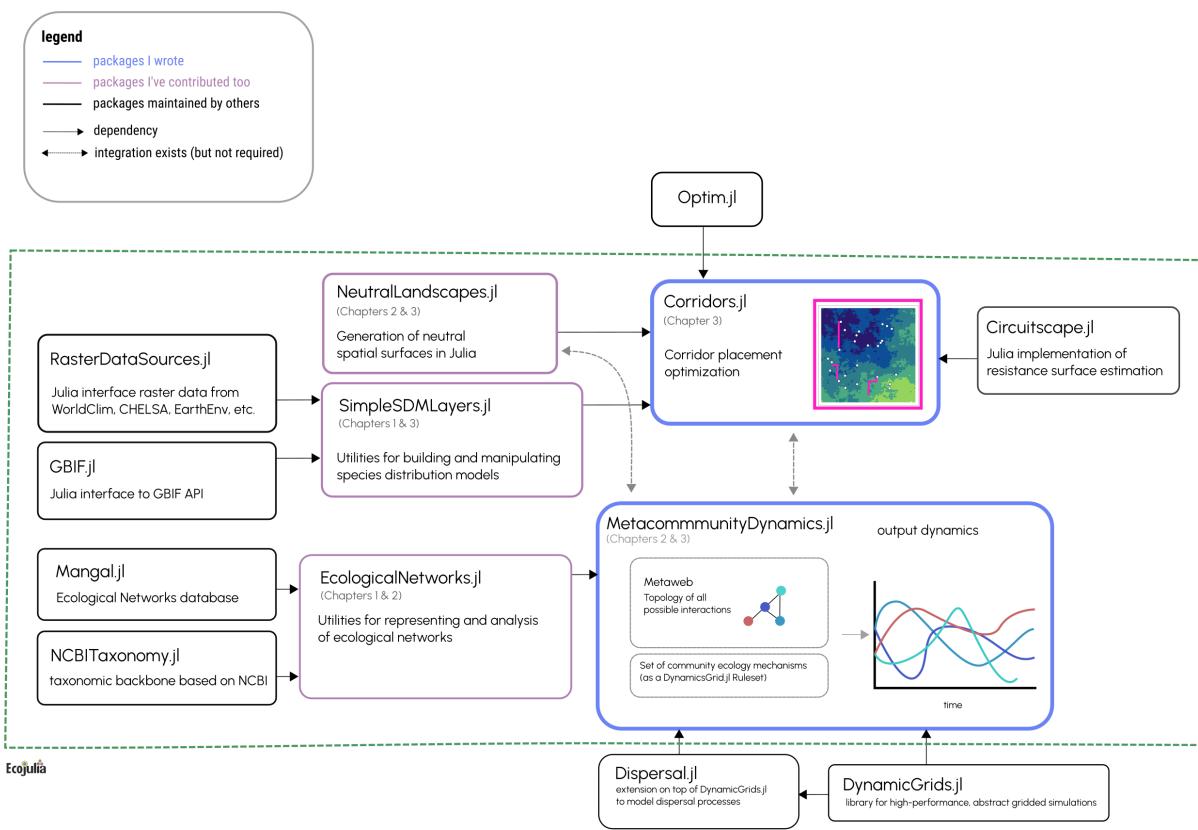


Figure 9: The structure of the software libraries used as part of MCD.jl