

A quantitative study examining mutualism in metacommunities using agent-based modelling in Netlogo.

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Abstract

This project aimed to describe how mutualistic interactions in metacommunities are influenced by changes in ecological conditions. Most research surrounding mutualistic interactions in metacommunities utilized positive interactions (i.e mutualism) as a covariate in their numerical models. These models attempted to predict changes in population dynamics however, we wanted to consider how different ecological factors can predict changes in mutualism. We used a pre-existing framework for a metacommunity model that several previous McMaster students had created in the software called 'Netlogo'. This model was an agent based model involving a landscape composed of 81 habitat patches and up to 50 species of agents dispersed across the 4D synthetic environment. The model encompassed variables in four dimensions: effective dispersal, (ED), species specialization (SS), interhabitat differences (IH), and species interaction (SI). We predicted that positive interactions would be more abundant and hence, more beneficial under increased dispersal potential and increased interhabitat differences. The initial experiments conducted in Netlogo were all organized into one large excel spreadsheet. We then analyzed the data using 'Statistica' to compare and contrast the changes in mutualism under different ecological conditions. Our findings revealed that mutualistic interactions are indeed positively correlated with species abundance. Additionally, the IH and EF dimensions were found to have negligible effects on population growth while SI and EF*SI (an interaction term) promoted both mutualistic interactions and abundance. Our study failed to analyze the remaining results from our model however, the results we have thus far appear highly promising considering the uncertainty regarding agent- based modelling. Overall, this project provides insights into the potential ecological conditions that can promote mutualistic interactions within metacommunities.

Introduction – Review of the Literature

Mutualism can be described as an association between organisms of two different species in which each of them benefit. Nearly all organisms participate in several mutualisms throughout their lifespan (Afkhami, Friesen and Stinchcombe, 2021), and these interactions drastically affect their population dynamics and respective ecological communities. Some examples of mutualistic interactions in nature include plants associating with multiple pollinators, clown fish associating with sea anemones, and also gut microbes associating with humans.

Historically, research on ecological interactions focused on predator-prey and competition interactions opposed to mutualistic ones. However, in recent years, key papers have highlighted the impact of mutualistic interactions in ecosystems; namely through the use of metacommunity modelling (i.e a set of interacting communities linked by dispersal of multiple species). Most if not all of these metacommunity models use an algebraic approach where response variables of interest are predicted for by using mutualistic interactions as a covariate. These models excel in predicting the changes that may occur when positive interactions are regulated, but the reverse relationship is seemingly ignored. Questions regarding how mutualism or positive interactions persist in different environmental conditions are hypothesized but never modelled for.

Moreover, agent-based modelling is a novel software technique that can be used to design and analyze interactions between agents (species). These models can illustrate ecological metacommunities both visually and numerically and thus, different environmental conditions can be modelled for in particular through the use of code. This makes both the analysis and interpretation of mutualistic interactions in metacommunities a lot more feasible. By altering

ecological conditions, the agent-based model can be used to mimic and compare the virtual metacommunities to realistic ones around the globe.

Theoretical studies about population dynamics began in the early 20th century where the ‘Lotka and Volterra’ models were used to predict behaviours of populations using predation and competition (Holland 2012). Because these models only focused on antagonisms, the Lotka-Volterra models were quickly replaced by newer models that accounted for mutualistic (i.e positive) interactions. More research on the topic showed that mutualism had positive effects on population growth, and by the mid-late 20th century, researchers had concluded that mutualistic interactions provided a better understanding of the universal features of species interaction in general (Holland, 2012).

This leads us to the 21st century where researchers began modelling interactions between species on a larger scale (i.e metacommunity models). The models from the 20th century were considered the foundation for the updated newer models which incorporated an abundance of ecological conditions. One study in particular, “The Internal Structure of Metacommunities”, examined how mutualistic networks assembled in response to a progressively diminishing habitat (Fortuna, Krishma, and Bascompte, 2013). Some notable parameters from their model include the probability of colonizing an empty patch, the probability of becoming extinct, a critical distinction value, and the total number of animals interacting with the plant (i.e the mutualist interactions). When the researchers accounted for 95% of the total habitat being destroyed, they noticed that mutualistic interactions collapse accordingly. Thus, with respect to our research question, we can infer that ecological conditions that mimic a ‘destroyed’ habitat could show a reduced number of mutualisms.

Similarly, another metacommunity by Cosmo, Guimaraes, and Pires (2022) questioned how mutualism along with coevolution would affect the persistence of local populations under environmental changes. Some notable aspects of their numerical model include the probability of successful interactions, the mean trait value from one generation to the next, mean fitness, the contribution of mutualistic interaction, and sensitivity of species fitness. The researchers performed numerical simulations of their model using the Julia programming language and in their model, they used ‘mutualism strength’ as a covariate that predicted several response variables. The main takeaway from their study was that coevolution with mutualists expand the realized niche of species and promote dispersal potential. These findings are critical to our study considering that we again have an idea about the ecological conditions that mutualism could thrive in.

Overall, the research surrounding mutualistic frameworks in metacommunities all seem to take a bottom-up approach with respect to their conclusions. In other words, researchers seem to perturb the amount of mutualistic or positive interactions and then examine how ecological conditions are affected. However, there seems to be a lack of research regarding the reverse relationship, i.e, under what ecological conditions do mutualistic interactions seem most beneficial? Thus, this project will aim to provide a general answer to this question and ultimately reinforce or confirm many of the common hypothesis surrounding mutualisms and metacommunities.

Hypothesis

We predict that mutualistic interactions should be prominent in our agent based metacommunity model when effective dispersal and interhabitat differences are set to their 'highest' settings respectively.

Objectives:

This is a continuation of an ongoing project in which a previous student had developed a framework for a metacommunity model in the software 'Netlogo'. The overall objective is to explore how mutualism is impacted by the different environmental conditions outlined in the existing agent-based model.

Experimental Design

This study utilized an already existing Netlogo metacommunity model that was designed by a previous McMaster student. This agent based model was designed as a landscape consisting of 81 habitat patches and up to 50 species. The environmental conditions of the landscape were defined through four different variables: effective dispersal (EF), species specialization (SS), inter-habitat differences (IHD), and species interactions (SI). To summarize, the effective dispersal dimension governed the dispersal rate of the model, the species specialization dimension divided the population into specialists (niche habitat range but more reward) and generalists (wide habitat range but less reward), the inter-habitat differences dimension changed habitat diversity, and the species interactions dimension impacted both positive and negative associations between individuals. Furthermore, each of these dimensions also encompassed a range of different settings. For example, the SS dimension had four different levels: High, Low,

Random, and None. All four dimensions had between four and five different settings each which amounted to 400 different possible ecological combinations.

During the initial setup of the code, each individual agent was given an energy value of ten (energy = food), was assigned a suitability range, and each patch was assigned a suitability value. Each agent was also assigned a specialization value that determined the range of habitat types that were suitable for them. After setup, the code runs and the agents are compelled to disperse to different patches. If an agent had landed on a patch without food or on a patch that was out of their suitability range, they would die or lose energy respectively. On the contrary, agents that landed on a patch that was within their suitability range were obligated to reproduce or interact (positively or negatively) with other individuals.

To reiterate, our goal was to determine ‘under what ecological conditions does mutualism accord major benefits for participating species?’ and thus, we first began listing all 400 possible combinations of ecological settings. We then kept the combinations that had the SI dimension fixed along with one other variable among the remaining three (the other two should be set to random). An example of a sufficient combination is as follows: SS (NONE), IHD (RANDOM), EF (RANDOM), SI (SPECIALIST-GENERALIST DEFAULT). We decided to fix the SI dimension in particular because this is how mutualism was activated in the model. The different settings of the SI dimensions are summarized below:

- If SI = “HIGH”: all of the species can interact both positively and negatively
- If SI = “LOW”: only 20% of species experience positive interactions and a separate 20% experience negative interactions
- If SI = “SPECIALIST-GENERALIST”: specialists interact positively with specialists and negatively with generalists (the reverse is true for generalists)
- If SI = “SPEC-GEN-SLIDER”: no rewards or penalties between specialists and generalists

The various configurations of the SI dimension altered the amount of mutualistic interactions within the metacommunity. Hence, given this method of selection, we promptly cut our list of 400 possible combinations down to 48.

Next, to obtain adequate results, we used the 'Behaviour Space' option in Netlogo to run experiments (experiments = running the code with specific parameters). The students who had previously written the code had also developed an experiment to test for mutualistic interactions in 'Behaviour Space'. In this experiment, there were 10 species within the model and four different variables that were being measured: species overall abundance, species abundance in each path range, mean food in each path range, and the standard deviation of food in each patch range. For our study, we set the amount of runs for each experiment to five and thus ran five experiments for each of our 48 combinations. The Netlogo software automatically placed the results of each experiment in an excel spreadsheet. We then organized all the data into one large spreadsheet which ultimately had 240 rows (48 combinations x 5 runs each = 240). In order to interpret our data, we renamed each of the columns (or variables) into phrases that were much simpler. This involved reading the code thoroughly and following the logical steps until we could make sense of each of the columns. Additionally, many of the entries in our spreadsheet were filled with the following string: 'Runtime PrimeException error'. This error was dealt with by replacing the phrase with an empty cell.

From here, Professor Kolasa used the Statistica software to compare and contrast the results from the different combinations. Considering the ample evidence in literature demonstrating the linkage between mutualistic interactions and positive population growth, we only used the 'species overall abundance' variable to compare our results.

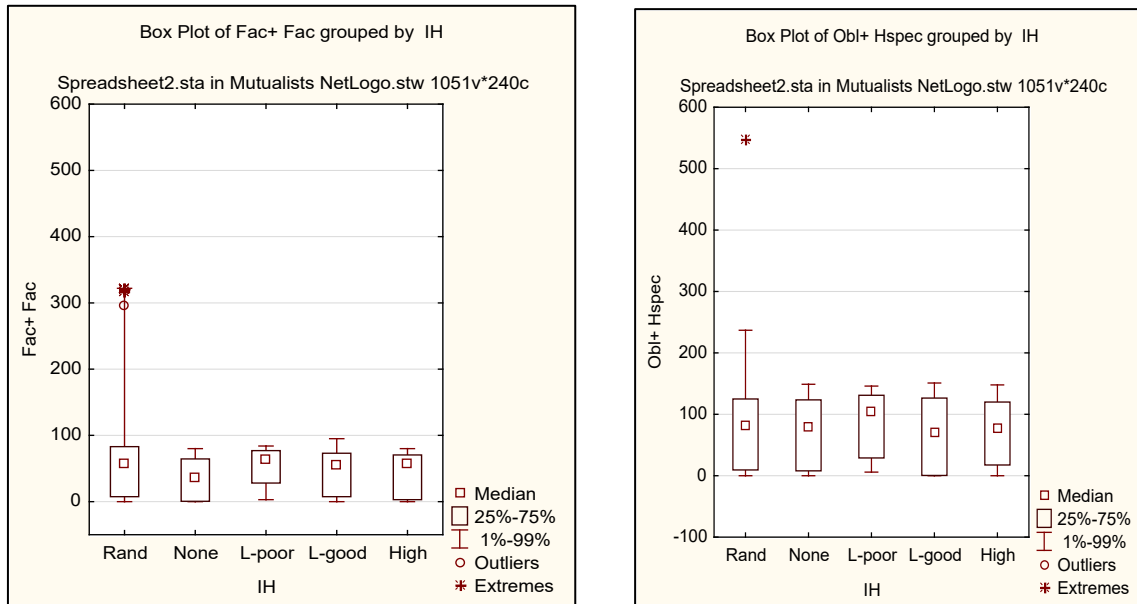
The data from the experiments in Behaviour Space calculated species abundance using labels for each particular species. The labels are defined below:

In our 10 species model:

- Species 1 and Species 3 almost always act positively with one another (+15 rewards). They are labelled as obligate + obligate or (obl + obl).
- Species 2 and Species 8 also act positively with one another (+10 reward). They are labelled as obligate + highly specialized or (obl + hspec).
- Species 4 and Species 5 have an equal amount of positive and negative interaction. They are labelled as obligate + highly specialized or (obl + hspec)
- Species 6 and Species 7 have an equal amount of positive and negative interactions. They are labelled as highly specialized + highly specialized or (highly specialized + highly specialized).
- Species 9 has an equal amount of positive and negative interactions but is usually a generalist which mean low rewards for mutualisms. Labelled as facultative (or fac).

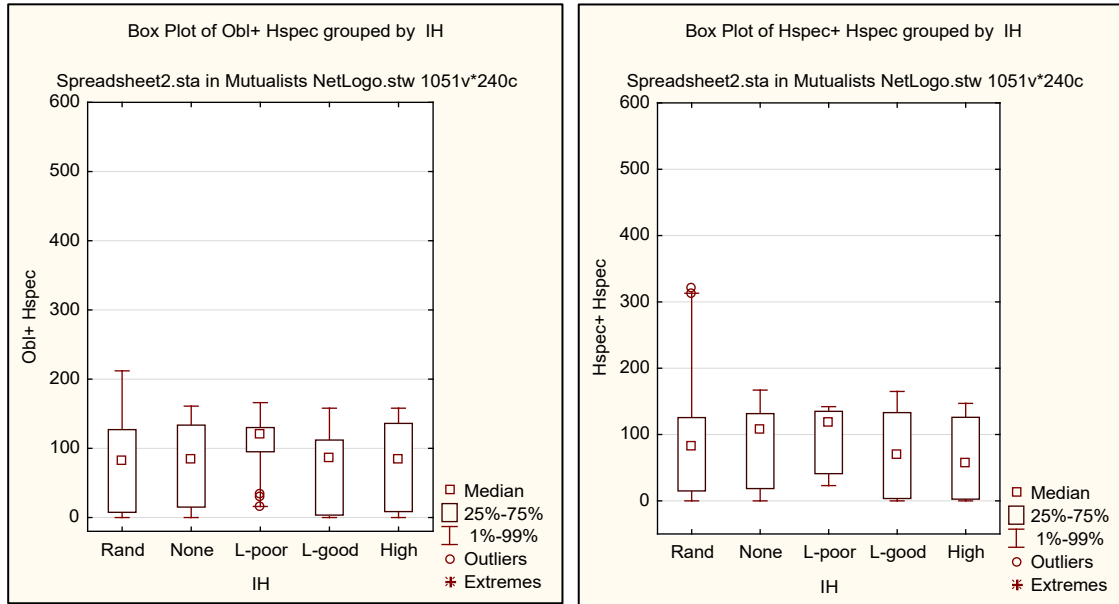
Results

Box plots were used to visualize the differences in species abundance between each treatment of the 'Interhabitat Differences' (IH) dimension. In particular, figure 1 shows the total species abundance of species 1 and species 3 (fac + fac) for each treatment (Rand, None, L-poor, L-good, High). There was extreme overlap between each of the five boxplots and a single outlier in the IH-NONE boxplot.

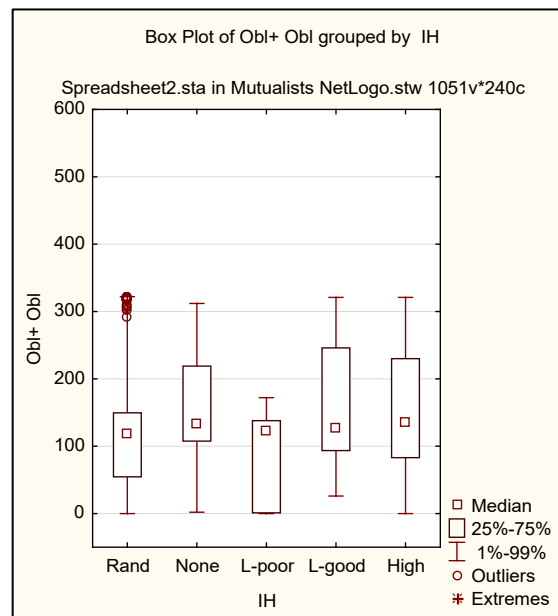


Figures 1 and 2: (Left) Comparing the species abundance (Fac + Fac) with different settings of the Interhabitat Differences dimension. (Right) Comparing the species abundance (Hspec + Hspec) with different settings of the Interhabitat Differences dimension.

Figures 2, 3, 4, and 5 shows the total species abundance of species 2 and species 8 (obligate + highly specialized), species 4 and species 5 (obligate + highly specialized), species 6 and species 7 (highly specialized + highly specialized), and species 9 (facultative) respectively. These figures show a very similar trend to figure 1 where the boxplots for each category of the IH dimension show extreme overlap. Moreover, the 'L-poor' box plot of figure 3, the 'Rand' boxplot of figure 4, and the 'Rand' boxplot of figure 5 have multiple outliers.



Figures 3 and 4: (Left) Comparing the species abundance (Obl + Hspec) with different settings of the Interhabitat Differences dimension. (Right) Comparing the species abundance (Obl + Hspec) with different settings of the Interhabitat Differences dimension.



Figures 5: Comparing the species abundance (Obl + Obl) with different settings of the Interhabitat Differences dimension. (Right) Comparing the species abundance (Obl + Hspec) with different settings of the Interhabitat Differences dimension.

Figure 6 presents a comparison of the boxplots from figures 1 through 6 arranged horizontally (side by side). The trendline illustrates an upward trajectory across various species treatments. Notably, Species 9 appeared to exhibit the lowest total abundance in the metacommunity, while the combined abundance of Species 1 and 3 consistently showed the highest total abundance across all different settings of the IH dimension.

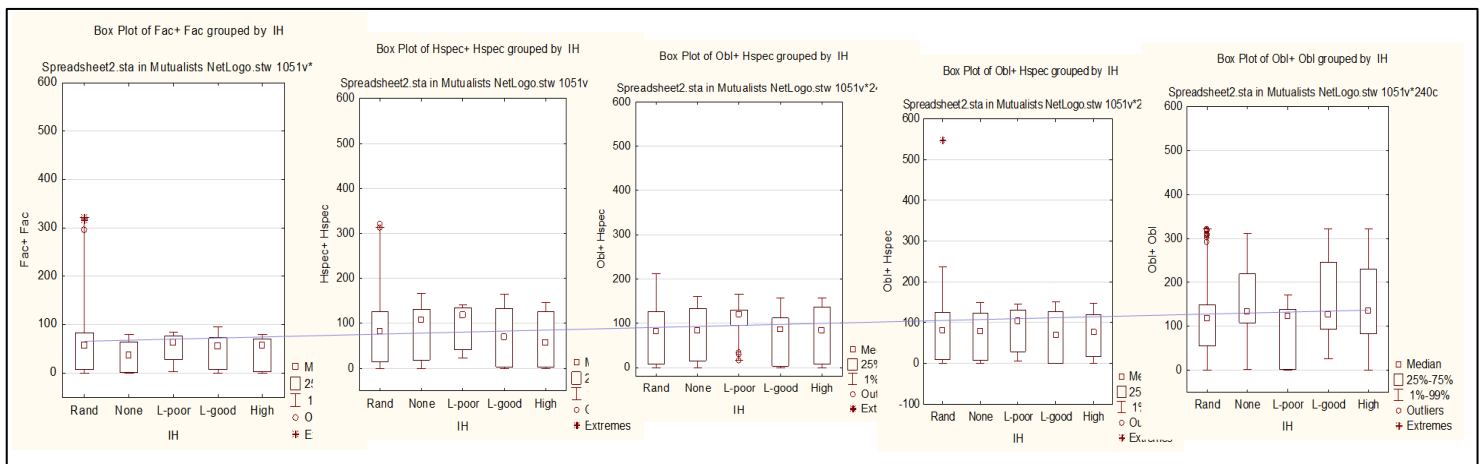


Figure 6: Comparing figures 1,2,3,4 and 5 in a horizontal alignment.

Figures 7,8,9, and Table 1 show results from a reduced data set in which the ‘Species Specialization’ (SS) and ‘Interhabitat Differences’ (IH) dimensions were set to random. As a result, the ‘Species Interactions’ (SI) and ‘Effective Dispersal’ (EF) dimension were controlled for. We used F-tests in ANOVA to statistically assess the equality of species abundance (Total N) between each of treatment of the ‘Effective Dispersal’ dimension (High, Low, None, and Random) and the ‘Species Interactions’ dimension.

There was a significant difference in abundance (Total N) between each SI treatment (p-value <0.05). When SI was set to ‘Spec-Gen default’, the population of the metacommunity hovered around 150 individuals. On the other hand, the population seemed to reach its maximum of around 575 individuals when the SI dimension was set to either ‘Low’ or ‘Spec-Gen Slider’. Moreover, there was no significant difference in species abundance between the four levels of the ‘Effective Dispersal Dimension’ (p-value ≈ 0.59). The population of the metacommunity was consistently within 405 and 430 individuals when ED was controlled for.

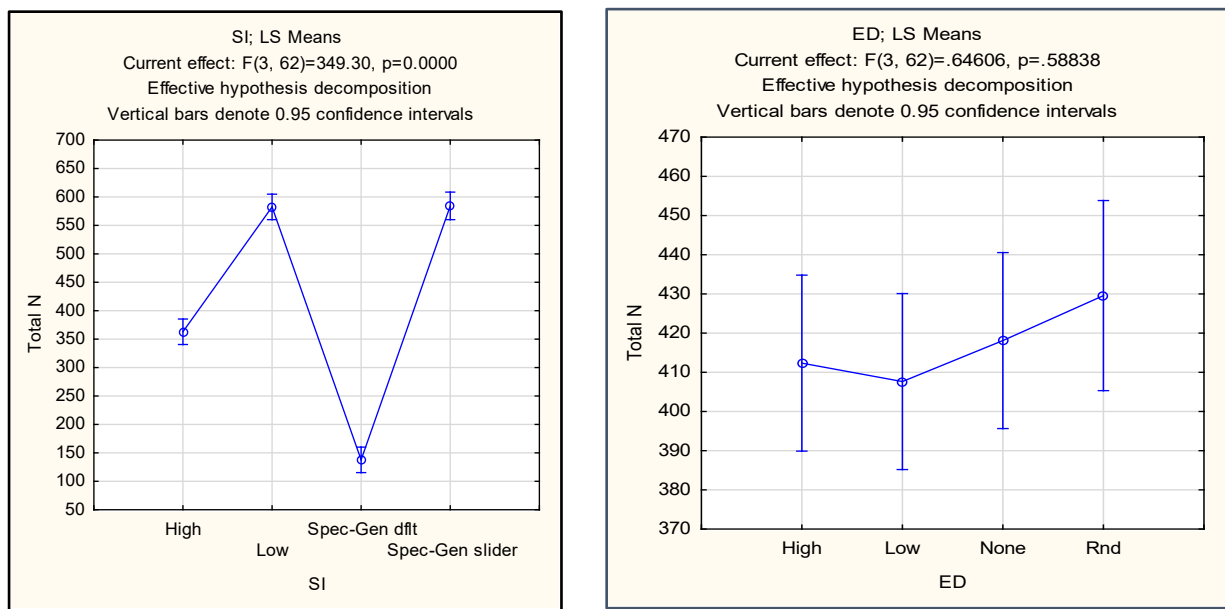


Figure 7 and 8: (Left) We ran an ANOVA test to see if the species total abundance significantly differed between the different settings of the ‘Species Interaction’ dimension. (Right) We ran an ANOVA test to see if the species total abundance differed significantly between the different settings of the ‘Effective Dispersal’ dimension.

The ANOVA test on the interaction term between ED and SI (i.e. ED*SI) showed significant changes in species abundance (p-value < 0.05). No matter what setting of ED we used, whenever SI was set to ‘Spec-Gen default’, the population of the metacommunity consistently reached a minimum (between 100 and 200 individuals). In contrast, whenever SI was set to ‘Low’ or

‘Spec-Gen Slider’, the population would consistently reach a maximum of almost 600 individuals given any random ‘Effective Dispersal’ treatment.

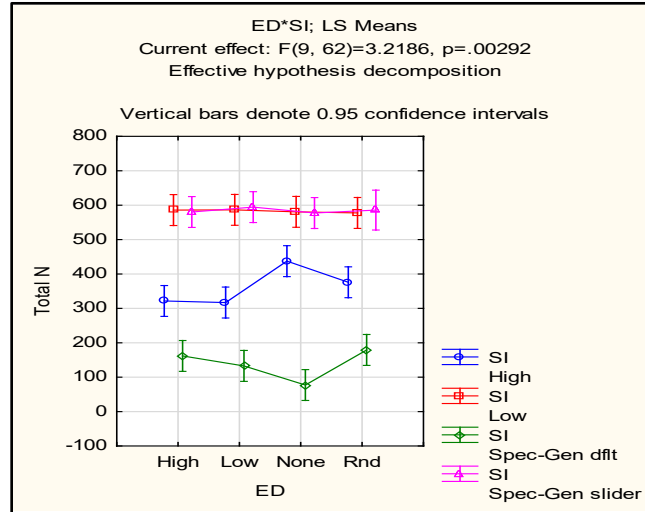


Figure 9: We ran an ANOVA test to see if the species total abundance differed significantly between different settings of the interaction term between ‘species interaction’ and ‘effective dispersal’ (SI*ED).

Univariate Tests of Significance for Total N (Spreadsheet in Mutualists NetLogo)					
Sigma-restricted parameterization					
Effective hypothesis decomposition					
Effect	SS	Degr. of Freedom	MS	F	p
Intercept	13349338	1	13349338	5292.361	0.000000
ED	4889	3	1630	0.646	0.588382
SI	2643219	3	881073	349.302	0.000000
ED*SI	73067	9	8119	3.219	0.002917
Error	156387	62	2522		

Table 1: A table summarizing the ANOVA tests in figures 6,7, and 8.

Discussion

Our project aimed to identify the ecological factors that promote or hinder the prevalence of mutualism among species. We predicted that mutualistic interactions would be most abundant in metacommunities that possessed a wide range of habitats and increased species dispersal. First,

our results indicated that the ‘Interhabitat Differences’ dimension did not significantly affect total species abundance considering the substantial overlap in the boxplots across all the different treatments. The overlap signified that there were no statistical differences between the means of the four groups (Rand, None, L-poor, L-good, High). However, a side-by-side comparison of the boxplots showed an increasing trendline with respect to the combination of species that were being tested. Specifically, the abundance of species 1 and species 3 consistently exceeded 100 individuals on average, this was not seen in any other combination of species. These results support the claim made in previous literatures that positive interactions contribute to population growth. Species 1 and Species 3 are the strongest mutualists within this metacommunity considering they both obtain a +15 reward when they interact; this is the highest reward among all mutualists. Therefore, the observation of Species 1 and Species 3 exhibiting the highest abundance aligns with the philosophy that mutualistic interactions foster positive population growth. In conclusion, the findings mentioned above contradict our initial hypothesis; yet, we can use these results in a diagnostic sense and confirm that we indeed have a traditional metacommunity model characterized by a strong association between mutualistic interactions and population growth.

Moreover, the results from our reduced subset highlighted the importance of ‘Species Interactions’ (SI) and ‘Effective Dispersal’ (ED) in modulating mutualistic interactions. When the ‘Species Specialization’ (SS) and ‘Interhabitat Differences’ (ID) dimensions were set to random, we observed a significant difference in species abundance across the different SI treatments. Most notably, the ANOVA tests showed how the population would thrive under the ‘Low’ and ‘Spec-Gen slider’ settings but became small under the ‘High’ setting. These results made logical sense considering when SI was set to ‘Low’ or ‘High’, there was a reduced amount

of negative interactions within the metacommunity. However, when SI was set to 'High', the amount of negative interactions were maximized. From these results, we can reinforce the notion that positive interactions in particular contribute to population growth. Furthermore, we failed to observe a significant difference in species abundance across the different settings of the ED dimension. This implies that ED alone cannot induce changes in species abundance which also contradicts our initial hypothesis. We believe that the ED dimension encourages individuals in the code to disperse to empty or non-suitable patches rather than towards other individuals. This suggests that ED does not have a direct impact on the amount of mutualistic interactions occurring at a given time. Finally, we observed significant differences in species abundance across the different treatments of the SI and ED interaction term (ED*SI). From these results, we deduced that the effect of ED on species abundance (and mutualistic interactions) is dependent on the SI setting. Under conditions where SI favoured mutualistic interactions (i.e 'Low' or 'Spec-Gen Slider'), the population reached maximum levels in each ED treatment. The interaction term seems to promote species dispersal in addition to more interactions between individuals which ultimately leads to more mutualisms and thus, a more bountiful population. Overall, mutualistic interactions are favoured in metacommunities when increased dispersal directly influences the frequency of such interactions.

Our study contributes to the growing body of literature on mutualistic interactions in ecology. By using an agent-based modelling approach, we were able to explore the effects of environmental variables on metacommunities visually opposed to numerically. Yet, there were some limitations with regards to our study. For instance, we only had a handful of ecological dimensions in our code which implies that our model might have oversimplified the complexities of real-world systems. Our code fails to acknowledge the nuances that makes species and ecological systems

unique. For example, we did not consider the size of each species, the type of food they eat, weather, natural disasters, human intervention, etc. These factors contribute to a more holistic understanding of metacommunities however, our model nonetheless yielded significant findings that supported previous literature.

One important point to consider is that our results only represented a portion of what we could have potentially achieved. We have not seen the ANOVA tests regarding the ‘Species Specialization’ (SS) dimension, the ‘Interhabitat Differences’ (IH) dimension, or the remaining interaction terms from our model. Also, the original Netlogo code had several additional parameters of interest that were not discussed in this study. Most notably, the value of the rewards and penalties between species (specialists and generalists in particular) may accord major benefits to species participating in mutualisms. We advocate for future studies to explore the parameters we ignored and seek potential relationships with respect to positive interactions.

Moving forward, future research should aim to refine our understanding of mutualistic interactions. This can be achieved by reinforcing the associations we have already discussed and through incorporating additional ecological factors. Our study in particular has demonstrated how ecological dimensions that facilitate dispersal along with species interactions can increase the amount of mutualisms in a metacommunity. Whether it be through numerical simulations or agent-based modelling, future studies can use similar tactics and attempt to identify links between mutualistic interactions and different ecological parameters. Ultimately, a comprehensive understanding of mutualistic frameworks in metacommunities is crucial for informing conservation efforts and ecosystem management strategies aimed at preserving biodiversity and ecosystem stability.

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