

The effect of adaptive plasticity on biodiversity in microbial communities

Written by Elles Jetten s2564564

MSc Biology; Modelling in Life Sciences

Supervised by Sander van Doorn

Theoretical Research in Evolutionary Life Sciences

14-07-2021

Table of Contents

Abstract.....	3
Introduction	4
Model.....	5
Results.....	7
Local stability.....	7
Numerical simulations and expanding model with plasticity	9
Effective interactions, comparing simulations with plasticity with without plasticity	12
Discussion.....	15
References.....	17
Appendix.....	19

Abstract

The human microbiome plays an important role in human health. Ecological theory is thought to be important for predicting its functioning. In light of this, recently Coyte et al. have investigated the effects of different compositions of cooperative and competitive interactions between species on the stability of the community. Here I take their model as a reference point. A factor that has not been considered much in this field is the effects of adaptive plasticity of species on the stability of communities. In this report I try to answer the question, how does adaptive plasticity affect the community diversity? Here the generalized Lotka-Volterra model that is used, is analysed using an analytical approach, namely local stability analysis, and a numerical method is used to determine some stable equilibria of different systems.

With the local stability analysis, I will look into multiple randomly generated communities and try to find all biologically relevant equilibria, their stability and the speed at which communities return to them after a small perturbation. Results show that a low connectivity and high fraction of cooperative interactions within a community result in more stable communities, which is measured through different criteria.

Numerical simulations will look at a single stable equilibrium that arises when a random community is initialised at low densities and allowed to run its course and species diversity of resulting communities is looked at. Results from the numerical simulations show that effects of connectivity and interaction strength are in line with past research, namely the higher they are the less diversity remains in resulting communities. The effect of competition seems predominantly preventing species loss. However, communities solely comprised of species that have cooperative interactions with each other do not lose too much diversity. The effects of adaptive plasticity on diversity were found to prevent extinction of species from communities. When looking at the effective interactions that species have while capable of plasticity, it shows that it does not move in a specific direction, i.e., it does not move more toward cooperative interactions. The effects may be due to added variation that moves interactions more towards neutral values, which is known to have a stabilizing effect. In conclusion, adaptive plasticity may be a mechanism that enables communities to grow larger and more stable.

Introduction

The human microbiome plays an important role in human health. Changes in microbiome composition in the human gut have for example been linked to development of gastro intestinal disease (Frank, Daniel N et al., 2007), obesity (Turnbaugh et al., 2009), and even anxiety and depression (Foster & McVey Neufeld, 2013). Ecological theory describing what affects community composition can lead to increased understanding of microbial community dynamics, for example in microbial development in infants, during recovery after large perturbations and during invasion of pathogenic species (Costello et al., 2012). Additionally, ecological insight would help to build a framework to work towards personalized medicine in cases where the human microbiome leads to pathogenesis (Gonzalez et al., 2011; Lozupone et al., 2012).

The stability of bacterial communities in human microbiomes is thought to be important to human functioning and health. Overall observations have been that natural ecosystems can grow very large and complex, and that this complexity adds to their stability. However, Robert May questioned whether large systems such as microbial communities could even be stable (May, 1972). Results from his model suggests that stability of communities would decrease when species diversity increases. Since then, people have been investigating into reasons why large complex systems as we see them in nature are so stable and complex. A factor that May did not include for example in his model are spatial dynamics, which can have a stabilizing effect (Gravel et al., 2016).

One factor that has also not been considered in the complexity-stability debate is the effects of plasticity of species on stability of communities. Previous models have assumed an unchanging set of interactions for each species. However, it is known that bacteria can adapt their phenotypes to changing environments (Kümmerli et al., 2009). This plasticity is usually assumed to exist in order for species to maximize their own growth. The question is whether species maximizing their own growth would be good for the diversity of a complex community.

Recently Coyte et al., (2015) have investigated the effects of cooperative and competitive interactions between species on the stability of a community. They used analytical and numerical methods to explore what influences the stability of species-rich community equilibria. Here stability is defined as the ability of a community to return to its equilibrium after a small perturbation, how long it takes to do so and whether oscillations occur after the perturbation. They predict that cooperative interactions as well as high species diversity destabilizes communities. They also found that competitive interactions and low connectivity have a stabilizing effect.

Another measure of stability that is used by Coyte is community permanence. Permanence reflects whether a species in a community is able to return to equilibrium after being brought to a low density.

This study provides clear predictions for what is expected to affect stability of communities that have been investigated through multiple modelling methods. The model used is a

generalized Lotka-Volterra model, which is commonly used to investigate population dynamics. Their results into the effects of different kinds of interaction on community dynamics also provides a nice starting point to confirm some results and extend and investigate on new ones with plasticity considered. For these reasons, this paper will be taken as a reference point as a way to extend on previous a previous known model. The question posed now is what are the effects of adaptive plasticity on the stability of microbial communities? To answer this, I present an extended model to investigate the effects of enabling adaptive plasticity within microbial communities.

In this report I will first give an overview of the model for microbial communities and their interactions. There are two methods used for the analysis of the model, and I will go over the analysis method and results one by one. First, results obtained will be compared to previous conclusions made by Coyte and May. Finally, I will look at the extended model with adaptive plasticity and its effects on stability.

Model

The model that is used and analysed is a generalized Lotka-Volterra model. I will first describe the general model assumptions that apply to both the analytical and numerical methods used to examine the different systems. In the results section the different methods of analysing this model will be discussed before showing the results. The Lotka-Volterra equations are coupled ordinary differential equations used to describe species densities

$$\frac{dx_i}{dt} = x_i \left(r - s_i x_i + \sum_{j=1, j \neq i}^S a_{ij} x_j \right) \quad (1)$$

In this equation, x_i stands for the specific density of species i . The number of species within the community is equal to S , and therefore the index i , runs from 1 to S . The parameter r is the intrinsic per capita rate of growth, which is assumed to be equal for all species and set in all cases at $r = 2.0$. The growth rate of each species depends as well on the intraspecific competition coefficient, the strength at which a species competes with itself, given by s_i . This is set in all systems to 0.2. Finally, the species growth depends on the interactions, a_{ij} , it has with all other species present. The effects of these interactions on the per capita growth depends as well on the species densities of species j , with which species i has an interaction with. All the interactions of the species within a community may be represented in a so-called interaction matrix which would have the dimension $S \times S$. The interactions of species j on species i can then be found in the i th row and the j th column. On the diagonal of this matrix is s_i , the competitive effect of the species on itself.

Communities and their interactions are created randomly. In all following results the assumption is made that species either have cooperative, competitive or no interactions. This is done to start with a very simple model that has easy to interpret results and extensions will also become easier to interpret. When generating random interaction matrices, the connectivity, C is the chance of an element in the interaction matrix to equate

to 0. For example, $C=0.3$ means that 70% of randomly drawn interactions equal 0. An interaction coefficient of 0 means that the two species do not influence each other's growth. When it is determined that two species do interact, their interactions are drawn in a pair-wise manner. Interactions are drawn from a half-normal distribution, a normal distribution with a mean of 0.0 where the absolute of all values is taken. The standard deviation of the underlying normal distribution is $\sigma = 0.05$ for all simulations unless stated otherwise. The coefficients a_{ij} and a_{ji} are drawn together so that the species i and j will either cooperate (+/+) or compete (-/-) with each other and the sign of the interaction is decided by the ratio for cooperative and competitive interactions. Because there are only competitive and cooperative interactions possible the chance of cooperative interaction can be obtained by $p_{coop} = 1 - p_{comp}$.

To measure community diversity, the Shannon Index is used according to equation 2, where p_i is the proportion of species i in the population. For each number of species, a maximum Shannon index is reached when the species are present in the exact same abundance in the population, as is illustrated in figure A1.

$$H' = - \sum_{i=1}^S p_i \ln p_i \quad (2)$$

The relationship between stability and species diversity is a complicated one. There is an important debate going on about the relationship of complexity and stability within communities, and how there could exist large complex communities that are stable. Investigations into this relationship can be done from different angles. The approach taken by Coyte et al., (2015), and May, (1972) is one where they look at random communities with different characteristics, like species diversity, connectivity and interaction composition, and they determine all equilibria and the stability of those equilibria. This more classical approach assumes that there is an equilibrium with all species present, and then investigates whether that equilibrium is stable and how stable it is.

Here however, the approach is taken from another angle. Communities with different characteristics are generated and only a stable equilibrium is looked for. One of the important measures of the resulting equilibria is the species diversity. This is opposed to the approach taken by May and Coyte where they look at all equilibria and see what characteristics lead to unstable equilibria. These unstable equilibria, where communities move away from the equilibrium point after a small perturbation, never actually occur in real life systems.

Results

Local stability

For the local stability analysis, I look at stable and unstable communities that result from communities with randomly drawn interaction matrices and examine the composition of the resulting community in terms of proportion of cooperation, competition, connectivity and diversity. Communities are initialized with 10 species, and their equilibria are calculated through a numerical solving method. In all instances biologically irrelevant equilibria and results are filtered from the analysis, meaning equilibria with negative species densities are filtered out. The stability of these equilibria is then determined by examining the eigenvalues of the Jacobian matrices. The real parts of the eigenvalues say something about the local stability of the system around the equilibrium. If all the real parts of the eigenvalues of an equilibrium are negative it is stable and will return to the equilibrium after a small perturbation. The lower this number is the quicker the community will return to equilibrium after a perturbation. The imaginary part of the eigenvalue determines whether or not oscillations occur when the equilibrium is being approached by the system.

As mentioned before, communities are initiated by generating an interaction matrix. The interactions in this matrix are zero with a chance determined by the connectivity. If they are non-zero, they have a chance of being negative dependent on the fraction of competitive interactions and positive dependent on the fraction of cooperative interactions. In this case the chances for connectivity and competitive interactions are also drawn randomly, creating large variation between communities. After stable equilibria have been determined some species may have gone extinct and the resulting community composition may have changed. The connectivity and the proportion of competitive interactions is therefore calculated and plotted here in the results.

In contrast to the approach of Coyte et al., I do not look at the shift in all possible eigenvalues as a consequence of changing the proportion of cooperative, competitive and connectivity in large systems, but at single systems and their equilibria and eigenvalues. All communities that are analysed are assumed to have a species pool of 10 species. This is opposed to the research of Coyte et al., where the results are only applicable for very large communities.

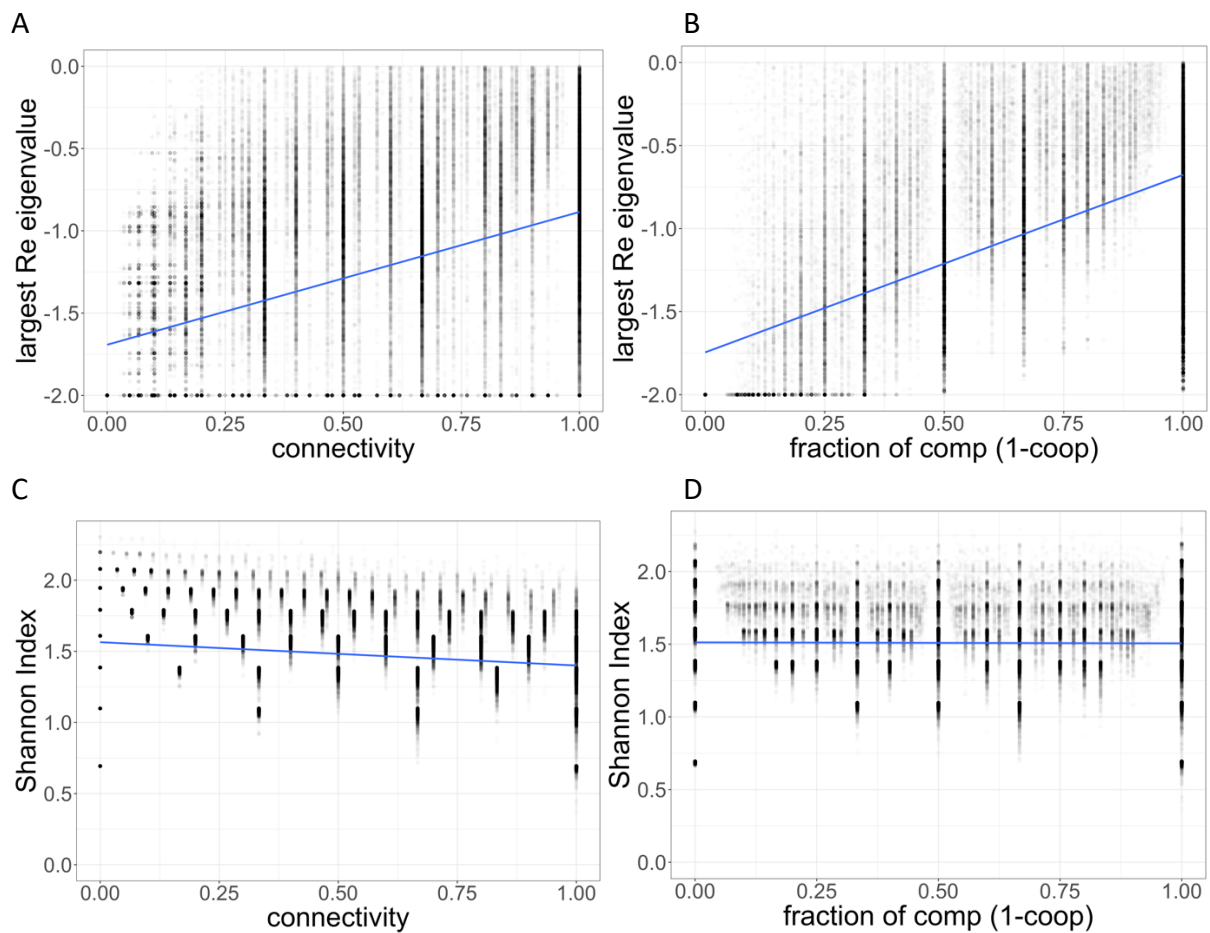


Figure 1. the largest real part of the eigenvalues underlying the community equilibrium and the Shannon index against the proportions of interactions and connectivity. The lower the largest real part of the eigenvalue is, the quicker the system returns to the equilibrium after perturbation. In 1A and 1B we see a larger proportion of cooperative interactions and no connections in the community is associated with a lower stability. When the proportion of competitive interactions is higher, the largest real part of the eigenvalues is larger. Figure 1C and 1D shows the Shannon index against the proportion of different interactions. 1C shows that the more unconnected the community, the higher the diversity is. In figure 1D, we see no clear relation between the fraction of competitive interactions and species diversity. The blue lines are linear models fitted to the points.

First, I looked at the stable communities with different proportions of cooperation and competition and looked at the species diversities and stability of them. One measure of stability we can look at is the largest real part of the eigenvalue which, as mentioned before, describes the speed at which the community returns to the equilibrium after a small perturbation. Looking at figure 1A and 1B, the stable communities show lower values of the largest real part of the eigenvalues of the system for larger proportions of cooperation and low connectivity. As mentioned before, the lower the largest real part of the eigenvalue is, the quicker the community will return to equilibrium after a perturbation. A quicker return of the system could mean that the system has less chance to be thrown off of their equilibrium even more after the perturbation and thus increases its stability. In figure 1D we can see the proportion of competitive interactions or the proportion of cooperative interactions of the communities does not predict what the Shannon index of the stable community is. However, in figure 1C a relation between the diversity and the connectivity of the community can be seen.

So far, we have characterized properties of stable equilibria. However, now we will look at how common stable equilibria are relative to unstable ones and how community characteristics change these proportions. Here unstable equilibria mean that the system will move away from this point after a small perturbation. In figure 2A there is again a clear relationship between the connectivity and the stability of a given equilibrium within the community. In figure 2B there seems to be more unstable communities when there is a slightly higher proportion of competitive interactions.

Comparing these results to the results produced by Coyte et al., the results that show relationship between connectivity and stability are the results that seem to be robust to the method of analysis. However, there is an unexpected difference for the relationship of the proportion of competitive interactions and stability. It seems that a higher fraction of competition has a destabilizing effect in communities in the results presented here. Possible reasons will be considered further in the discussion section of this report.

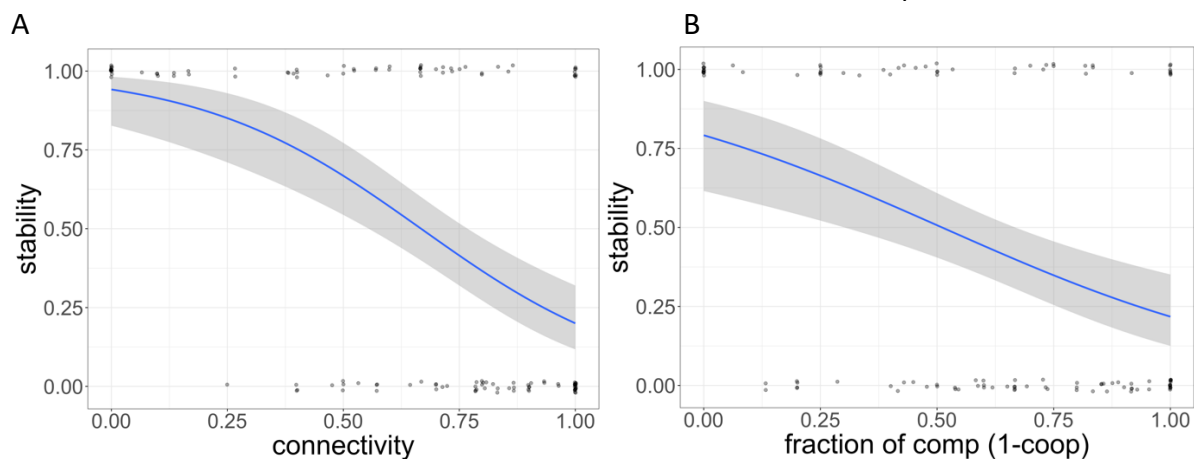


Figure 2. the fraction of stable equilibria with different proportions of competition and cooperation that are present within the identified stable and unstable equilibria. In this figure, 0 stability means an unstable equilibrium and 1 stability means a stable one. In 2A there is an association between the stability of an equilibrium and the proportion interactions that are zero. In 2B there is a somewhat less clear association between the stability of a given equilibrium and the proportion of competitive interactions in the community, but it is slightly negative. The blue lines indicate a fitted logistic curve with the grey area representing the standard error.

Numerical simulations and expanding model with plasticity

In the next part of this research numerical simulations will be used to let randomly generated communities grow from low species density initial conditions to a stable equilibrium. From this equilibrium we look at the remaining species present and calculate the Shannon index as a measure of diversity. This method differs from local stability analysis because for every community only a single stable equilibrium is found. The community grows from the initial conditions towards one stable equilibrium, and dependent on the initial conditions and the basin of attraction of equilibria present in the system it might find another equilibrium. This method allows to analyse larger communities than local stability analysis due to computational reasons.

An additional reason to use this method is the fact that it can be extended with plasticity.

Plasticity is implemented by expanding the Lotka-Volterra equations by allowing every species to exhibit two variant strategies. The variants of the same species can have different interactions with other species. Each species has a default state, and the assumption is that new grown cells always start off in this state. Dependent on the per capita growth rate of the two species they can switch to and from the variant. At each step the per capita growth is calculated, the difference in this growth between the variants is used to determine the switch rate of variant two to one, as described by the equation 3, shown here below

$$v_{21} = \frac{1}{(1 + e^{-\beta*(\delta_2-\delta_1)})} \quad (3)$$

The switch rate from one to two is described by equation 4, shown below.

$$v_{12} = 1 - v_{21} \quad (4)$$

Here δ_1 and δ_2 are the per capita change in densities for variant 1, the default state, and variant 2, the alternative strategy. These switch rates determine what proportion of the species switch to the other strategy. It is multiplied by v_{\max} , a parameter that determines the speed at which the switching can take place. figure 3 illustrates what the switch rate might look like. It shows the graph of the switch rate function and an example of values given by a difference in per capita growth rate. The switch rate is multiplied by the densities of the variants and added to the growth equations of both variants in the following way

$$\frac{dx_i}{dt} = x_i(r - s_i(x_i + x'_i)) + \sum_{j=1, j \neq i}^S a_{ij}x_j + a_{ij}'x'_j + x'_i r + v_{\max}(-v_{12}x_i + v_{21}x'_i) \quad (5)$$

$$\frac{dx'_i}{dt} = x'_i(-s_i(x_i + x'_i)) + \sum_{j=1, j \neq i}^S a_{i'j}x_j + a_{i'j}'x'_j + v_{\max}(-v_{21}x'_i + v_{12}x_i) \quad (6)$$

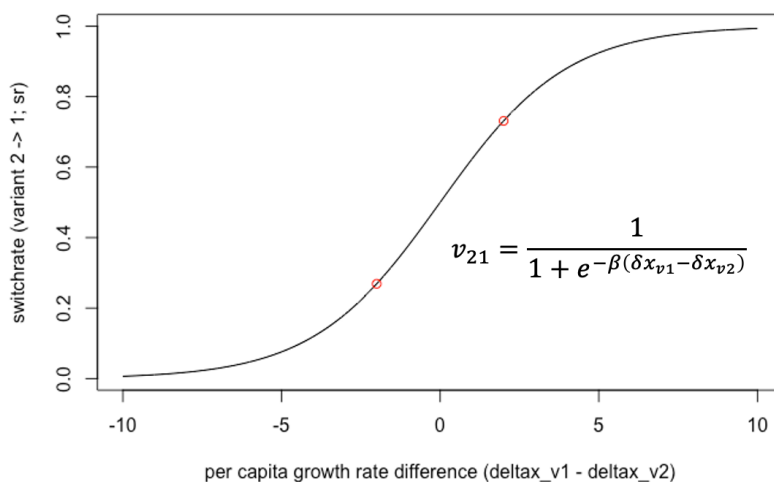


Figure 3, the function used to determine the switchrate from variant 2 to variant 1. The red dots are an example of the value of the switchrate when the per capita growth rate difference is: $\delta x_{v1} - \delta x_{v2} = 2$. The equation to determine the switchrate from variant 1 to variant 2 is equal to $v_{12} = 1 - v_{21}$, which in this example would be -2 and produces the value of the left red dot in the graph.

A carrying capacity for the entire community is added as well. This is to prevent cases where species show unbounded growth. In biological systems this would not be realistic, as there will always be constraints imposed by the environment at some point, whether that is because of resources or spatial reasons. The carrying capacity is implemented after each update step. When the total species density of the community exceeds the carrying capacity the community is normalized to be equal to the carrying capacity, taking into account the different growth rates of each species. This is achieved by dividing every species by the total species density in the community at that point and multiplied by the maximum carrying capacity. The carrying capacity in all simulations is set at 500. All species are initiated at 0.5 and the equilibrium of a single species without any interactions or than its own intrinsic growth rate and density dependence is 10. So, the carrying capacity only affects communities that have species that grow a lot beyond this isolated equilibrium.

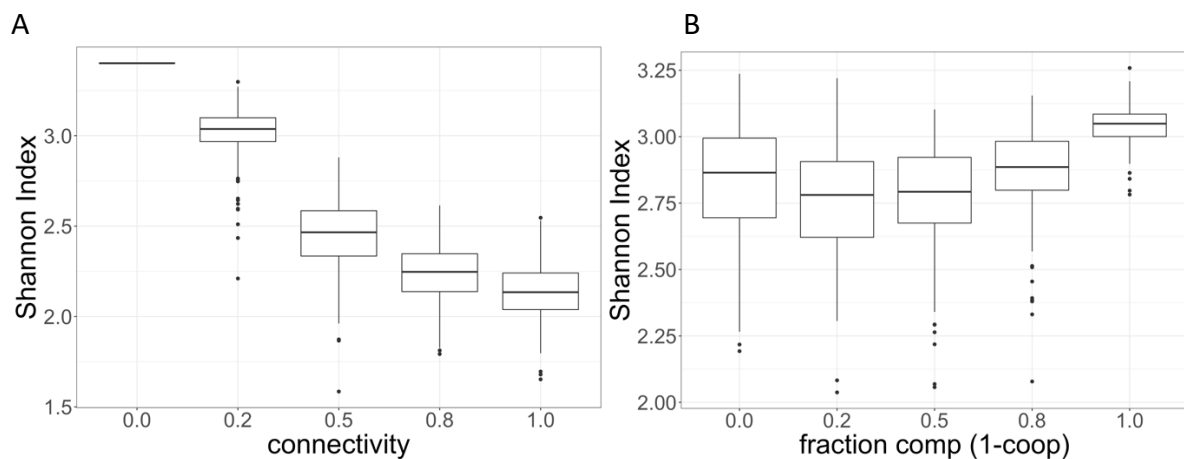


Figure 4. the Shannon index of resulting communities against different parameters used while generating random the communities. No plasticity is enabled for these simulations. The communities were initiated in each case with 30 species. In figure 3A we can see that high connectivity results in less diverse communities. Figure 3B shows the relationship between competition, cooperation and diversity found. The connectivity used to create random matrices is set to $C=0.3$, and the chance of competition when there is an interaction is set to 0.6. All communities are initiated with 30 species.

Figure 4 shows the effects of different parameters on the diversity of the resulting communities. As expected, as seen in figure 4A, the effect of connectivity decreases the diversity in resulting populations. This is in line with predictions made by Coyte and May (Coyte et al., 2015; May, 1972), in that high connectivity results in more instability in complex communities, so that the remaining stable equilibria tend to harbour low species diversity.

Figure 4B shows that the highest species diversity is found in communities with either a large fraction of cooperative or competitive interactions. The lowest diversity is found in communities with a small but non-zero fraction of competitive interactions and increasing the fraction from that point onward increases stability. A result that is in line with previous

predictions is the effect of increasing the standard deviation of the half-normal distribution from which interactions are drawn, and thus increasing the chance of high interaction strengths. This decreases the Shannon index of resulting stable communities, as can be seen in figure A2.

Finally, in figure 5 we can see the effects of the species ability for adaptive plasticity on the diversity of the stable equilibria that are attained in the numerical simulations. Here species with a v_{\max} of 0.0 show no ability to adapt their interactions, whereas higher values of v_{\max} correspond to species that can switch increasingly rapidly between alternative variants. Simulations of species communities with higher values of v_{\max} show higher diversity in stable equilibrium communities. This indicates that allowing for species to adapt their interactions with community members to maximize their own growth can increase the diversity of the entire community.

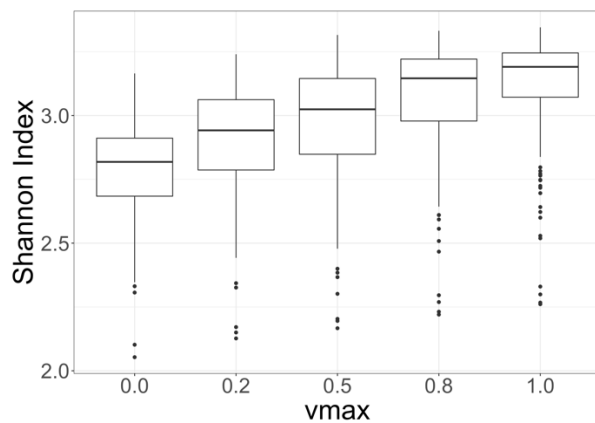


Figure 5. The Shannon index is plotted against v_{\max} , the parameter that determines adaptive plastic ability of species. A higher v_{\max} shows a positive effect diversity. The connectivity used to create random matrices is set to $C=0.3$, and the chance of competition when there is an interaction is set to 0.6. All communities are initiated with 30 species.

Effective interactions, comparing simulations with plasticity with without plasticity

In the final section of the results, we will look into further details of individual simulations, comparing the runs that have plasticity enabled or disabled. In the runs where plasticity is possible, the v_{\max} is set to 1.0, in the runs without it is set to 0.0. In figure 6 the species densities of communities with and without the capability for plasticity can be seen over time. It is clear from the graphs that communities without plasticity as seen in figure 6A, have more loss of species while reaching an equilibrium compared to the community where plasticity is possible as seen in figure 6B. What is interesting as well is the apparent difference in the variation of the species densities reached by the species. The highest densities between the simulation with and without plasticity are far apart from each other.

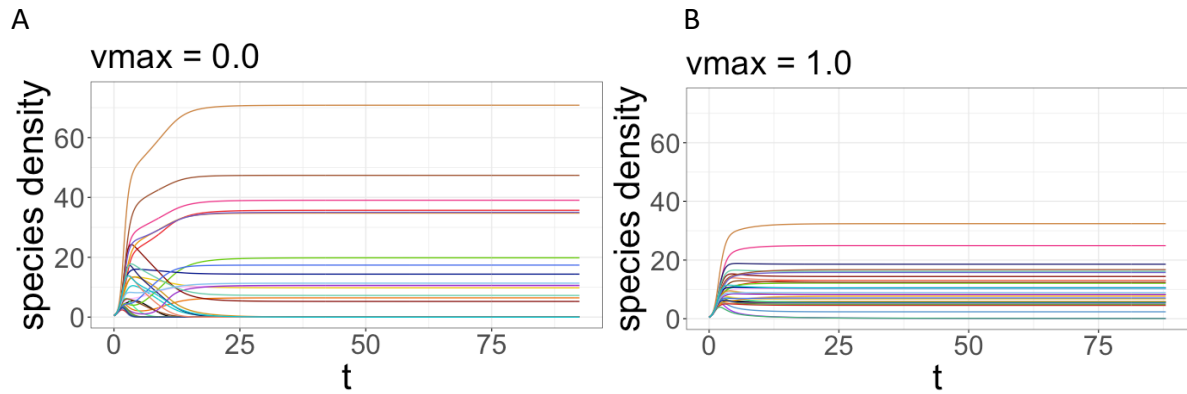


Figure 6, single runs with 30 species. 6A shows a community without this capability with $v_{\max} = 0.0$, and 6B shows a community with the capability for plasticity with $v_{\max} = 1.0$. The two variants per species are added together into single lines.

To investigate further into the community dynamics with and without plasticity as seen in figure 6, here I look into which interactions are effectively used by each species. This is achieved by taking the interactions of the default and alternative variant of each species and weighting them by the species densities of both the relevant species' variants. The calculation of the effective interactions is shown in equation 7.

$$\overline{a_{ij}} = \frac{(x_i x_j a_{ij} + x'_i x_j a_{i'j} + x_i x'_j a_{ij'} + x'_i x'_j a_{i'j'})}{(x_i + x'_i)(x_j + x'_j)} \quad (7)$$

The effective interactions in the case where plasticity is not enabled will be equal to the interaction a_{ij} , as all variant species will have a 0.0 density. By plotting the effective interactions of the same community after reaching equilibrium when plasticity is and is not possible, we can observe whether and in what direction change their interaction based on maximizing their own growth.

To compare the results of the change in effective interactions to a case where no bias towards certain interaction kinds can occur, a linear prediction is made where interactions are randomly shuffled. There is expected to always be a shift from the baseline interactions towards 0.0, because the mean of a random interaction is almost equal to 0.0. Therefore, interactions of the variant species have been shuffled, creating points where no bias towards any interaction exists. These points have then been used to create a linear model, to compare to the points and line where the points have not been shuffled, and therefore a bias can exist towards for example more cooperative interactions.

In figure 7 this has been done for the community with the same interaction matrix as the community seen in figure 5. The red line indicates the possible biased regression line and the blue one is the baseline expectation. The effective interactions of the species have not shifted too much, as can be seen by the closeness of the blue and the red line. It would be expected for species to avoid competitive interactions and move towards more cooperative interactions as this maximizes their own growth. However, it seems this has not happened

in a major way. The red line is slightly above the blue line for strong positive interactions, but it is very close. In that sense this result is somewhat surprising.

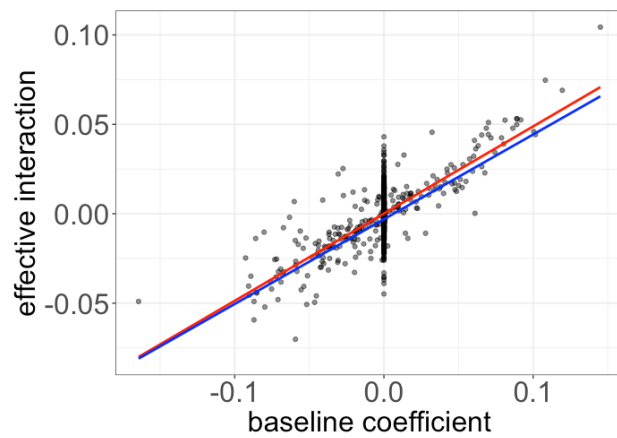


Figure 7, Shown here are the effective interactions of the same community where plasticity is and is not enabled. On the x-axis the baseline coefficients are shown. These are the effective interactions where $v_{max} = 0.0$ and therefore no plasticity is possible, they are equal to the interaction coefficients of the default variant. On the y-axis the effective interactions of the same system are shown where plasticity is possible and $v_{max} = 1.0$. The red line indicates a linear model fitted to the points. The blue line is fitted to shuffled effective interactions and represents a controlled expectation where no bias due to adaptive plasticity is present.

Discussion

Results from my analytical investigation into randomly generated communities show that lower connectivity and higher cooperation result in more stable equilibria for different measures of stability. This was true as well when looking at the largest real part of the eigenvalues of stable systems and for the diversity of the resulting communities in stable versus unstable equilibria.

These results do not match results found in the paper by Coyte et al. and there may be several reasons why. The community sizes that are investigated in the paper by Coyte are assumed to be very large, such that definite conclusions are limited to the infinitely large communities from random matrix theory. In this investigation only communities of 10 species were used due to the time it takes to solve larger systems and compute their corresponding eigenvalues. This difference in community size could be the reason different effects are found of the fraction of cooperative interactions on the stability. They mentioned that these effects become more prominent the higher the connectivity of the community is. It could very well be that a higher diversity has the same effect, since more interactions are possible.

Another thing to note is that the equilibria looked at in this report were found through numerical methods which might not always find all equilibria. Perhaps there could be a bias in the equilibria it does find. It also does not find stable community compositions in the cases where species grow unbounded. However, this unbounded growth is more an artefact of the model used than a biologically relevant result. The environment would always at some point constrain the growth of bacteria (e.g., due to resource or space limitations) and lead them to a stable equilibrium.

Although local stability analysis provides an interesting perspective on what affects stability of equilibria, the relevance of it on biological systems are not immediately clear. For example, the presence of multiple unstable equilibria in a system does not directly predict what the behaviour of the system will be. Only the stable equilibria will be reached. Especially since the interactions that affect the equilibrium in biological systems are not random but result from an evolutionary process which in turn is affected by stable equilibria of stable communities. This may cause unintuitive and creative ways in which systems avoid instability.

Results from the numerical simulations show that effects of connectivity and interaction strength are in line with expectations. The effect of competition predominantly gives rise to communities with higher species diversity, however, communities solely comprised of species that have cooperative interactions with each other do not lose too much diversity. This is in line with the idea that the destabilizing effect of cooperation comes from species that are in a positive feedback together and become the dominant species in the community. Any species that are in competition with the dominant species would be competitively excluded.

The effects of adaptive plasticity on diversity have been found to be positive here. If the exclusion of species arises from the fact that you would always be outcompeted when you

are in competition with a dominant species, it makes sense that when species are given an opportunity to escape from having that interaction, it will prevent competitive exclusion. As could be seen from looking at the effective interactions in the cases with and without plasticity enabled, it does not seem that competitive interactions in general are avoided.

The stabilizing effect of plasticity observed in Figure 6, can, in principle, be due to two mechanisms. The first would be that plasticity moves species towards less competitive interactions, especially with strong species. From results in figure 7 this can be ruled out at least in this case. A second mechanism through which the stabilizing effect can take place is that the plasticity introduces variation, so that interactions become weaker on average. Weaker interactions have already been known to have a stabilizing effect.

However, it may be that specific competitive interactions with strong species would be avoided under other circumstances. In this model it is assumed that species have a choice between two distinct variants and do not have the possibility to switch strategies between interactions with a subset of other species in the community. If this was enabled, there may have been a more visible bias of species towards particular types of interactions. To enable this may be a good extension on the model presented here.

Another extension that would be interesting for future research is to allow for predator-prey or parasitic like interactions (+/-). Allesina & Tang, (2012) predicted stabilizing effects from predator-prey like interaction and destabilizing effects from cooperative, +/+ and competitive -/- interactions. It would be interesting to see if the effects of plasticity on species diversity as seen in results in this report would be compounded in the case where these interactions were also allowed.

Finally, this model of adaptive plasticity has taken the first steps in demonstrating the effects of plasticity in microbial communities. Here plasticity is however assumed to always be adaptive, and species are assumed to “know” what exactly will maximize their growth. A good continuation of investigating the effects of plasticity is to look more towards mechanistic models that explicitly model switching of metabolic strategies.

References

- Allesina, S., & Tang, S. (2012). Stability Criteria for Complex Ecosystems. *Nature*, *483*(7388), 205–208. <https://doi.org/10.1038/nature10832>
- Costello, E. K., Stagaman, K., Dethlefsen, L., Bohannan, B. J. M., & Relman, D. A. (2012). *Toward an Understanding of the Human Microbiome*. *336*, 9.
- Coyte, K. Z., Schluter, J., & Foster, K. R. (2015). The ecology of the microbiome: Networks, competition, and stability. *Science*, *350*(6261), 663–666. <https://doi.org/10.1126/science.aad2602>
- Foster, J. A., & McVey Neufeld, K.-A. (2013). Gut–brain axis: How the microbiome influences anxiety and depression. *Trends in Neurosciences*, *36*(5), 305–312. <https://doi.org/10.1016/j.tins.2013.01.005>
- Frank, Daniel N, St. A., Allison L., Feldman, Robert A., B., Edgar C., & Harpaz, Noam, P., Norman R. (2007). Molecular-Phylogenetic Characterization of Microbial Community Imbalances in Human Inflammatory Bowel Diseases. *PNAS*, *104*(34), 13780–13785.
- Gonzalez, A., Clemente, J. C., Shade, A., Metcalf, J. L., Song, S., Prithviraj, B., Palmer, B. E., & Knight, R. (2011). Our microbial selves: What ecology can teach us. *EMBO Reports*, *12*(8), 775–784. <https://doi.org/10.1038/embor.2011.137>
- Gravel, D., Massol, F., & Leibold, M. A. (2016). Stability and complexity in model meta-ecosystems. *Nature Communications*, *7*(1), 12457. <https://doi.org/10.1038/ncomms12457>
- Kümmerli, R., Jiricny, N., Clarke, L. S., West, S. A., & Griffin, A. S. (2009). Phenotypic plasticity of a cooperative behaviour in bacteria. *Journal of Evolutionary Biology*, *22*(3), 589–598. <https://doi.org/10.1111/j.1420-9101.2008.01666.x>

Landi, P., Minoarivelo, H. O., Brännström, Å., Hui, C., & Dieckmann, U. (2018). Complexity and stability of ecological networks: A review of the theory. *Population Ecology*, 60(4), 319–345. <https://doi.org/10.1007/s10144-018-0628-3>

Lozupone, C. A., Stombaugh, J. I., Gordon, J. I., Jansson, J. K., & Knight, R. (2012). Diversity, stability and resilience of the human gut microbiota. *Nature*, 489(7415), 220–230. <https://doi.org/10.1038/nature11550>

May, R. M. (1972). Will a Large Complex System be Stable? *Nature*, 238(5364), 413–414. <https://doi.org/10.1038/238413a0>

Turnbaugh, P. J., Hamady, M., Yatsunenko, T., Cantarel, B. L., Duncan, A., Ley, R. E., Sogin, M. L., Jones, W. J., Roe, B. A., Affourtit, J. P., Egholm, M., Henrissat, B., Heath, A. C., Knight, R., & Gordon, J. I. (2009). A core gut microbiome in obese and lean twins. *Nature*, 457(7228), 480–484. <https://doi.org/10.1038/nature07540>

Appendix

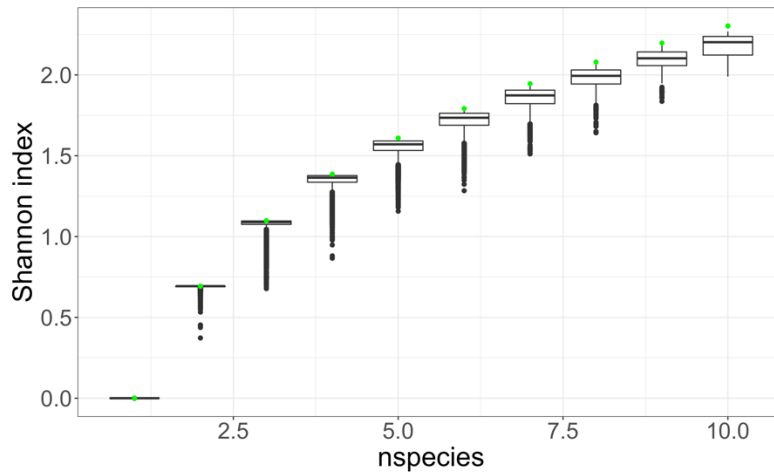


Figure A1. The number of species present in every stable equilibrium and their corresponding Shannon index shown on the y-axis. The equilibria calculated from 10 species with a random interaction coefficient matrix. The green dots indicate the maximum Shannon index value that can be reached per number of species. These equilibria were obtained using $\sigma = 0.05$, $C = 0.3$, and the proportion of competition to cooperation $3/2$.

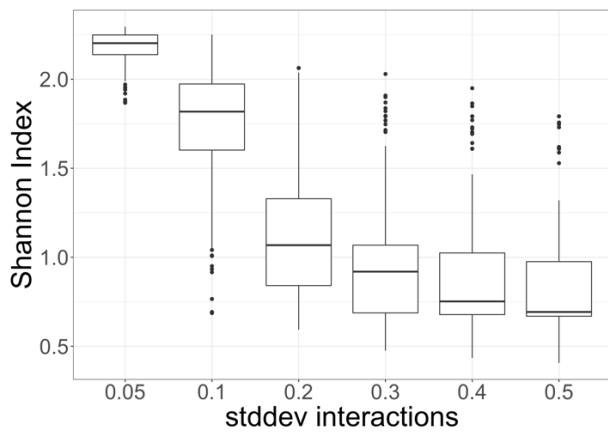


Figure A2 shows the effects of increasing the standard deviation of the half normal distribution from which the interaction strength between species is drawn on the diversity in the resultant community. Larger interaction strengths lower the diversity in communities markedly.