

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 in the temperature of both Earth's
4 terrain and oceans, and both agricultural and urban development has rapidly reshaped Earth's land cover.
5 The bulk of this change has occurred within the last several hundred years, a geological instant, inducing
6 a sudden shift in conditions to Earth's climate and biosphere. As a result *ecological forecasting*—modeling
7 how ecosystems and their services will change in the future—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 difficulty 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 a
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 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 over time, yielding models in the form of differential equations in continuous-time settings,
21 $\frac{dx}{dt} = f(x)$, or difference equations in discrete-time settings, $x_t = f(x_{t-1})$, where $f : \mathbb{R}^n \rightarrow \mathbb{R}^n$ is an
22 arbitrary function describing how the system changes on a moment-to-moment basis (e.g. in the context of
23 communities, f could be Lotka-Volterra, Holling-Type-II or DeAngelis-Beddington functional response).
24 The form of this functional response in real systems, and whether it is meaningfully non-zero for a given
25 species interaction, is effectively unknown and must be predicted (Strydom *et al.* 2021b), and some forms
26 of these dynamics are inherently more “forecastable” than others (Beckage *et al.* 2011; Chen *et al.* 2019;
27 Pennekamp *et al.* 2019). The initial success of these forms of models can be traced back to the larger
28 program of ontological reductionism, which became the default approach to modeling in the sciences after
29 its early success in physics, which, by the time ecology was becoming a quantitative science (sometime in

30 the 20th century, depending on who 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 a model
39 increases, so does the ability of the scientist to discern clear relationships between them given a fixed
40 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 last 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 observation 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 Québec 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 to 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 do 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 provide a framework for
61 ecosystem monitoring and forecasting (fig. 1, left), and each chapter addresses some aspect of this pipeline
62 to data from a monitoring network to forecasts to mitigation strategy (fig. 1, right).

63 [Figure 1 about here.]

64 The primary research challenges this thesis addresses are: how do we design ecological samples to detect
65 change? How do we build the software infrastructure to assimilate data from a variety of sources? And
66 how do we propagate uncertainty from data to forecasts? The flow of chapters follows the flow in fig. 1
67 (left), from data collection via a monitoring network, to forecasting an essential biodiversity variable
68 (EBV), to optimizing mitigation strategy based on constraints. In chapter one, we discuss how simulation
69 can aid in the design of ecological samples and monitoring network design. In chapter two we use data to
70 forecast the uncoupling of a plant-pollinator network. In chapter three, we apply simulation methods in
71 landscape ecology to optimize corridor placement to 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 **Context**

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

82 **Objective**

83 The goal of this chapter is to use simulation models to investigate the relationship between species relative
84 abundance, sampling effort, and probability of observing an interaction between species in order to aid in

85 the design of samples of ecological interactions across space, and to provide a null expectation of the
86 false-negative probability for a dataset of a given size. Further, it then proposes a method for optimizing
87 the spatial sampling locations to maximize the probability of detecting an interaction between two species
88 given a fixed number of total of observations and the distributions of each species. This addresses the
89 optimization of monitoring network part of the flow from data to mitigation at the top of fig. 1, left.

90 [Figure 2 about here.]

91 **Methods**

92 We begin by proposing a method to compute a null expectation of the probability of an interaction
93 false-negative as a function number of total observations of individuals of *all species in the species pool*.
94 This is done by simulating the process of observation, where the probability that an observation is of a
95 given species is that species' relative abundance. We show that the realized false-negative rate can be quite
96 high, simply as a byproduct of the distribution of relative abundance in communities. We use a log-normal
97 distribution of relative abundance (Hubbell 2001) and simulating the process of observation on food-webs
98 generated using the niche model (Williams & Martinez 2000) with connectance parameterized by the
99 flexible-links model (MacDonald *et al.* 2020). An example of this relation for networks with varying
100 species richness is shown in fig. 4.

101 [Figure 3 about here.]

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

110 **Results**

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

115 [Figure 4 about here.]

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

120 [Figure 5 about here.]

121 **Progress**

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

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

127 **Context**

128 Interactions between plants and pollinators form networks which together structure the “architecture of
129 biodiversity” (Bascompte & Jordano 2007). The functioning and stability of ecosystems emerge from these
130 interactions, but anthropogenic change threatens to unravel and “rewire” these interaction networks
131 (CaraDonna *et al.* 2017), jeopardizing the persistence of these systems. Plant-pollinator networks face two
132 possible forms of rewiring in response to anthropogenic environmental change: spatial and temporal.

133 Range shifts could cause interacting species to no longer overlap in space, and shifts in phenology could
134 cause interacting species to no longer occur at the same time of year.

135 **Objective**

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

139 [Figure 6 about here.]

140 **Methods**

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

149 As the data we have is spatially sparse and likely to contain many interaction false-negatives, we begin by
150 predicting a metaweb of interactions across Colorado as they exist *in the present*. We do this using a set of
151 candidate interaction prediction models: relative abundance only, phylogenetic embedding only (a la
152 Strydom *et al.* (2021a)), niche embedding only (encompassing both phenology and environmental niche,
153 similar to Gravel *et al.* (2019)), and all pairwise combinations of those constituent models. After validating
154 and selecting the best performing model, we then predict how these distributions of each of these species
155 will change under the CMIP6 consensus climate forecast (Karger *et al.* 2017), and then finally quantify the
156 reduction in spatial overlap between species for which there is a predicted interaction.

157 **Results**

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

161 **Progress**

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

166 **Chapter Three: Optimizing corridor placement against ecological
167 dynamics**

168 **Context**

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

173 **Objective**

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

180 **Methods**

181 [Figure 7 about here.]

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

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

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

204 **Progress**

205 Currently I have an algorithm for proposing landscape modifications and a simple implementation of
206 simulated annealing. The only gap left is implementing Circuitscape estimation of resistance surfaces and

207 running benchmarking tests for the resulting chapter.

208 **Chapter Four: MetacommunityDynamics.jl: a virtual laboratory for** 209 **community ecology**

210 **Context**

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

216 **Objective**

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

222 [Figure 8 about here.]

223 **Methods**

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

231 **Results**

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

237 [Figure 9 about here.]

238 **Progress**

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

246 **Discussion**

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

252 Biodiversity science would be wise to use the success of numerical-weather prediction and the Earth
253 monitoring system that supports it as a template. Further, we should embrace methodological advances in
254 computational statistics that can enable more robust prediction of the dynamics of complex systems than
255 is possible using the tools of analytic models—not just because they can provide more efficacious

256 predictions, but also because they enable a more direct representation of uncertainty, which is crucial for
257 developing ecological forecasting models which provide actionable information to stakeholders, and to
258 find a way for humans to live sustainably on Earth, the only planet on which life has ever been known to
259 occur.

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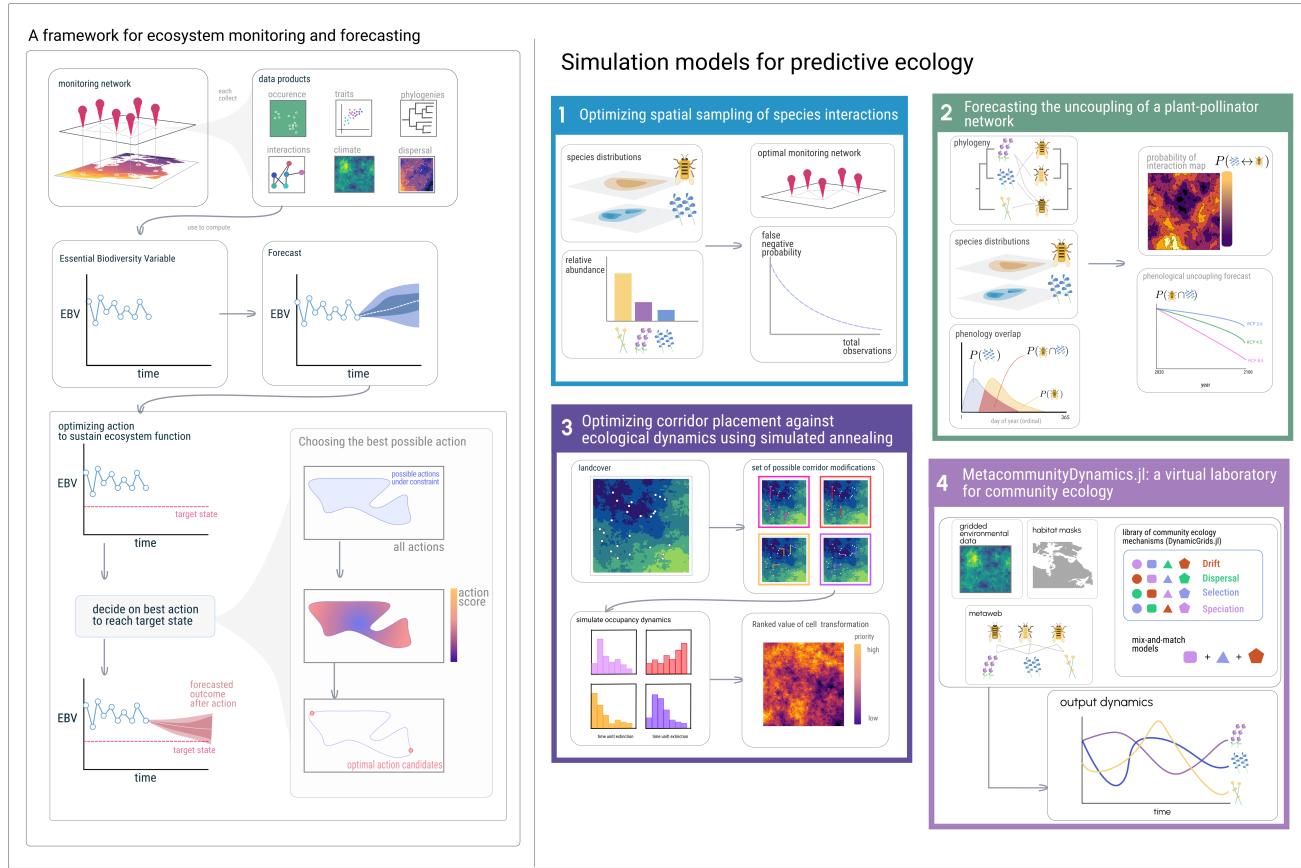


Figure 1: Left: a framework for ecosystem monitoring, forecasting, and mitigation. From the top, a set of biodiversity observatories which form a monitoring network. Each collect various biodiversity data products. From this raw data, we derive essential biodiversity variables (EBVs), and forecast how 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.

Species A occurs?

Species B occurs?

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

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

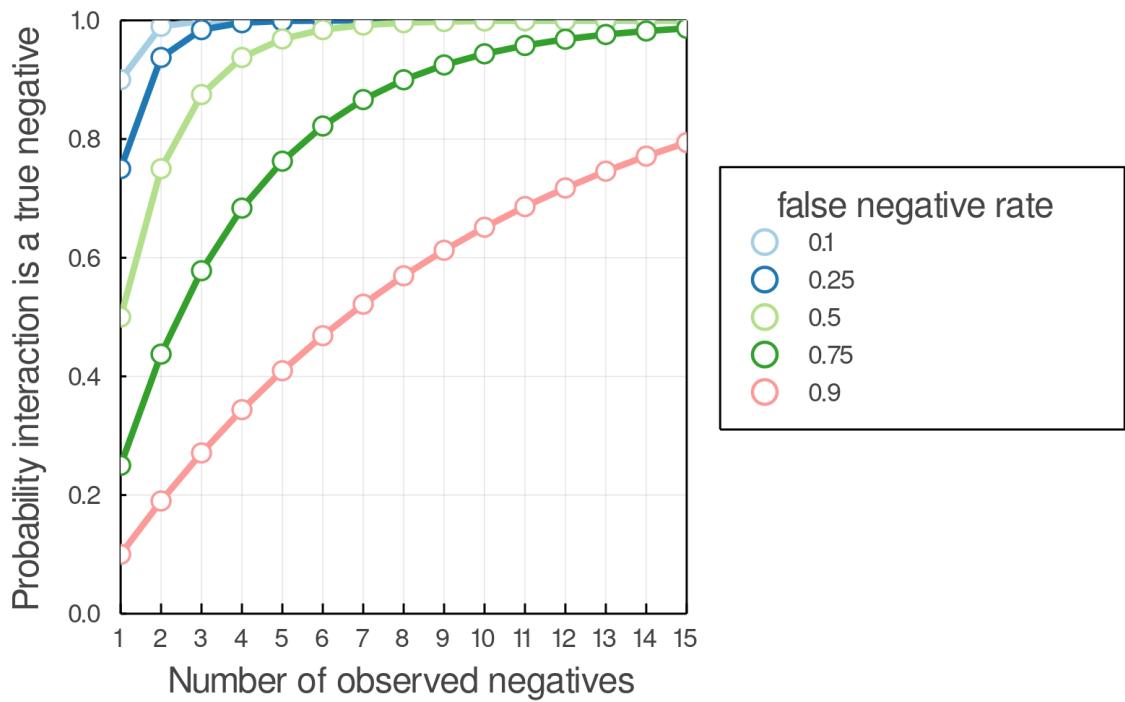


Figure 3: Relationship between total number of observed interactions negatives (x-axis) and the probability that an interaction is a true-negative as a function of different realized false-negative rates (colors), assuming each observed negative is independent—the same as the negative-Bernoulli distribution.

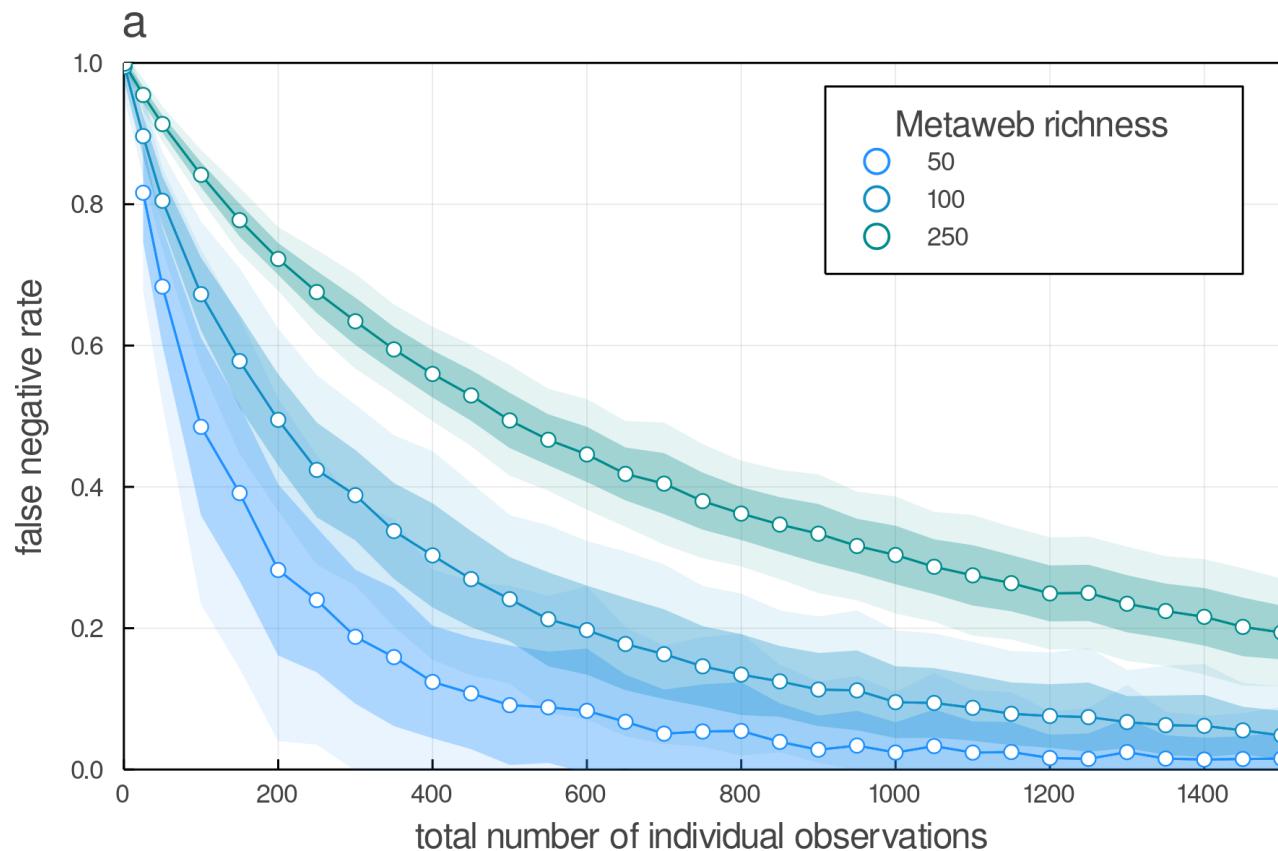


Figure 4: The realized false-negative-rate of interaction detection (y-axis) as a function of the total number of observations of all species in the species pool (different richnesses in different colors). Each point is the mean of 50 replicates, with one standard-deviation in the first shade, and two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

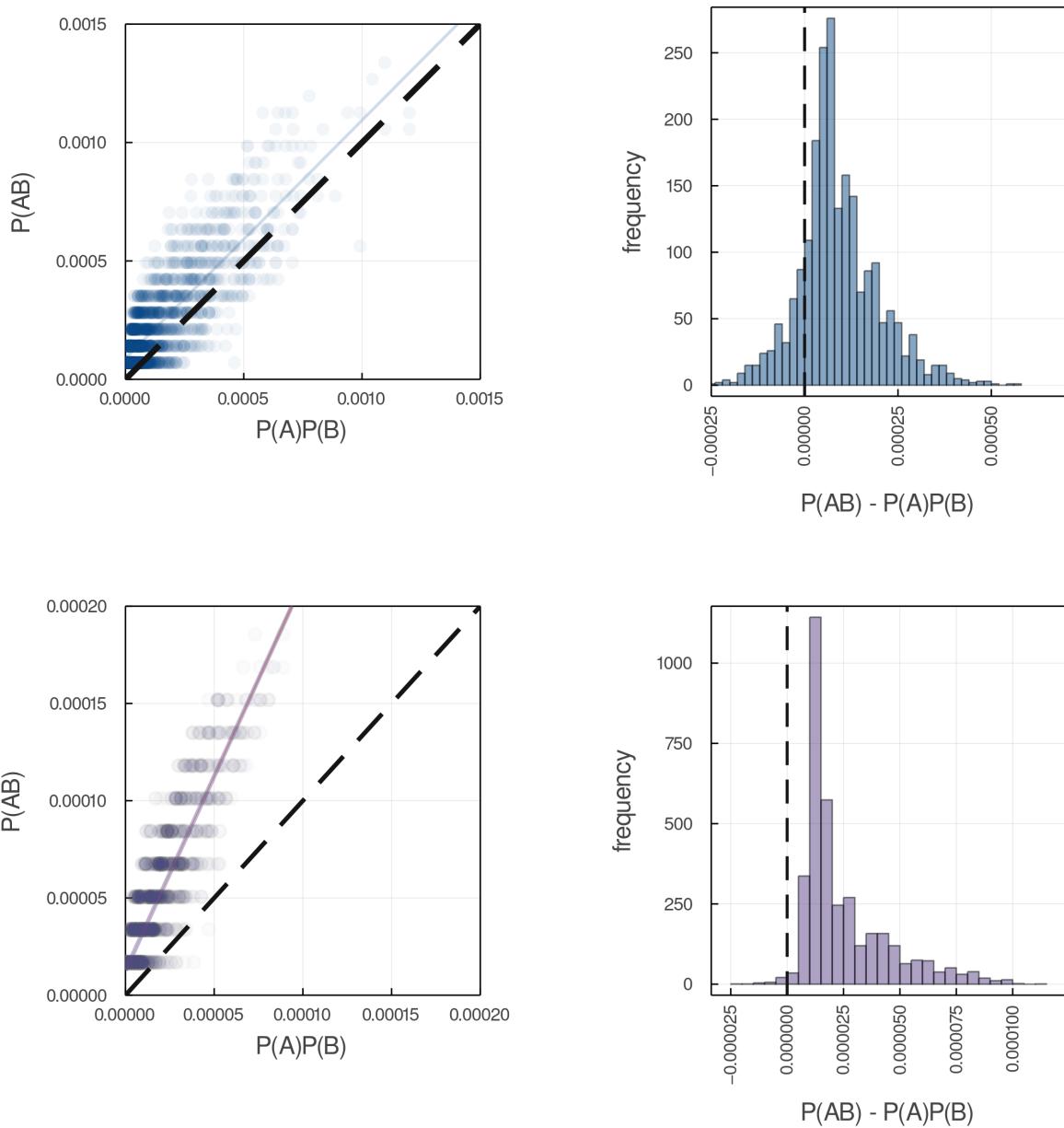


Figure 5: Demonstrates positive associations in co-occurrence. Left: the product of the marginal probability of observing two species (A and B) in a sample (x-axis) against the computed joint probability of observing these species together (y-axis). Dashed line indicates $y = x$, meaning no association 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.

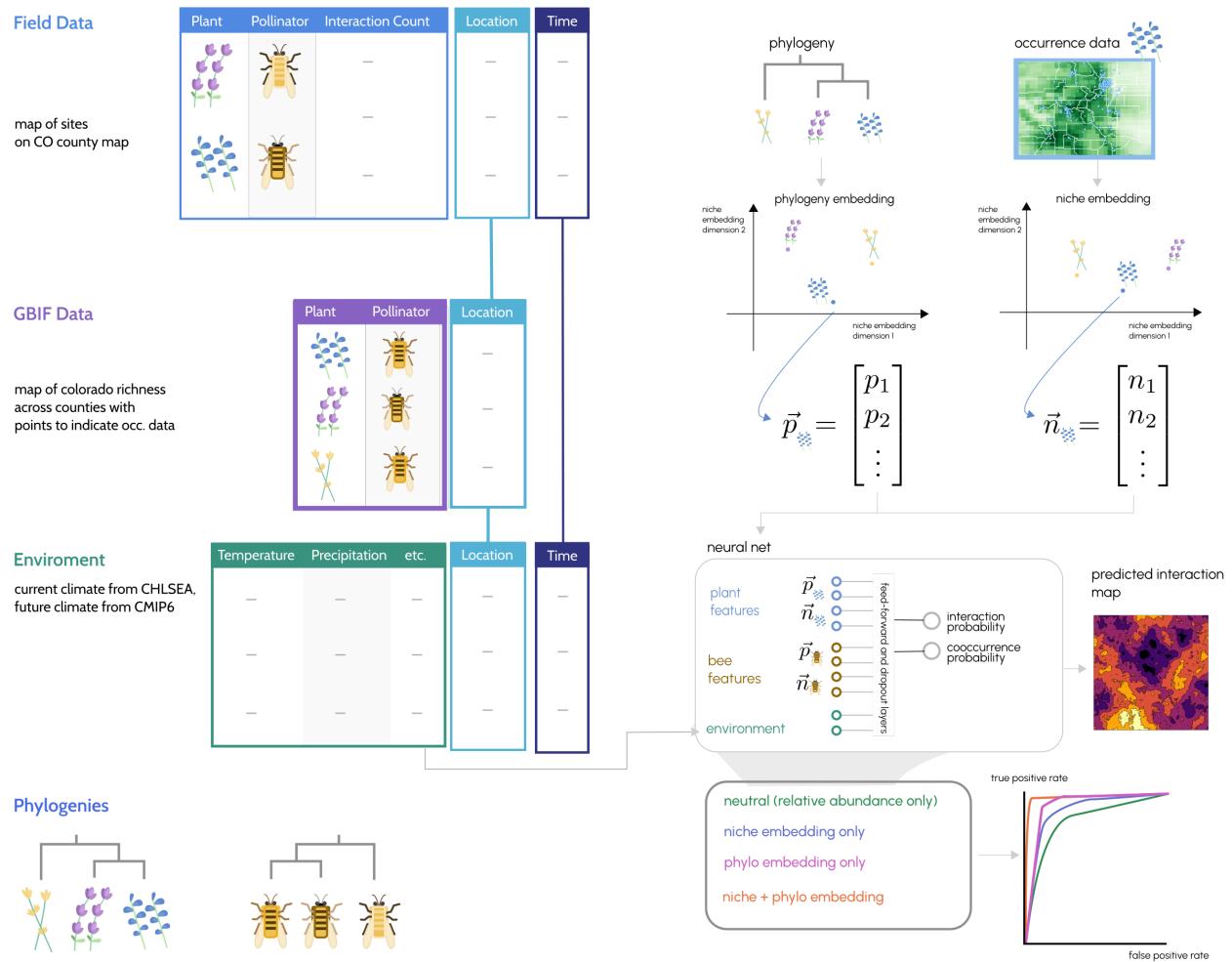


Figure 6: Chapter two conceptual figure. Left: the sources of data and how they can be combined. Right: The flow from data to interaction prediction using a few different interaction prediction models.

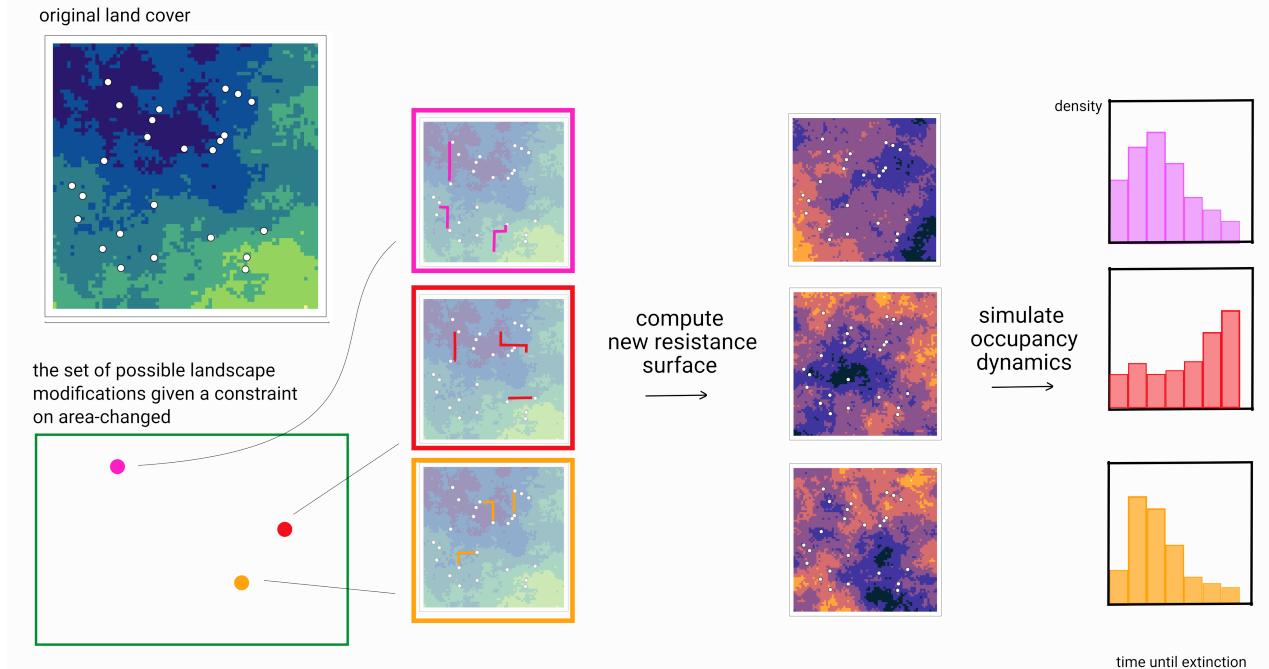


Figure 7: A conceptual example of how we go from a map of landcover with a set of points where occurrence of a species has been recorded (top left), to the set of all possible landscape modifications (green box, where each point in the green box is a unique landscape modification, with three examples 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).

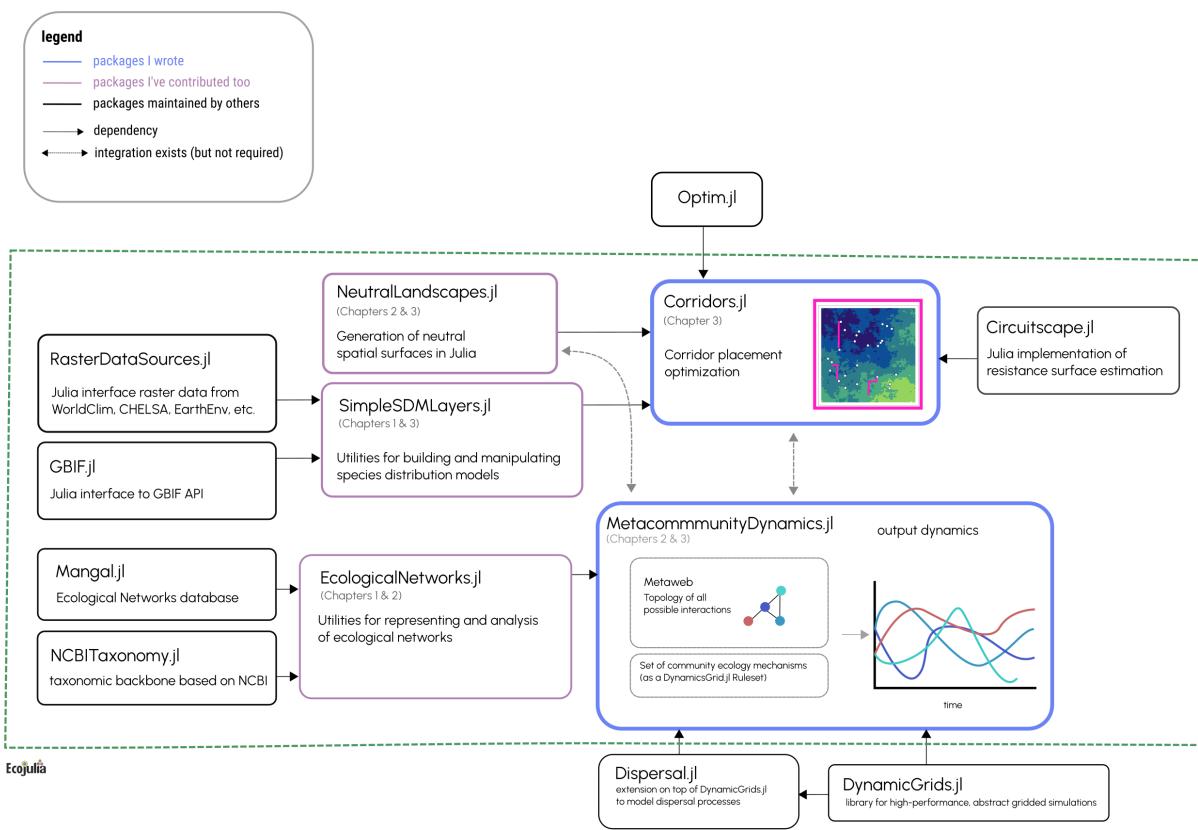


Figure 8: The structure of the software libraries used as part of MCD.jl

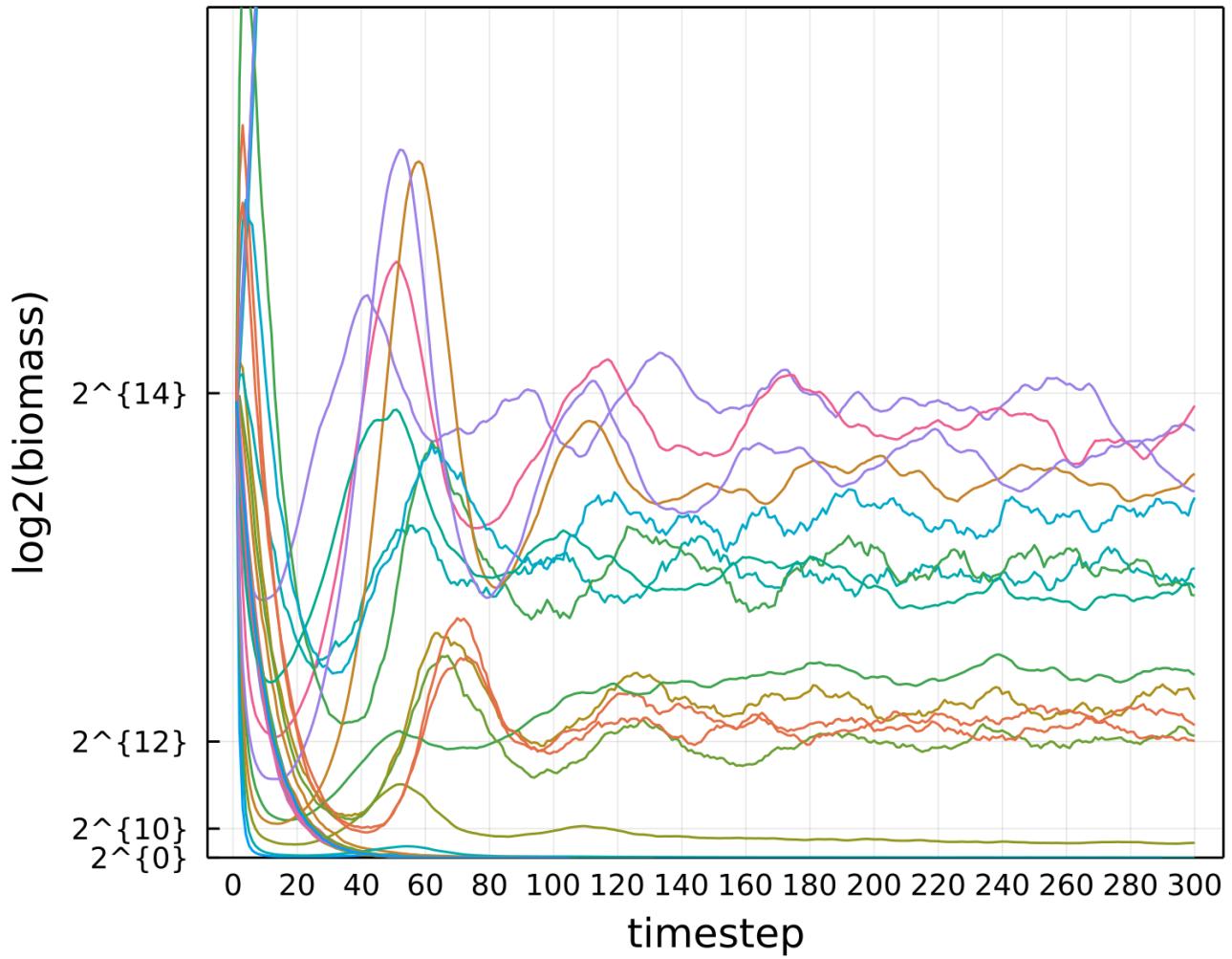


Figure 9: Sample output of simulated food web dynamics from MetacommunityDynamics.jl. Timestep (x-axis), and biomass of each species (y-axis).