



The effect of climate change on the biodiversity of a multilayer network of plant-plant and plant-pollinator interactions

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The effect of climate change on the biodiversity of a multilayer network of plant-plant and plant-pollinator interactions

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Summary

Pollinators are highly under threat, causing a risk for biodiversity, ecosystem stability, food security and CO₂ sequestration. Pollinators have a mutualistic interaction with plants (plants benefit from pollinator, pollinators from nectar). Recent studies show soil organisms determine aboveground plant species composition. This is caused by the plant-soil negative feedback: The soil becomes less suitable for a plant species by growing there. Plant diversity and interactions that are mediated via the soil can be modelled in a plant-plant network. Increasing temperatures and increasing or decreasing moisture content cause changes in the abundances of soil organisms. Because some of the mutualists and pathogens increase and others decrease, the hypothesis is that the heterogeneity in the competitive interaction strengths of this plant-plant network will therefore increase with climate change (Some will increase, others decrease). Changes in the plant biodiversity, caused by these changes in the soil, might affect the pollinator biodiversity. To study the effect of this climate induced increased heterogeneity on plant and pollinator biodiversity, a new multi-layer model was created. The model combines the plant-plant network with a mutualistic plant-pollinator network. The study shows that plant richness will decrease because the plant-plant networks become increasingly unstable with changing climate. Also, both plant and pollinator densities will become less even, what might generate a higher risk of extinction by other factors. Furthermore, climate induced soil modifications might make plant communities more dependent on the pollinator network to generate network stability. Therefore, soil conservation and restoration will improve plant richness conservation and might also improve pollinator richness.

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Preface

On a sunny day, early in my studies, I was sitting on a chair, in front of my house, reading a book. I don't remember what I was reading but it must have been something interesting, because when there came a weird noise I kept on reading. When the noise became too loud to ignore, I looked up, saw only an empty field of grass in front of me, so I returned to my book. Only a little later, the noise became so loud I looked around where I could come from. It wasn't from behind my house, I certainly came from the other side. But all I could see in front of me was the grass, with a flower here and there, and the block of houses surrounding it. It was a constant noise and it seemed to move. I was staring at the end of my street, expecting an electric land mower to come around the corner any second. But the sound became closer, while there was still nothing to see. A neighbour left his home, looked at me, also in wonder of the sound, then ignored it and cycled away, leaving me still in wonder of the sound. I started to walk around. The fact that there could be such a loud noise without me being able to identify the source, annoyed me a bit. Now the sky also seemed to suddenly grow darker... The sky... it was coming from the sky! Then it saw them: an enormous swarm of honeybees! A hundred thousand bees were flying around in magnificent patterns. They filled the entire sky above the field of grass. I don't remember I ever saw so many animals moving at the same time. It was impossible to follow individuals, they didn't seem to be individuals anymore. In a wonderfully orchestrated choreography they were dancing around, all keeping the same distance. Astonished by their beauty I kept on gazing, unprepared to what came next. Suddenly, at a signal unnoticed by me, they all came down at once, right in front of me. The queen had decided to land on my bike, that was parked just half a meter in front of me. Her hive followed her, to protect her in her search for a better place to live.

I will never forget the sight and sound of these honeybees that came to visit me on that sunny day. Some things you can't learn from books and this was certainly one of them. Ever since, I've been even more interested in the bees, butterflies and bumblebees that pollinate our food and all the beautiful flowers that grow on the land. I also learned how they are under (human induced) severe threat of extinction. To research them is step one, but knowledge without action that stays in papers or books doesn't help to save our pollinators or halt further climate change. I therefore hope, that my research and other research on pollinators, biodiversity and climate change will find its way outside academia and will be a wakeup call that moves us to further action to protect the earth we live on.

Introduction

Biodiversity of soil organisms, plants and pollinators is under pressure due to global environmental change. Especially pollinators are vulnerable to extinction and have experienced decline over the last decades (Potts et al. 2010; Burkle et al. 2013). This decline is caused by a combination of disease, parasites, habitat loss, the use of insecticides and climate change (Bryden et al. 2013; Potts et al. 2010; Henry et al. 2012; Lever et al. 2014). As most of the flowering plants depend on pollinators for their reproduction this is a threat for food production and biodiversity (Kaiser-Bunbury et al. 2010; Klein et al. 2007; Ollerton et al. 2011) Furthermore, the loss of vegetation would cause a loss of carbon storage and thereby enhance the greenhouse effect and the loss of other ecosystem services (Cardinale 2012; Rockström et al. 2009).

Another threat for pollinator biodiversity are shifts in plant species biodiversity. Plant extinction and changes in evenness of plant species (closeness in numbers of individuals for each species in a community) affect pollinator populations. So far, the effects of environmental change on pollinators have been studied with plant-pollinator interaction networks, which is the combination of all interactions between plants and pollinators. In these studies, plants are assumed to be dependent on pollinators and pollinators on plants. To predict the effect of environmental change on pollinators there have been several studies about plant-pollinator interaction networks, which is the combination of all interactions between plants and pollinators (Bastolla et al. 2009; Bascompte et al. 2006,2009; Dakos et al. 2014; Rohr et al. 2014; Saavedra et al. 2013). The strength of the mutualistic interaction, i.e. a pollinator and a plant benefiting from each other, can decline under changing circumstances. A typical example of the effect of climate change is an earlier flowering season for plants because of increased temperatures in early spring. However, their pollinators do not shift equally. When plants and pollinators no longer peak at the same time, they can profit less from each other (Memmott et al. 2007; Rafferty et al. 2015; Johansson et al. 2015). Plants and pollinators can indirectly affect species in the network, even though they are not directly connected to them: For example, the increase of one pollinator species can cause the decline of another pollinator because they are feeding on the same plant and competition increases (Johansson et al. 2015).

Plant diversity can also change independently of pollinators and thereby affect the pollinators. Therefore, plants might be not affected as strong by pollinators as pollinators are affected by plants because plants are also affected by soil organisms. To explain the biodiversity of plant species, several explanations have been proposed. The classical explanation is plant-plant competition for resources (e.g. Tilman 1994), which had only limited success. More recently, plant-soil negative feedbacks have been proposed to determine plant biodiversity. A plant-soil negative feedback is a feedback between plants and the soil, where the growth of a plants species makes the soil less suitable for this species and, to a lesser extent, other plant species. The higher the density of the plant, the stronger is the negative effect (Bever et al 2003; Comita et al. 2010; Johnson et al. 2012; Mangan et al. 2010). These feedback interactions can be described and modelled with a plant-plant interaction network, that includes all the interactions of plants. These interactions are the effect of one plant on the growth of another plant species. They represent the effect the plant has on the soil community and thereby on the other plant species. In these networks, the structure and strength of plant interactions determines the abundances of plants. This plant-soil negative feedback theory hereby provides another mechanism for the coexistence of species (Eppinga et al. 2017).

From a theoretical view point, there have been only few studies combing different types of ecological interactions (Philosof et al. 2016; Kefí et al. 2014, 2016). Network studies focus in general only on either competition, mutualistic or trophic interactions (i.e. predators eating prey). They are not yet combined because until now the tools to do so were lacking (Kefí et al. 2016). Some first theoretical studies show the need to understand how these different types of interactions combine (Fontaine et al. 2011; Philosof et al. 2016). Therefore, more research on how different interaction types are interrelated is required.

More specifically, research on the combination of mutualistic interaction networks and competitive interaction networks is very limited. One study did indicate that there is a relationship between competition of plants and the mutualism of their pollinators. (Saavedra et al. 2013). The mutualistic network responds very differently in a strong mutualist regime (where mutualism is stronger than competition) than in a weak mutualist regime (where competition is stronger than mutualism) (Saavedra et al.2013). However, in this modeling study, only a difference in interspecific relative to intraspecific competition was assumed but no competitive differences between the plant species nor between pollinator species were considered. Other studies of mutualistic models have also not included the structure of the plant-plant competition thus far (Bastolla et al.2009; Rohr et al.2014; Dakos et al.2014; Bascompte et al.2006; Bascompte 2009; Gao et al.2016 et al.; but see Lever et al. 2014, which included them partly). Because the plant soil feedbacks can be modelled in a plant-plant network and can explain plant biodiversity, it is expected to impact the mutualistic network in a similar way as plant-plant competition. Therefore, plant soil feedbacks are expected to indirectly affect the biodiversity of pollinators.

The negative plant-soil feedback is expected to increase for some plants under climate change and thereby change plant abundances (Bardgett & van der Putten 2014). The change of belowground biodiversity affecting aboveground plant abundances is already been detected for several plant species (Bardgett & van der Putten 2014). These soil-mediated plant composition changes will cause abundances of plant species to change independently of their pollinators. This is expected to affect the structure and dynamics of the mutualistic network. To my knowledge, this effect has not been researched so far.

Therefore, the aim of this research is to investigate climate change induced modifications of the plant-pollinator networks, occurring because of changes in plant-plant interactions. This understanding will improve predictions of biodiversity of pollinators and plants under climate change. This could help the conservation and restoration of ecosystems.

This results in the following research question:

What is the effect of changes in plant-soil negative feedback in a plant-plant network on the biodiversity of a plant-pollination network?

Sub questions:

- What is the effect of heterogeneity of plant-soil feedbacks on species richness of plants and pollinators?

- What is the effect of heterogeneity of plant-soil feedbacks on species evenness of plants and pollinators?

To investigate these questions, simulations with a newly constructed model of a multilayer network of a plant-plant (including soil-mediated plant interactions) and a plant-pollinator (with mutualistic interactions) network will be performed. Details about the mentioned concepts will be explained in the Theory section. Details of the model are described in the Methods section.

Theory

The model that is used is a multilayer network, which combines different types of interactions in an ecological network. At first, a short overview of current network theory is described, plant-pollination networks in specific. Thereafter two theories on coexistence are explained that can both be modelled in a plant-plant network. Henceforth more details are given on the underlying mechanisms of the plant soil feedback and how this will be affected by climate change. To conclude, arguments are given why it is therefore appropriate to use a multilayer network, of a plant-pollinator and a plant-plant network, for the research question.

Since Robert May (1972) there is a search for mechanisms that make ecosystems stable, since random systems are not stable. There is a growing body of network theory research linking network structure and dynamics (e.g. Alcántara & Rey 2012; Gilarranz et al. 2015). The emphasis has been on stability and resilience of the networks (Allesina & Tang 2012; Gao et al. 2016; Suweis et al. 2015; Thébault & Fontaine 2010). In soil food webs with many trophic levels, weak links reduce the need for intraspecific competition to stabilize the network. They are stable when the matrix of the network has a negative eigenvalue (Neutel et al. 2002). In mutualistic networks, the highly nested structure makes them more stable to perturbation (Bastolla et al. 2009; Bascompte et al. 2003, 2006, 2009; Rohr et al. 2014). However, feasibility, which is the capacity of a system to keep species alive (all densities stay positive), might be more important than stability for persistence (Saavedra et al. 2016). For example, early in a flowering season, with only a few plant and pollinator species present, the plant-pollinator network might not be stable. But the early flowers can sustain the pollinator populations long enough until new flower species start blooming when summer approaches and pollinators can switch their source of nectar. The composition of the plant-pollinator network is flexible and changes during the season. These changes in composition can be expressed in a flexible interaction strength between plants and pollinators (the interaction strength becomes zero when the interaction is absent). This means that if interaction strengths are flexible, a network does not need to be stable to be feasible (Saavedra et al. 2016; Kaiser-Bunbury 2009, 2010; Bascompte et al. 2010). This indicates a need for models with flexible interaction strengths, to be able to study feasibility and not only stability.

Textbox 1. Definitions

Species richness: the number of plants and pollinator species.

Species abundance: the abundances of the species, expressed in biomass or number of individuals.

Species evenness: a measure for diversity which quantifies how equal the abundances of the species within a community are.

Network degree: the average number of connections a species (node) has to other species.

Nestedness: a measure for the structure of a network. A network is nested when the specialist species, with few interactions, interact only with a subset of the generalist species, that have many connections (Bastolla et al. 2009). The exact definition of nestedness is still debated (Jonhson et al. 2013).

Plant coexistence can be explained by the competitive structure of a plant community (Allesina & Levine 2012) and by the plant-soil feedback (Bever et al. 2003; Eppinga et al 2017). The competitive structure can stabilize a plant community by intransitive cycle loops. These loops exist of at least 3 three species. Imagine for example a community with competing species *a*, *b* and *c*. If species *a* wins the competition with species *b* on a specific trait (e.g. water uptake), species *b* wins from species *c* on a different trait (e.g. light competition by plant height) and species *c* wins from species *a* (e.g. nutrient uptake), all three species will survive. The intransitive loop causes this community to be stable and determines the relative abundances at the equilibrium of this plant-plant network (Nahum et al. 2011; Allesina & Levine 2012). These intransitive networks can be stable without considering the intraspecific competition, but only communities with an uneven number of species can be stable (Allesina & Levine 2012).

The plant coexistence can also be explained by the negative plant-soil feedback. The negative plant soil feedback can stabilize the population density of a single species by the negative effect a species has on

its own growth rate, through the negative plant soil feedback. This is called the conspecific effect. A heterospecific effect, is the effect of species *a* on the growth rate of species *b* in an environment dominated by species *a*. This effect is mediated by the negative plant-soil feedback. Species *a* and *b* can coexist if the conspecific plant-soil negative effects are stronger than the heterospecific. The net feedback is thereby negative (Comita et al. 2010; Johnson et al. 2012; Mangan et al. 2010; Bever et al. 2003; Eppinga et al. 2017). A community of more than 2 species can also coexist through plant soil feedbacks. This can be modelled with a plant-plant network where plant-soil feedbacks generate a negative frequency-dependency. The negative frequency-dependency determines patterns in plant species abundances and species richness (Eppinga et al 2017). With this plant-soil feedback also communities with an even number of species can be stable. In real communities, both the intransitive structure of the plant-plant network and the negative frequency-dependency that are mediated by negative plant-soil feedback are likely to determine plant frequencies (Eppinga et al 2017).

The plant-soil negative feedback has several explanations. One of the possible underlying mechanism is that plants species have species-specific soil microbe herbivores and pathogens. If a plant species is abundant at a specific site, the abundance of its herbivores and pathogens also increases. Thereby the soil becomes less inhabitable for this specific species (Bardgett & van der Putten 2014; Comita et al. 2010; Johnson et al. 2012; Mangan et al. 2010; Bever et al. 2003). A second explanation is strong intraspecific competition for resources (Bever et al. 2003; Allesina & Levine 2012). The third is autotoxicity, which implies that plant litter can be toxic for its own species (Mazzoleni et al. 2015). In particular, DNA is proposed as the toxic element (Mazzoleni et al. 2015). These mechanisms could explain the coexistence and the biodiversity of species. Furthermore, it could explain why it is needed to rotate crops on an agricultural field. Moreover, the relative strength of the negative feedback determines the relative abundance of plant species: the stronger the feedback, the lower the relative abundance of a plant species. To a lesser extent, this negative plant-soil feedback is also negatively affecting competing plant species (Bever et al. 2003). A positive feedback by mycorrhiza is also possible (Bever et al. 2003). Therefore, the plant-soil feedback is a key driver of plant diversity, abundance and succession (Bardgett & van der Putten 2014).

Climate change affects the plant-soil feedbacks and thereby the aboveground plant abundances (Bardgett & van der Putten, 2014). Although above and belowground global spatial species richness patterns are not correlated because they are driven by different factors, evidence is growing that belowground species composition does affect aboveground diversity on a local scale (Bardgett & van der Putten, 2014). Belowground soil organisms play a key role in ecological and evolutionary adaptation of plants to climate change. Rhizosphere microbes can affect natural selection from plant traits as tolerance, nutrient acquisition, drought tolerance and disease resistance (Bardgett & van der Putten, 2014). A stronger average negative plant-soil feedback is expected because higher temperature will cause faster metabolism of soil organisms, as is already observed in mycorrhizal fungi (Bardgett & van der Putten, 2014). More heterogeneity between plant-soil interactions is expected because soil organisms and plants are expected to have different responses to climate change factors (temperature, drought and rainfall variability etc.). This different response across soil microbe taxa has been observed (Bardgett & van der Putten, 2014).

The first reason plant-pollinator networks are expected to be sensitive to plant-plant interaction changes, is because this has already been a measured effect of invasive plant species: Invasive plant species have altered plant abundances in a plant-plant community on Mauritius and thereby caused a decline of pollinators (Kaiser-Bunbury et al. 2009, 2010).

The second reason to expect the changes in the plant-soil feedback to affect the plant-pollinator network, is because in real ecosystems different layers of interaction networks affect each other (Keff et al. 2015, 2016). In these observations, it matters which species of a non-trophic interaction network are linked to which species of a trophic network layer. The species that connect the networks are on positions that maximize persistence and total biomass compared to randomly linking the 2 networks

(Kefí et al. 2015, 2016). One of the first studies analysing a real multilayer ecological network shows that the negative feedback of sessile species, such as seaweeds (algae), is affecting other mobile species layers, like animals, of the network (Kefí et al. 2015, 2016). In terrestrial ecosystems plant-plant networks are expected to affect the structure of the mobile species network likewise (Kefí et al. 2016). This suggests that the plants in a plant-plant network are likely to be also non-randomly connected to the mutualists of a mutualistic network. It can be expected that mutualistic networks are not only dependent on the strength but also sensitive to the structure of the plant-plant network.

All this taken together, a multilayer network approach is appropriate because pioneer studies from multilayer networks show that the structure of layers of networks are highly dependent on each other. Furthermore, mutualistic network studies so far do not include changes in the plant-plant network. Therefore, they lack a mechanism for how plant-pollinator interactions change under environmental change. As belowground diversity and thereby the strength of plant-plant interactions is expected to change due to climate change, it can be expected this will affect the plant-pollinator networks. This can only be studied in a multilayer network.

Methods

Model

The multilayer network model (MLM) is a set of 2 types of differential equations, one set for plants and one set for pollinators. It is a combination and a modification of the plant-plant network negative frequency dependence model of Eppinga et al. (2017) and the plant-pollinator mutualistic model of Saavedra et al. (2013). The MLM introduces two main differences with respect to the original mutualistic model of Saavedra et al. (2013). Plant abundances are calculated as relative frequencies (P_i) while pollinators are calculated as abundances (A_i) following Eppinga et al. (2017). Furthermore, intra- (or conspecific) and interspecific (or heterospecific) competition is not equal for all plants. This is only partly following Eppinga et al. (2017) that used equal heterospecific effect coefficients within each plant species, but different coefficients between species. The total number of plant species (n_p) together with the total number of pollinator species (n_a) are the total number of differential equations in the model. The equations are as follows:

$$\frac{dP_i}{dt} = P_i \left(\sum_j^{n_p} \sigma_{ij} P_j - \sum_j^{n_p} \sum_k^{n_p} \sigma_{jk} P_j P_k + c \frac{\sum_l^{n_a} \gamma_{il}^{(P)} A_l}{1 + h \sum_l^{n_a} \gamma_{il}^{(P)} A_l} - \sum \left(c \frac{\sum_l^{n_a} \gamma_{jl}^{(P)} A_l}{1 + h \sum_l^{n_a} \gamma_{jl}^{(P)} A_l} \right) P_j \right) \quad (2)$$

$$\frac{dA_i}{dt} = A_i \left(\alpha_i^{(A)} - \sum_l^{n_a} \beta_{il}^{(A)} A_l + \frac{\sum_j^{n_p} \gamma_{ij}^{(A)} P_j}{1 + h \sum_j^{n_p} \gamma_{ij}^{(A)} P_j} \right) \quad (3)$$

Equation 2 has one part of the Eppinga et al (2017), one part of the Saavedra et al (2013) model, and a part to combine the models. This equation calculates the relative abundance of each plant species i , P_i , where i varies between 1 and n_p . The boundary conditions of the P_i are: $\sum_i P_i = 1$ and $0 \leq P_i \leq 1$. In this equation, the first two terms on the right-hand side (r.h.s.) ($\sum_j^{n_p} \sigma_{ij} P_j - \sum_j^{n_p} \sum_k^{n_p} \sigma_{jk} P_j P_k$) calculate the frequency dependent feedback of a plant-plant network that includes plant-soil negative feedbacks. The coefficients (σ_{ij}) of the interaction matrix (σ) quantify the negative effect on the growth of species i in an environment dominated by species j , for each pair of species i and j . All values are sampled between 0 (strong negative frequency dependence) and 1 (no frequency dependence) (Eppinga et al. 2017). In ecosystems, the negative conspecific effect of a species has on itself is stronger than the heterospecific effect on other species (Comita et al. 2010; Johnson et al. 2012; Mangan et al. 2010, Bever et al. 2003). Therefore, the values of the off-diagonal elements of the interaction matrix (the effect of species j on i) are higher than the values of the elements of the diagonal of σ (the effect of species i on i) and all are below 1 to represent a negative feedback. Because the coefficients of σ define a plant-plant network that represent plant-soil negative feedback, this network, represented by the first two terms on the r.h.s., is called a plant-soil network (PSN) in the following.

The first term on the r.h.s. in equation 2 ($\sum_j^{n_p} \sigma_{ij} P_j$) is the sum of all the effects the plant species i experiences from all the other plants (j) and are dependent on the (relative) abundance of plant j (P_j). This means that the relative competitive effect of the plant-soil negative feedback effect caused by the presence of species j on species i , is dependent on the abundance of this species (P_j). Therefore, the abundance of species i (P_i) is dependent on the presence of all the other species.

The second term on the r.h.s. in equation 2 ($-\sum_j^{n_p} \sum_k^{n_p} \sigma_{jk} P_j P_k$) is a consequence of assuming zero-sum dynamics (no plant species can increase without another decreasing). It can be interpreted as the average fitness of the plant community (Allesina and Levine 2011). This part of the equation converts species densities into relative densities. The assumption behind this is that the growth of the soil

community is proportional to the plant abundances (Bever 2003; Eppinga et al. 2017). A second assumption is that productivity of the plants is high (Eppinga et al. 2017).

The third and fourth terms on the r.h.s. of equation 2 ($+c \frac{\sum_l^{na} \gamma_{il}^{(P)} A_l}{1+h \sum_l^{na} \gamma_{il}^{(P)} A_l} - \sum \left(c \frac{\sum_l^{na} \gamma_{jl}^{(P)} A_l}{1+h \sum_l^{na} \gamma_{jl}^{(P)} A_l} \right) P_j$)

calculate the effect of pollinators on relative plant frequencies. In this part, the fitness effect is calculated that plants experience from pollinators. The plant pollinator network, or also called plant mutualist network (PMN) is defined in the interaction matrix γ .

The third term on the r.h.s. in equation 2 ($\frac{\sum_j^{na} \gamma_{ij}^{(P)} A_j}{1+h \sum_j^{na} \gamma_{ij}^{(P)} A_j}$), is the mutualistic benefit of plants from

pollinators. It is a Holling type II functional response ($f(P) = \frac{aP}{1+ahP}$), because of a saturation effect: if a plant is visited by pollinators, there is no added effect of new pollinators visiting the plant because it is already pollinated. The half-saturation constant (h), determines the extent of the saturation (units of biomass⁻¹). $\sum_j^{na} \gamma_{ij}^{(P)} A_j$ is the sum of the mutualistic benefits from the abundance of every pollinator species (A_j) and γ_{ij} is the mutualistic interaction strength of pollinator species j on plant species i . γ_{ij} includes a mutualistic trade-off given by:

$$\gamma_{ij} = \frac{\gamma_0 y_{ij}}{k_i^\delta} \quad (4)$$

where, γ_0 is the basal value of the mutualistic interaction strength, representing how much the growth of a plant species benefits from pollination. γ_0 is kept equal for all species which implies that pollinators have no food preferences for one plant over the other and plants benefit from pollinators equally in the present model simulations. The interaction matrix y defines the structure of the plant-mutualist network (PMN). $y_{ij} = 1$ if plant species i and pollinator species j interact, 0 if they do not. k_i is the species degree of a pollinator species i , i.e. the number of plant species it pollinates. The interaction strength of this pollinator is inversely related to its species degree. This means that if a pollinator pollinates a lot of other plants as well, the interaction strength is less strong because a large proportion of this pollinator population will spend its time pollinating other plant species. However, if a pollinator only pollinates this plant species the interaction strength is stronger because all individuals of this species will search for this particular plant species (Burkle et al 2013). This is called the mutualistic trade-off. In the model, this trade-off can be turned on ($\delta=0$) and off ($\delta=1$) with parameter δ (Dakos & Bascompte 2014).

In the third term on the r.h.s., c is a conversion factor that determines the relative influence of the PSN on the plant pollinator network. Because the units of $\gamma_{ij}^{(P)}$ are inversely related to the pollinator biomass ($1/\sum A_j$), c determines how strong the interaction between plant i and pollinator j is. If c is close to zero, plant frequencies are not limited by pollinator abundance. This is when pollinator abundances are high and there are enough pollinators to pollinate all the plants. Because of the functional response function, this is not a finite number of pollinators. If c is close to 1, pollinator abundances are low compared to the total (but unknown) biomass of the plants.

The fourth term on the r.h.s of equation 2 ($-\sum \left(c \frac{\sum_l^{na} \gamma_{jl}^{(P)} A_l}{1+h \sum_l^{na} \gamma_{jl}^{(P)} A_l} \right) P_j$) adjusts the mutualistic effects of the pollinators on plant abundances to effects on relative plant frequencies. This factor ensures that the plant species are calculated in frequencies.

Equation 3 calculates the abundance of pollinator species A_i . The first term on the r.h.s of equation 3 ($\alpha_i^{(A)}$) is the intrinsic growth rate (α) of a pollinator species i .

The second term on the r.h.s of equation 3 ($\sum_l^{na} \beta_{il}^{(A)} A_l$) is the competition between pollinators. The pollinator-pollinator interaction matrix β defines the competitive effect of pollinator species l on pollinator species i . For the pollinators, a mean field approximation is used for the intraguild competition factor $\beta_{il}^{(A)}$ (Saavedra et al. 2013). This means the effect of plants on pollinators is not affected by spatial effects. The competitive strength is the same for all the pollinators.

The third term on the r.h.s of equation 3 ($\frac{\sum_j^{np} \gamma_{ij}^{(A)} P_j}{1+h \sum_j^{np} \gamma_{ij}^{(A)} P_j}$) is the mutualistic benefit pollinators experience from plants: their source of food. This is also a Holling type II functional response ($f(P) = \frac{aP}{1+ahP}$), because there is a limited amount of nectar pollinators need to reproduce. $\gamma_{ij}^{(A)}$ is also inversely proportional to the species degree (equation 4). In this case, k_i is the degree of a plant species i . If a plant species is also pollinated by other pollinators, only a proportion of the population of this plant species contributes to the growth of the pollinators. If the pollinator pollinates a plant species that is only pollinated by this plant species, the whole population of this plant species contributes to the growth of the pollinator because there is no indirect competition (Burkle et al 2013, Dakos & Bascompte 2014).

Network diagnostic measures

The plant equilibrium values of a PSN can be calculated directly. These equilibrium values can be used to check if a PSN is feasible without the effect of pollinators. Average pair-wise feedback and community feedback are also properties of the PSN. Nestedness is a property of the PMN. The Shannon and Pielou index are diagnostic measures of the plant frequencies and pollinator abundances.

Equilibrium values and feasibility condition

The equilibrium values of the plant frequencies in the MLM, without the effect of pollinators ($c=0$), can be calculated directly. The equation is then simplified to:

$$\frac{dP_i}{dt} = P_i \left(\sum_j^{np} \sigma_{ij} P_j - \sum_j^{np} \sum_k^{np} \sigma_{jk} P_j P_k \right) \quad (5)$$

The equilibrium values can be calculated with applying Cramer's rule to σ , using the following equation:

$$\hat{P}_i = \frac{\det A_i}{\sum_{j=1}^n \det A_j} \quad (6)$$

Where A_i indicates a matrix equal to σ , except for the i th column, which is replaced by a column vector of ones. Cramer's rule replaces a column of a matrix for an equal value. Because the plants are calculated as frequencies, the relative equilibrium values can be calculated. The determinant of the obtained matrix for a species i (A_i) needs to be divided by the sum of the determinants of the matrices obtained for all the other species (A_j) to calculate the relative abundance of species i (Eppinga et al 2017).

The feasibility condition is fulfilled if all relative equilibrium values are above zero, therefore:

$$0 < \frac{\det A_i}{\sum_{j=1}^n \det A_j} < 1 \quad (7)$$

Where A_i is the same explained in the previous section (Eq. 6). The feasibility condition means that if all plant equilibrium values are between 0 and 1, the PSN is feasible and all plant survive because of the structure of the PSN (Eppinga et al 2017).

Average pair-wise feedback and Community feedback

The pair-wise feedback (I_s) of 2 species can be calculated as:

$$I_s = \sigma_{11} - \sigma_{12} - \sigma_{21} + \sigma_{22} \quad (8)$$

Where σ_{11} is the effect of species 1 on itself, σ_{12} the effect of species 2 on species 1, σ_{21} the effect of species 1 on species 2 and σ_{22} the effect of species 2 on itself. To calculate the average pair-wise feedback, the pair-wise feedback was calculated for all species pairs. The sum of all these pair-wise feedback was divided by the number of species (Bever 2003, Eppinga et al 2017).

The community feedback can be calculated as follows:

$$I_c = (-1)^n \sum_{j=1}^n \det A_j \quad (9)$$

where $\sum_{j=1}^n \det A_j$ is the same as in equation 6 and n is the number of species. The first term on the r.h.s. $(-1)^n$ ensures that matrices, with both even and uneven numbers of species, have a negative I_c when the PSN meets the feasibility condition of equation 7. I_c is a necessary, but not a sufficient condition for plant species persistence (Eppinga et al 2017).

Nestedness

Nestedness is a measure for the structure of an ecological network. A plant-pollinator network is nested when the plants that have few connections have connections to a set of pollinators that have a lot of interactions with plants. The specialists are thus connected to generalists. Nestedness can be calculated following Bastolla et al. (2009) and Lever et al (2014):

$$N = \frac{\sum_{i>j}^{n^p} N_{ij} + \sum_{i>j}^{n^a} N_{ij}}{\frac{n^p(n^p - 1)}{2} + \frac{n^a(n^a - 1)}{2}} \quad (10)$$

Where n^p is the number of plant species and n^a the number of pollinator species. The first sum in the numerator is across all pairs of plant species, the second sum is across all pairs of pollinator species. N_{ij} is the nestedness of a pair of species. The nestedness of this pair of species of two plants (or two pollinators), i and j , can be derived as follows:

$$N_{ij} = \frac{n_{ij}}{\min(n_i, n_j)} \quad (11)$$

Where n_i is the number of interactions of species i and n_j is the number of interactions of species j . n_{ij} is the number of times species i and j interact with the same mutualistic partner. This nestedness index ranges from zero to one.

Shannon index and Pielou's evenness index

The Shannon-index is a measure to describe species diversity. In the index both the number of species as their abundances are considered. The equation is:

$$H' = - \sum_{i=1}^{n_p} (P_i \ln P_i) \quad (12)$$

Where n_p is the number of (plant) species. P_i is the relative abundance of species i . For the pollinator species, the abundances first have to be converted to relative abundances ($P_i = A_i / \sum A_j$) The Shannon index was calculated separately for pollinators and plants. The Shannon index was calculated to calculate the Pielou evenness index.

The Pielou's evenness index calculates how close in numbers each species is. For example, if the abundances of 2 different plant species are the same, the evenness is very high. If the first species is

very abundant and the second has only a few individuals, the evenness is very low. Pielou's evenness index is described as:

$$J' = \frac{H'}{H'_{max}} \quad (13)$$

Where H' is the Shannon index as described above and H'_{max} is the maximum possible value of H' . This can be calculated as:

$$H'_{max} = - \sum_{i=1}^{n_p} \frac{1}{n_p} \ln \frac{1}{n_p} \quad (14)$$

Where n_p is the number of species of and i is also the number of species and thus is H'_{max} calculates the maximum Shannon index for this number of species. Pielou's evenness index (J') is a value between 0 and 1. The higher J' , the more even the community is.

Simulations & Analysis

To test for the effect of climate induced changes in the soil on plant and pollinator composition (species evenness and richness), different plant-soil networks (PSN) and plant-mutualist-networks (PMN) were created. The different initializations of the coefficients of the plant-plant interaction matrix σ represent different scenarios of climate change effects. Conspecific coefficients were kept lower than heterospecific coefficients, representing a stronger conspecific plant-soil feedback. All conspecific coefficients were chosen between 0.05 and 0.3 and all heterospecific coefficients between 0.3 and 0.9, following Eppinga et al. (2017). Table 1 shows an overview of the values of the parameters that are used (unless stated otherwise).

The transient can take very long to get to an equilibrium or regular cycle (*See Appendix S1*). This effect is stronger when species are close to an unstable equilibrium value. Therefore, initial values were not set close to the equilibrium value. Instead, the initial values of all plants were set on equal values and the initial values of all pollinators were also set on equal values. and. Which species dies out first in an unstable PSN, is also dependent on the initial value. Other initial values might result in different networks of surviving species. By starting all simulations at equal values this effect was reduced as much as possible. The plant frequencies and pollinator abundances were almost always at equilibrium after 1500 timesteps if there is a stable equilibrium. Therefore, the number of time steps was set on 1500.

If the frequency or abundance of a species becomes lower than 0.0001, the species were classified as extinct. The simulations and analyses were performed in Matlab.

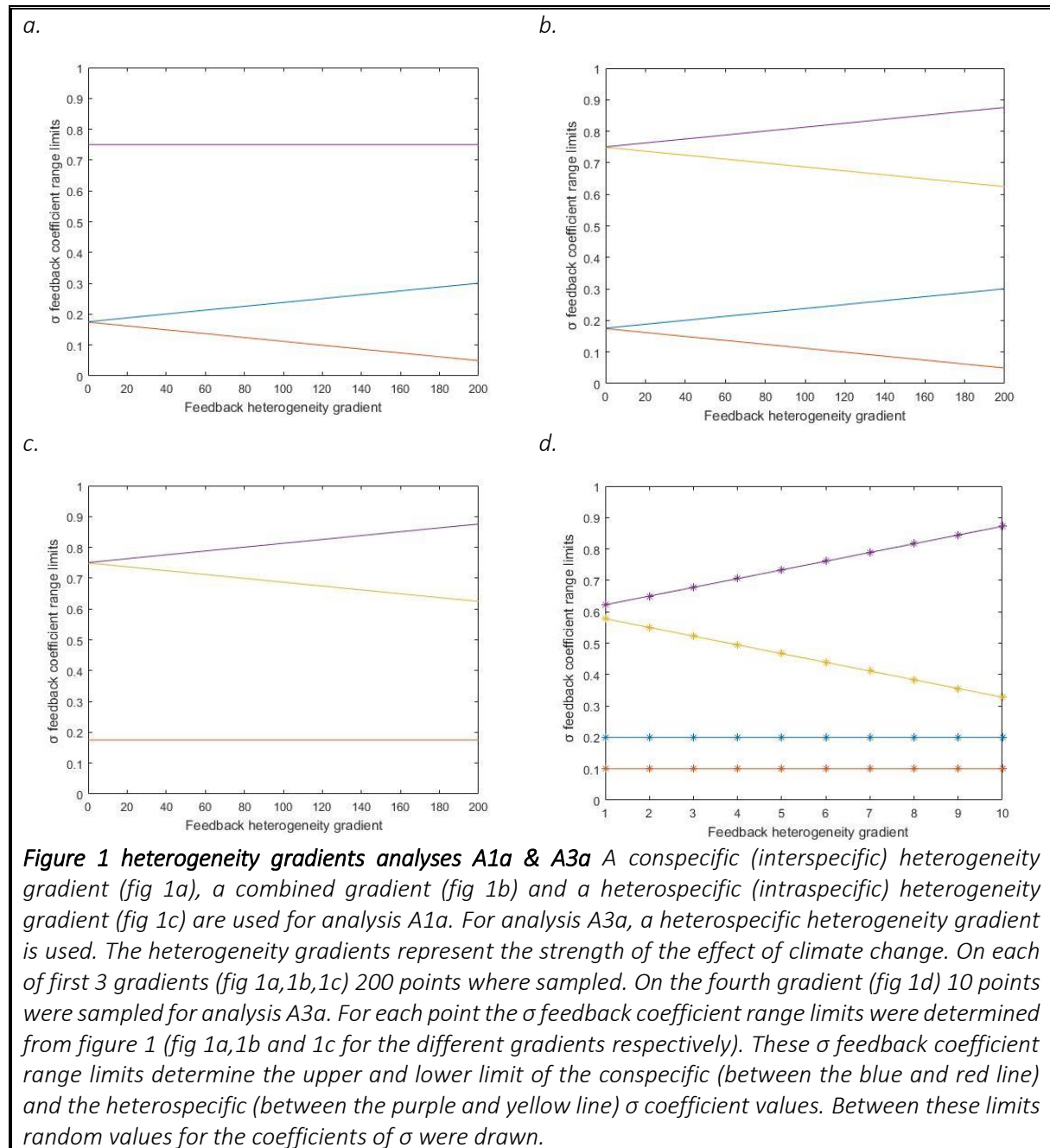
A.1 Analysis of the effect of PSN heterogeneity on average pair-wise feedback and nr. of stably coexisting species

The first analysis (A1a) was performed to test which type of heterogeneity of σ would lead to changes in the stability of the PSN and thereby affect plant species composition. These simulations were performed without an effect of pollinators on the plants ($c=0$). Three types of heterogeneity gradients were considered: a conspecific heterogeneity gradient (*fig. 1a*), a heterospecific heterogeneity gradient (*fig. 1c*), and a combined gradient (*fig. 1b*). The heterogeneity gradients represent the strength of the effect of climate change. On each of the 3 gradients 200 points were sampled. For each point the σ feedback coefficient range limits were determined from *figure 1* (*fig 1a,1b* and *1c* for the different gradients respectively). These σ feedback coefficient range limits determine the upper and lower limit of the conspecific (between the blue and red line) and the heterospecific (between the purple and yellow line) σ coefficient values. For each of the samples, 12 different matrices of 1000 species were created with the same upper and lower conspecific and heterospecific σ coefficient limits. For each of the 12 matrices, a community was assembled in the following way: After selecting two species randomly other species were added and the equilibrium values were calculated as in equation 6. Species were added until the community was no longer feasible (i.e., one of the species had negative equilibrium value, see equation 7). For each of the 12 runs the average pair-wise feedback (l_s , equation 8), the

number of stably coexisting species (counted as the number of species) and the community feedback (l_c , equation 9) were calculated for the assembled community. For each of the 200 points on the heterogeneity gradient boxplots were created for: i) the nr of stably coexisting species of the 12 runs ii) the average pair-wise feedback of the 12 runs and iii) the l_c of the 12 communities that were created in the 12 runs on. This was repeated for the 3 different gradients.

Based on these results, it was concluded that only a gradient in heterospecific heterogeneity of the PSN will affect plant species number of coexisting species. Therefore, this gradient was used in the analysis of the combined MLM.

To validate these calculations, the results of Eppinga et al. (2017) were first reproduced (analysis A1b).



A.2. Analysis of the effect of the conversion factor on species' frequencies and abundances and on evenness

The second type of analysis was performed to test the sensitivity of the MLM to parameter settings. The results of these analyses were used to parameterize the MLM. For the second type of analysis (A2a), a PSN of 100 plant species (n_p), with low heterospecific heterogeneity and a PSN with high heterospecific heterogeneity were created. Both PSNs have conspecific coefficients between 0.1 and 0.2. The PSN with low heterogeneity has heterospecific coefficients between 0.6 and 0.7 and is feasible and meet the condition of equation 7 (fig. S2a). The PSN with high heterogeneity with heterospecific coefficients between 0.3 and 0.9 and is unstable (does not meet the condition of equation 7) (fig. S2b). For 10 values of c between 0 and 1, plant frequencies and pollinator abundances were calculated with the MLM for the 2 different PSNs. The frequencies and pollinator abundances after 1500 time steps were plotted for each value of c . For all values of c the Pielou evenness index (with equation 12,13,14) was calculated for the plant frequencies and pollinator abundances.

A random y matrix (fig. S2c) was created with 100 pollinator species (n_a). The probability of interaction of the PMN was set to 0.2 resulting in a network degree of 0.2. The nestedness (calculated with equation 10 & 11) of this network is 0.2305.

These calculations were repeated with a nested network with a nestedness of 0.9 (fig. S2d), also with a probability of interaction of 0.2. To build such a nested network, the approach of Medan et al (2007) was adopted. The previously described random network was reassembled by randomly selecting a row (plant species) from the PMN. From this row 2 pollinator species (columns) a & b are selected. If the plant interacts with a and not with b and species a has less interactions than species b , the cells are swapped. Thereafter, a column (pollinator species) was randomly selected from the PMN. From this column 2 plant species (rows) c & d are selected. If the plant interacts with a and not with d and species c has less interactions than species d , the cells are swapped. By this algorithm the 'rich get richer', and thereby the nestedness will increase. The algorithm was repeated until a nestedness of 0.9 was reached.

These calculations were repeated for a sensitivity analysis of $\alpha_i^{(A)}$ (analysis A2b), $\gamma^{(P)}$ (analysis A2c), $\gamma^{(A)}$ (analysis A2d) and $\beta^{(A)}$ (analysis A2e) with c set to 1. These sensitivity analyses are performed with a stable PSN (fig. S2a). This is to ensure that the plants and pollinators have a stable equilibrium, thus allowing making graphs of the equilibrium values for each value of the changing parameter.

Because analysis A.2 a, b & c show that the conversion factor (c) has the same qualitative effect as the growth rate and the interaction strength ($\gamma^{(P)}$), it does not matter for the results of plant survival and evenness which parameter is taken. The main difference of interaction strength ($\gamma^{(P)}$) and conversion factor is the effect of the half saturation time. Based on these results (see below in results section) a conversion factor of 0.2 was chosen for the final type of analysis (A3). This represents a dependency of plants on both the PSN and the pollinators.

A.3. Analysis of the effect of heterogeneity on species richness and evenness

The third type of analysis was performed to tests for the effect heterospecific heterogeneity on species richness and evenness. This heterospecific heterogeneity represents the effect of climate change on the plant soil feedback. This analysis thereby simulates the effect of climate change on plant and pollinator richness and evenness. A monte Carlo sampling was performed to test for significance.

10 points were sampled on a gradient of increasing heterospecific heterogeneity of the coefficients of σ . For each of the 10 points the σ feedback coefficient range limits were determined from figure 1d. These σ feedback coefficient range limits determine the upper and lower limit of the conspecific (between the blue and red line) and the heterospecific (between the purple and yellow line) σ coefficient values. For each of the samples, 12 different matrices of 100 species were created with the same upper and lower conspecific and heterospecific σ feedback coefficient limits. For each matrix, the MLM was run for 1500 time steps. For each run: i) the number of surviving species (species richness)

(analysis A3a), ii) Pielou index (equation 12,13,14) (analysis A3b), iii) average pair-wise feedback (equation 8) (analysis A3c) and iv) community feedback (equation 9) (analysis A3d) were calculated for both plants and pollinators.

For each of the 10 points on the heterogeneity gradient a boxplot was created of the 12 runs and plotted over de heterogeneity gradient for: i) the number of surviving species ii) Pielous' evenness (of both plants and pollinators), iii) the average pair-wise feedback, iv) the l_c of the 12 original 100x100 communities. Analyses A3a,b,c were repeated with a nested network (analysis A3e)

Table 1. Parameters with their symbols, meaning and values (if not otherwise stated)		
Symbol	Value	Name /Meaning
Model		
$\beta^{(A)}$	0.5000	Competition of pollinators
h	0.1	Half-saturation time
$\gamma^{(A)}$	1	Interaction strength of plants on pollinators
$\gamma^{(P)}$	1	Interaction strength of pollinators on plants
δ	1	Switch for mutualistic trade-off ($\delta=0$ if off; $\delta=1$ if on)
$\alpha^{(A)}$	1	Growth rate of pollinators
k	calculated	Species degree: the number of interaction of a species
γ_0	1	Basal interaction strength
c	0.2	conversion factor: The higher c , the stronger the relative effect of the PMN versus the PSN
Simulation initial values		
n_p	100	Number of initial plants
n_a	100	Number of initial pollinators
P_i	0.01	Initial plant frequency
A_i	0.01	Initial pollinator abundance
y		Plant mutualist network (PMN) plant-pollinator network
N	0.2305	Nestedness of Bastola (equation 10&11)
	0.2	Network degree: Average number of connections between plants and pollinators
p	0.2	Probability of interaction in Y. ($p/100$ =Network degree)
σ		Plant soil network (PSN) plant-plant network with assumed plant-soil feedback

Results

Effect of PSN heterogeneity on community feedback, average pair-wise feedback and number of stably coexisting species (A1)

The results of Eppinga et al. (2017) could be reproduced (*Appendix S3*) with analysis *A1b*. With analysis *A1a* figure 2 was created. An increase of only conspecific heterogeneity (*fig. 2a*) does not significantly affect the number of stably coexisting species (*fig. 2a*). There is a small increase of the standard deviation of the average pairwise feedback (*fig. 2b*) At low conspecific heterogeneity, the standard deviation is about between -1.135 and -1.160 up to about between -1.125 and -1.175 at high conspecific heterogeneity. l_c stays close to zero over the conspecific heterogeneity gradient (*fig. 2c*).

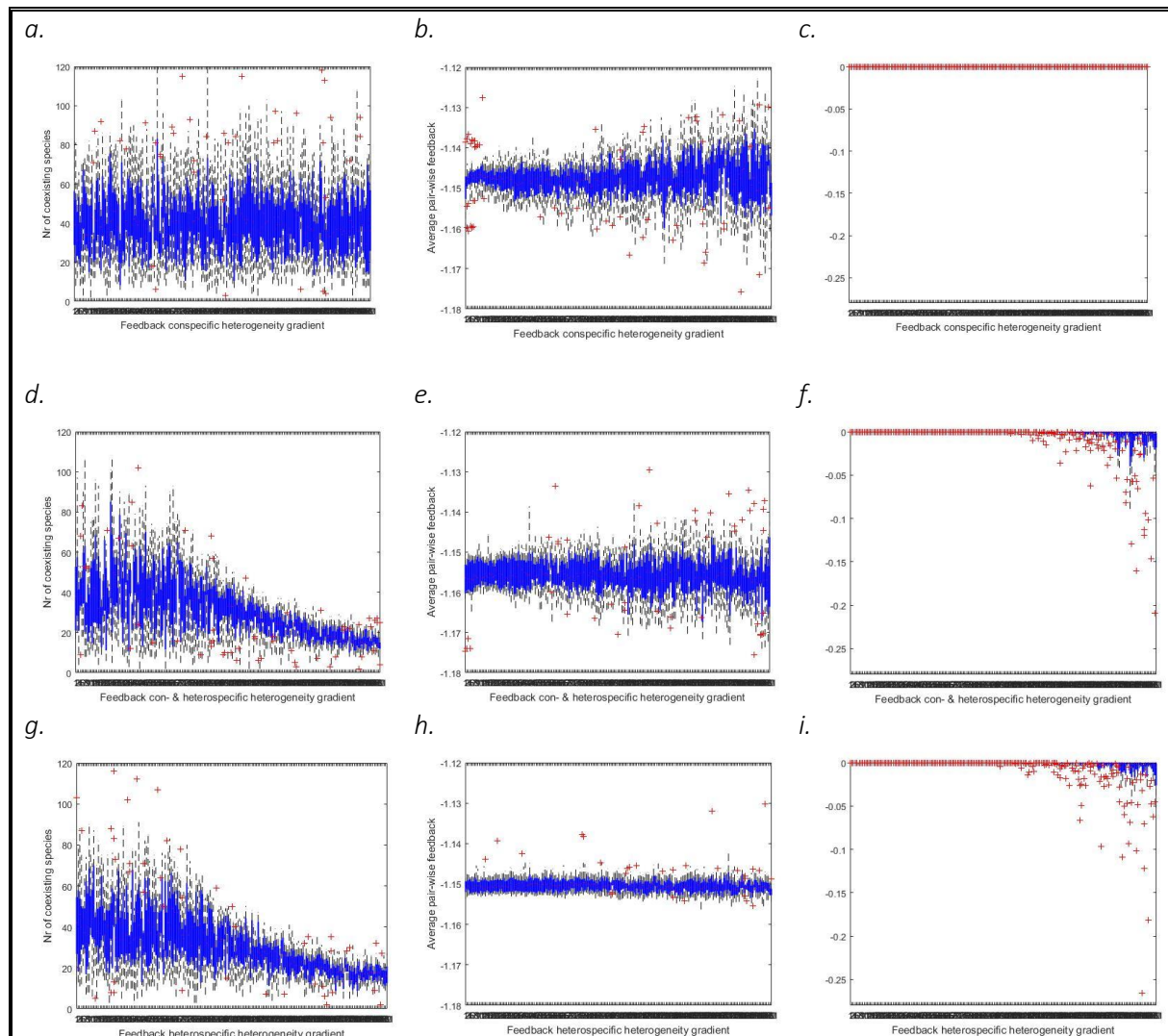


Fig.2. Effect of feedback heterogeneity of the PSN on nr. of coexisting species, average pairwise feedback and community feedback On the 3 gradients of fig 1 a,b&c, on 200 points the upper and lower limits of the con- and heterospecific parameter coefficients were sampled according analysis *A1a*. For each point, boxplots of 12 runs were created for the nr. of stably coexisting species (2a,d,g), the average pair-wise feedback (2b,e,h) and the community feedback (2c,f,i). This was done for a gradient of increasing conspecific heterogeneity (*fig 1a, 2a,b,c*), a gradient of increasing conspecific and heterospecific heterogeneity (*fig 1b,2d,e,f*) and a gradient of increasing heterospecific heterogeneity (*fig 1c,2g,h,i*) respectively. Each run adds a species to the PSN until the PSN is no longer stable. The number of stably coexisting plant species decreases with increasing heterospecific heterogeneity but not with increasing conspecific heterogeneity. Conspecific heterogeneity does also not affect the community feedback.

The increase of both conspecific and heterospecific heterogeneity (*fig.1b*) results in a decrease in number of stably coexisting species (*fig. 2d*). At low heterogeneity, the maximum size of a stable web is about 110. At high heterogeneity, the maximum size of a stable web 30 species. There is a small increase of pair-wise negative feedback spread (*fig.2e*). This means that the higher the combined conspecific and heterospecific heterogeneity, the smaller a stable PSN will be. l_c drops below zero at high combined heterogeneity (*fig 2f*).

An increase of heterospecific heterogeneity (*fig. 1c*) gives a lower number of stably coexisting species (*fig. 2g*). At low heterogeneity, the maximum size of a stable web is about 120. At high heterogeneity, the maximum size of a stable network is about 30 species. This means that the higher the heterospecific heterogeneity, the smaller a stable PSN will be. The average pair-wise feedback does not significantly change (*fig.2h*). These results were not tested for significance but based on the boxplots of figure 2.

These results of analysis A1a indicates that the effect of conspecific and heterospecific heterogeneity increasing at the same time (*fig. 2 d,e,f*) on nr. of stably coexisting species is dominated by the process of increasing heterospecific heterogeneity. Thus, in the following, the simulations of increasing heterogeneity are performed increasing only the heterogeneity of the heterospecific values. The analyses (A2 and A3) were also performed for an increase of conspecific heterogeneity but showed no significant results (not shown).

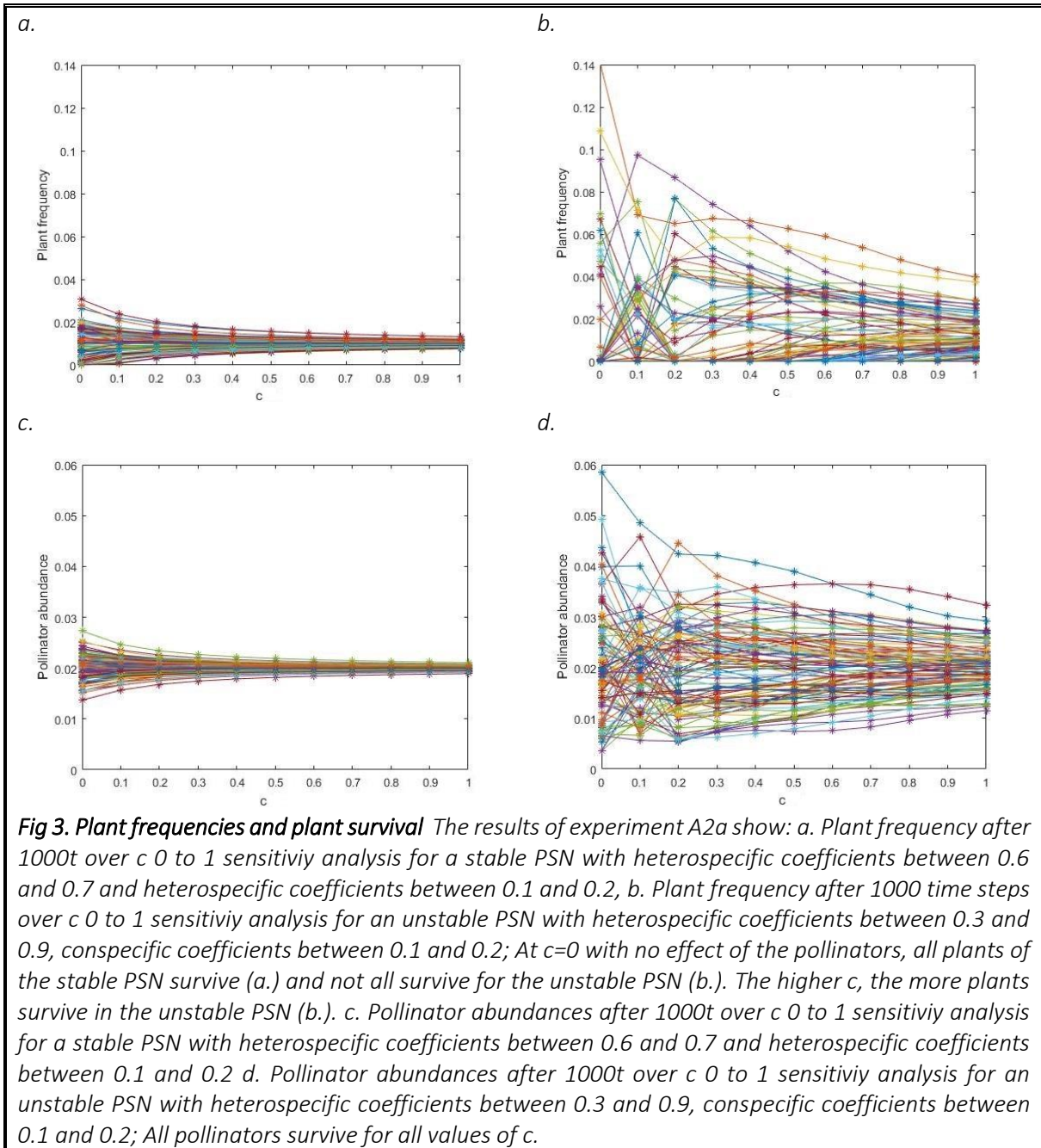
Sensitivity analysis of the conversion factor (A.2a) and other parameters (A.2b, c &d)

Experiment A2a. generates the sensitivity analysis of the conversion factor (c). The purpose of this analysis is to determine which parameters are valid to use for the final analysis A3. Figure 3a shows plant frequencies after 1000 time steps of a stable PSN (*fig S2a*) with a small heterogeneity in heterospecific feedback, over increasing interaction strength (c). For example, the points at time step 1000 in figure S41a are represented in figure 3a at $c=0$. All plants of this PSN survive regardless of the interaction strength (c) with the PMN. At $c=0$, where there is no effect of the pollinators, all plants survive, indicating that the PSN is feasible by itself, without the stabilizing effect of the pollinators. Figure S41a&b show this feasible PSN is also stable.

For a PSN (*fig S2b*) with a larger heterospecific feedback (*fig. 3b*), not all plant species survive at a small interaction strength (c) because the PSN is unstable. When the pollinators don't interact with the plants ($c=0$), not all plants survive, indicating an unstable PSN. With an increasing interaction strength (c), the dynamics are increasingly dominated by the pollinators and more plant species survive. All plants survive at $c=1$.

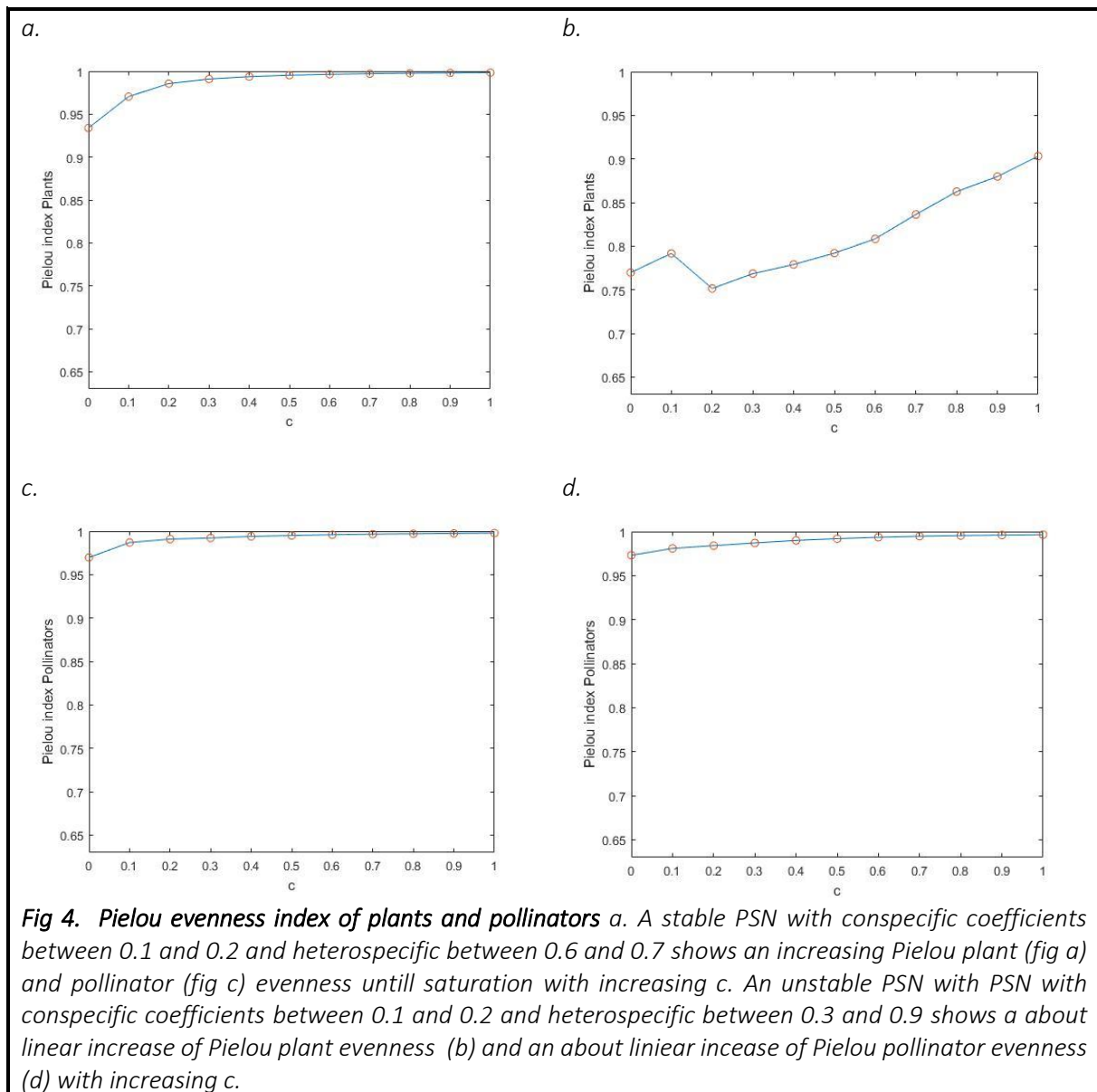
The higher the conversion factor (c), the faster the stable web goes to the equilibrium value (*fig. S4*). The plants of an unstable PSNs the plants do not always reach an equilibrium, at a low c ($c=0.1$ or $c=0$), even after >10.000 timesteps (not shown). The closer the initial values of plants are near the unstable equilibrium value of an unstable PSN, the longer it takes to get to regular cycling (*fig S1*). Parameter settings that do reach an equilibrium almost always do so before 1500 timesteps (not shown). In *fig. 2a,b,c&d* represent the frequencies and abundances after 1000 timesteps and are therefore not always necessarily an equilibrium.

Experiment A.2b calculates the Pielou evenness for plants and pollinators. Figure 4 shows the corresponding Pielou evenness values of analysis A2a (*fig. 3*). Pielou evenness of the plant frequencies, is affected by the conversion factor (c) but the effects are very small, except for the evenness of plants for an unstable PSN. When a PSN is stable, Pielou plant evenness increases until saturation with c (*fig. 4a*). If the PSN is unstable Pielou plant evenness increases 25% about linearly with increasing c (*fig. 4b.*).



Pielou evenness of the pollinators is also affected by the conversion factor (c) When a PSN is stable, Pielou evenness increases until saturation with increasing c (fig.4c). If the PSN is unstable Pielou pollinator evenness increases linearly with increasing c (fig. 4d). The effects on pollinator evenness are small.

A sensitivity analysis for $\alpha^{(A)}$ (analysis A2b) and $\gamma^{(P)}$ (analysis A2c) shows the same qualitative effect (compare fig 2a with fig S8a, S10a) for the plant frequencies as for c . Plant abundances converge to more even values with increasing $\alpha^{(A)}$ and $\gamma^{(P)}$. The abundances differ slightly because $h=0.1$ and not 0, thus the saturation functional response affects the $\gamma^{(P)}$ but not c . For the pollinators, the qualitative effect of c is the same as $\gamma^{(P)}$ but a lower growth rate of pollinators ($\alpha^{(A)}$) results in lower plant abundances (in contrast to plant abundances). Based on these results and the sensitivity analysis of $\gamma^{(A)}$ (analysis A2d, fig S5III) and $\beta^{(A)}$ (analysis A2e, fig S5IV), parameter settings for analysis A3 were chosen.



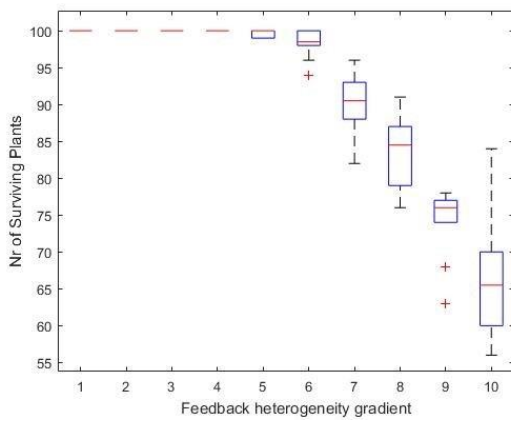
Effect of PSN heterogeneity on species richness of the plants (A.3a)

Plant species die out if the PSN is unstable and without the interaction with pollinators. However, when the plants interact with pollinators, the pollinators can balance the unstable PSN and the plant species survive. Not surprisingly though, the less unstable the PSN, the less plants will die out. Therefore, with an increasing heterospecific heterogeneity of PSN, fewer plants survive.

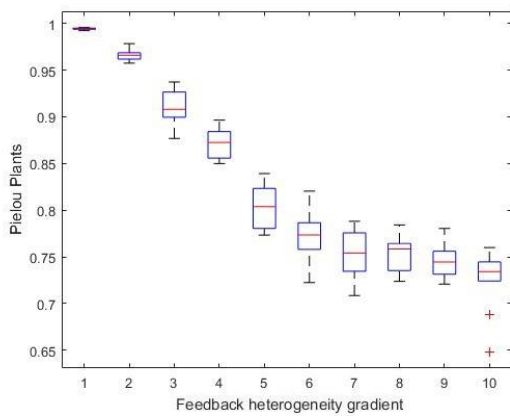
The results of analysis A3a are shown in figure 5. An increase of heterospecific heterogeneity results (fig. 5a) in lower plant species survival (at $c=0.2$). The boxplots at higher heterogeneity do not overlap with the boxplots at lower heterogeneity. The effect of heterospecific heterogeneity can therefore be considered a significant effect. Fig.5e shows that the average pairwise feedback for these samples does not change significantly with increasing heterogeneity (as in line with fig. 2h). The community feedback does not show a clear relation with decreasing heterogeneity for this small number of boxplots (fig. 3f, but see fig2i and S3).

The PMN that is used for these simulations is a random network (fig S2c) and has a very low nestedness. The plants are stabilized because they have an interaction with pollinators. The PMN thus does not need to be nested to stabilize the plants.

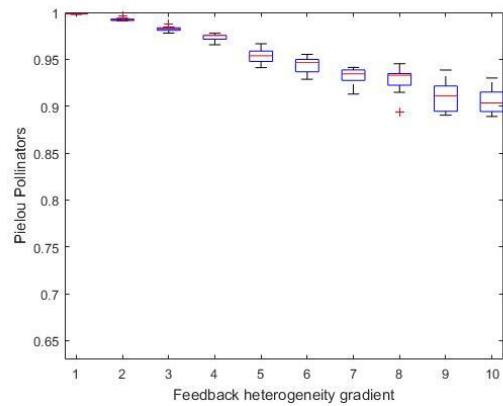
a.



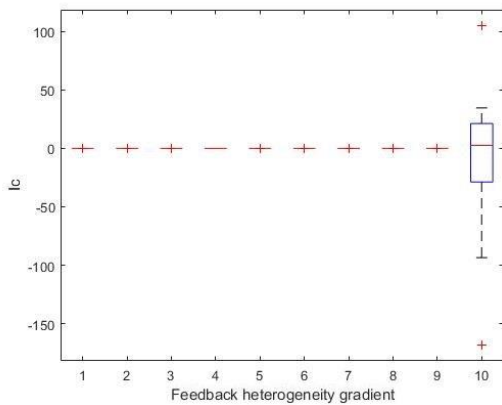
b.



c.



d.



e.

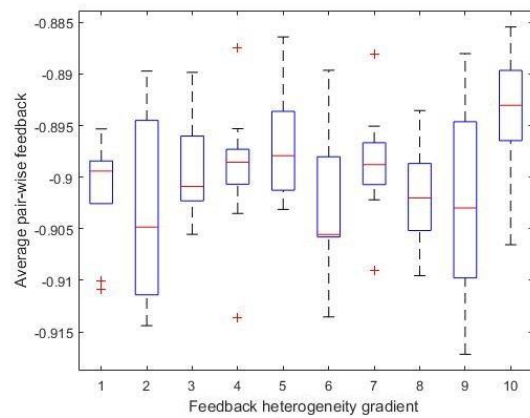


Fig 5. *Nr of surviving plants, Pielou evenness of plants and pollinators, community feedback and average pairwise feedback over a heterogeneity gradient* Boxplots with sample size 10 of the nr of surviving species for coefficient values of the points in fig 2d. of the 10 heterogeneity settings at $c=0.2$, following analysis A3a. The larger the heterospecific range the lower the number of surviving plant species (a.), plant (b.) and pollinator evenness (c.) The community feedback (d.) has a large standard deviation for high heterogeneity. Average pair-wise did not show a significant change (e.)

Effect of PSN heterogeneity on species richness of the pollinators (A.3a)

In experiment A3a, all abundances of pollinators are above zero, thus all 100 pollinators survive for all ranges of heterospecific feedback (*fig. 3c & fig. 3d*) when all the pollinator growth rates are equal and the mutualistic trade-off is present ($\delta = 1$)

Pollinator abundances are dependent on the PSN. In case the coefficients of σ are set to equal values and growth rates are set to equal values, all the abundances of pollinators become equal to each other (not shown). The unevenness of pollinator abundances is therefore fully determined by the PSN.

Pollinators can die out if parameters settings are changed ($\delta = 0$) to represent that the interaction strength is not dependent on the degree of a species. With this setting ($\delta = 0$), all plant species survive (not shown). However, there is no significant correlation of pollinator survival with a changing heterospecific range (not shown). Furthermore, the mutualistic trade-off has been observed (Burkle et al 2013, Dakos & Bascompte 2013) and thus a $\delta = 1$ is more likely to be in line with observations.

Effect of PSN heterogeneity on evenness of plant frequencies and pollinator abundances (A.3b)

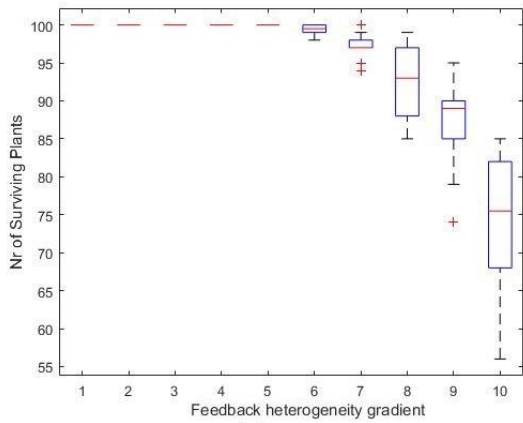
In experiment A3b, Pielou evenness of the plant frequencies, is affected by the heterogeneity of the PSN. If heterospecific range increases, Pielou plant evenness decreases about 25% at $c=0.2$ (*fig. 5b*).

Pielou evenness of the pollinators is also affected by the heterogeneity of the PSN. If heterospecific range increases, Pielou pollinator evenness decreases at $c=0.2$ (*fig. 5c*). The effect of heterogeneity is less strong on the pollinators than on the plants.

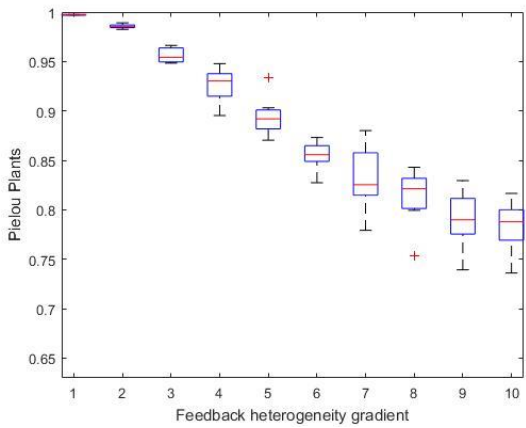
Effect of PMN nestedness on heterogeneity effects

In experiment A3e the results of experiment A3a&b were tested if they are affected by the nestedness of the PMN. Nestedness of the PMN does not affect the nr. of surviving plants, plant and pollinator Pielou evenness. There is no significant difference in nr. of plant species survival between the runs with and without a nested PMN (compare *fig. 6a* and *fig. 5a*). There is also no significant difference on in Pielou evenness of plants between runs with and without a nested PMN (compare *fig. 6b* with *fig. 5b*). Nestedness does affect pollinator evenness. The increasing heterogeneity of a nested network results in a higher standard deviation of pollinator evenness. This is different than the decreasing pollinator evenness with heterogeneity with a random PSN (Compare *fig. 6c* with *fig. 5c*).

a.



b.



c.

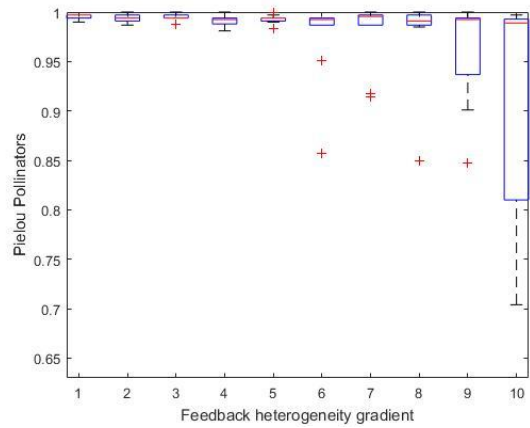


Fig 6. Effect of nested PMN on Plant survival, Pielou evenness index Plant and Pollinators All boxplots are with samplesize 10 for values of the points in fig 1d. of the 10 range settings at $c=0.2$, according analysis A3e. The nested PMN of figS2d was used. a. Boxplots of the nr of surviving species. The larger the heterospecific range the lower the number of surviving plant species. b. Boxplots of pielou plant evenness. The larger the heterospecific range the lower the plant evenness. c. Boxplots of pielou pollinator evenness. The larger the heterospecific range the lower the pollinator evenness.

Discussion

The study shows that plant richness will decrease if the plant-plant networks become increasingly unstable with changing climate (*fig.2 & 5a*). The increasingly unstable plant-plant networks might be partly stabilized by pollinator networks (*fig.3*). This might then pose a higher dependence of the plant-pollinator network on the pollinator network structure. Furthermore, plant and pollinator abundances will become less even (*fig.5b,c*), which might lead to a higher risk of extinction by other factors (Isbell et al 2008). Therefore, soil conservation and restoration will improve plant richness and might also improve pollinator richness.

Plant richness

The results of analysis A3 (*fig 5*) show that less plants survive at higher heterospecific heterogeneity. This means that with a changing climate, the species richness of plants will decline. A decline of species richness might lead to decreased carbon sequestration by the soil, loss of biodiversity of ecosystems and might also affect ecosystem stability (Cardinale 2012; Rockström et al. 2009). Furthermore, this decline of species richness can also have impacts on food security if agricultural crops are also affected (Klein et al. 2007; Cardinale 2012).

The results of the analysis A1 show that increased heterogeneity in heterospecific interaction coefficients decreases the plant richness of a PSN if they do not interact with pollinators. The first analysis (A1b) shows why heterospecific heterogeneity does affect plant richness and why conspecific heterogeneity does not. This is because conspecific heterogeneity does not affect the number of coexisting species but the heterospecific heterogeneity does. The second analysis (A2a) shows that a stronger effect of the PMN relative to PSN, increases plant survival. The lower plant survival with increasing heterogeneity in the MLM can be explained from the stability of the PSN.

To determine which type of feedback heterogeneity gradient would affect the stability of the PSN, analysis A1 was performed to determine the number of stably coexisting species over three combinations of gradients. The number of stably coexisting plants is a good indicator of PSN stability. Based on the results of *fig 2*, an increase of heterospecific heterogeneity was chosen for analysis A3. If heterospecific heterogeneity increases (*fig 1c*), the PSN becomes less stable resulting in smaller number of stably coexisting plants (*fig 2h*). The average pair-wise feedback is not affected (*fig 2i*). This gives an effect on number of surviving species and does not have an increased average pair-wise feedback standard deviation that only increases the influence of stochasticity in the initializations of the PSN and has no extra effect on number of surviving species. The conspecific heterogeneity (*fig 1a, fig 2a,b,c*) was not included in the analysis because this does not affect the number of stably coexisting species (*fig 2a*) but does increase stochasticity effects because of the increased standard deviation of the average pair-wise feedback (*fig 2b*). A stronger heterospecific heterogeneity means that the climate does affect the strength of the soil feedback effect of one plant species on another species. Neglecting the changes on the conspecific heterogeneity means that climate induced changes of the plant-soil feedback of a species on itself was not considered. The conspecific heterogeneity does not affect the stability of the PSN because if the conspecific coefficients are below the heterospecific, the value of the conspecific coefficient does not affect the structure of the PSN. All conspecific parameter values are chosen below the heterospecific parameter values. If conspecific values are higher than the heterospecific values, this would be more destabilizing but this is not in line with the field observations that show a stronger conspecific PSF than the heterospecific PSF (e.g. Comita et al. 2010; Johnson et al. 2012) and where therefore not considered.

The community feedback (I_c) did not give clear results for analysis A3 (*fig 5e*). In analysis A1 (*fig 2 c,f,i*) the community feedback shows a higher standard deviation at higher heterospecific heterogeneity for the stably coexisting communities (*fig 2i*). It seems that smaller stably coexisting PSNs have a more negative community feedback. A possible explanation is that by randomly adding a new species to a feasible community, the negative community feedback becomes less negative, moving towards zero. The community feedback, crosses zero when the species is added that makes the community unstable,

and the community feedback positive. At higher heterospecific heterogeneity the step size at which the negative community feedback decreases towards zero might be larger. This could then result in a stronger negative community feedback in the last feasible community before the addition of an extra species would make the community feedback positive. This result is not necessarily contradictory with the results of Eppinga et al (2017). In their results, the community feedback is not represented as a function of the feedback gradient. Rather, in their results, the community feedback is scaled to the number of surviving species ($-|I_c|^{1/(n-1)}$, figure S9f in Eppinga et al. 2017) and given as a function of average pair-wise feedback. There are two differences between Eppinga et al (2017) and the results of A1 that could also explain the results for the community feedback. In analysis A1, PSNs that were unstable but feasible were also included. This is because the stability of the resulting network was not calculated. However, the results of Eppinga et al (2017) could be reproduced for the number of stably coexisting species over average pair-wise feedback (S3), thus the number of unstable but feasible PSNs is very small. Furthermore, all the heterospecific coefficients have different values instead of row averages. This might affect the intransitive structure of the network, resulting in a different community feedback. Because the rest of the simulations (analysis A3) were started with the equal number of 100 plant species and non-stable networks were also included, I decided not to correct for number of stably coexisting species.

In the results of A1, the increased random heterospecific heterogeneity is destabilizing. At first this seems to be contradictory with the observation that intransitive structure can generate stability (Allesina & Levine 2012). However, the intransitive structure in the model is random. In real ecosystems, the intransitive structure might be arranged in such way that the intransitivity is stabilizing. If that is the case, the increased heterogeneity due to climate change reflects an increased disruption of the current intransitive structure.

To check if plants are dependent on pollinators for their survival the interaction strength of the effect of pollinators on plants was set to zero ($c=0$). This means plant growth is not limited by pollination because pollinator abundance is high. In the model, with these settings, a PSN with low heterogeneity is feasible (the number of stably coexisting species > 100), therefore all plant species survive (sample 1 in *fig 3a*). At high heterogeneity of the PSN, some species survive (sample 1 in *fig 3b*). This means that the PSNs that are used are not pollinator dependent when pollinator abundances are high. If the PSNs would be unfeasible at $c=0$, the PSN would be dependent on pollinators for feasibility and stability, even at high pollinator abundances. In real ecosystems, the plant populations become pollinator dependent when pollinator densities are low (Kaiser-Bunbury et al 2016). In that case, the total biomass of the pollinators is low compared to the total biomass of plants and the pollinators cannot pollinate all the plants. This could however not be studied with the MLM. Nevertheless, this limitation of the MLM does not affect the result that less plants survive at high heterogeneity.

Realistic values for the pollinator growth rates and the interaction strength are dependent on the relative strength of the effect of the PMN and the PSN (the parameter c). Because in real ecosystems plants only become pollinator dependent for their growth when pollinator abundances are very small (Kaiser-Bunbury et al 2016), it can be assumed that under normal conditions they are not pollinator dependent. Therefore, a growth rate, interaction strength or PSN/PMN ratio that represents dynamics that are not fully dominated by the pollinators (> 1) is realistic. Furthermore, half saturation time does not affect plants on the same time scale and can therefore be neglected. Therefore, the conversion factor that is chosen ($c=0.2$) can be considered representative.

The result that less plants survive at high heterogeneity in the MLM corresponds with the result that the number of stably coexisting species is lower at higher heterogeneity (*fig 2*). Heterogeneity negatively affects plant survival significantly even with pollinators interacting (*fig 2.c.*, $c=0.2$). This means that when climate change increases PSF heterogeneity, less plants will survive and go extinct. For the conversion factor ($c=0.2$) in analysis A3, both the PSF structure and the pollinators determine the number of surviving plants.

However, pollinators do decrease the negative effect of increased heterogeneity on plant survival. Higher growth rates of the pollinators ($\alpha^{(A)}$, *fig S5I*), higher interaction strength (*fig S5 II*) and a higher the pollinator dependence factor (*c, fig 2 a,b*) all decrease the negative effect on plant survival. This means that with the same growth rate, interaction strength and pollinator dependence factor, pollinators can sustain less plants when heterogeneity increases. Therefore, plant survival is only negatively affected by high heterogeneity if the number of initial species is higher than the number that can stably coexist and the growth rate of pollinators, the interaction strength or the pollinator dependence factor is low enough. This means species rich communities are more likely to be affected by climate induced heterogeneity of the PSF of the PSN. Furthermore, if pollinators grow too slow, their population will be too small to counterbalance the negative affect of the heterogeneity of the PSF. Also, if the positive affect of the pollinator on the plant, the interaction strength (parameter $\gamma^{(P)}$), is not strong enough, the pollinators will not counterbalance the negative affect. If growth rates of pollinators and the interaction strength stays the same, the increasing heterogeneity of the PSN can cross a threshold at which the plant can die out. This is shown for the conversion factor (*fig 2c*) but is also expected for the growth rate ($\alpha_i^{(A)}$) and interaction strength ($\gamma^{(P)}$) because the qualitative result of the sensitivity analysis is the same (*fig S5*). A more intuitive interpretation of an increase of the conversion factor would be an increase of the fitness of the plant population by an increased interaction strength.

There are also plant species that reproduce without pollinators (Kaiser-Bunbury et al. 2010). They are not considered in this study. However, they could affect the interaction of the plant-plant competition and plant-pollinator network. For example, species that don't need pollinators can be indirectly affected by the strength of pollinator interaction by their pollinator profiting competitors. These plants are likely to have a competitive advantage if pollinator abundances decrease because they are not dependent on pollinators but their competitors do.

Pollinator richness

There is no effect of heterogeneity on pollinator survival in the results. All pollinators survive in all the runs. Models (Saavedra et al 2013, Rohr et al 2014, Bastolla et al 2009) and observations (Kaiser-bunbury et al 2016) show that lower species richness of plants does affect pollinator richness. The contradicting result can be explained from the combination of settings that was chosen.

In the settings, the interaction strength was corrected for species degree (divided by k , so $d=1$). With this mutualistic trade-off, I followed Dakos & Bascompte (2014) because in real ecosystems this trade-off has been observed (Burkle et al 2013). Furthermore, in the MLM, the growth rates of the pollinators were assumed to be equal to each other ($\alpha_i^{(A)}=1$, for all the species). With these settings, pollinator dynamics are stabilizing. Therefore, nestedness does not affect the results of the number of surviving plants, but does affect the Pielou evenness of the pollinators (compare *fig 5 with fig 6*). This is because the abundance of pollinators is also affected by the nested PMN and not only by the PSN. The random PMN and the settings of the growth rates of pollinators were chosen because if the pollinator dynamics are stabilizing, all the destabilizing affects are caused by the PSN heterogeneity. The effects of the PSN are therefore not distorted by effects of the structure of the plant-pollinator network. Real ecosystems do have nested pollinator networks, that can be a stabilizing property of the PMN (Saavedra et al 2013). The PMN can be stable by the right combination of growth rates, initial values, interaction strength and interspecific competition. Because the stability of the PMN depends on many factors, it goes beyond this research to examine all these factors.

The main explanation that pollinators all survive in the model, but not in the observed ecosystems is that in the model all pollinator growth rates are kept equal. This affects the mutualistic trade-off and the saturation functional response. The mutualistic trade-off is not always present. The trade-off implies that if a plant species is pollinated by a pollinator that also pollinates other plant species is relatively less pollinated by this pollinator because it indirectly competes with the other plants that are pollinated by this species (Dakos & Bascompte, 2014). This generates a negative frequency dependent feedback. If

the density of plant species a is low, the high abundance of the pollinators is generated by the presence of the more abundant plant species b . Species a cannot sustain the pollinator population by itself but plant species a does profit from the high abundance of the pollinators. However, it is likely that if a field is full of one species of plants, and the others are rare, the chance of a pollinator pollinating this species is much higher. Therefore, if pollinator abundances are too low to pollinate all the plants, the interaction strength is no longer relative to the degree of the pollinator species.

This effect is normally accounted for by the saturation function (in equation 2 in the third term on the r.h.s), but because the plants are not calculated in abundances this response does not work. This functional response means that the abundance of the pollinator determines the speeds at which a pollinator pollinates with a plant. Because all the pollinators are calculated at the same time, this implies, 'who first comes, is served first'. This mechanism ensures plants to be pollinator depend at low pollinator abundances, but not at high abundances. This could not be accounted for in the model. Furthermore, this mechanism does not work because all growth rates are kept equal. This results in a negative frequency dependent feedback.

Because the pollinator survival can be explained from the setting of the model, it is not likely they represent the survival of pollinators in real ecosystems. Plant species richness is found to affect pollinator richness in other studies (Saavedra et al 2013, Rohr et al 2014, Bastolla et al 2009, Kaiser-Bunbury et al 2016)). Therefore, although not directly measured by the results, it is very likely that increased heterogeneity does also affect pollinator survival in real ecosystems because plant richness is affected.

Plant and pollinator evenness

Evenness of species populations describes if the populations in a community are relatively even or that some species dominate and other species are rare. If species are rare, they might have a higher risk of extinction (Isbell et al 2008). The evenness (Pielou index) of both plants and pollinators decreases with increasing heterogeneity of the PSN (*fig 5 b,c*). The evenness of plants and pollinators increases with the conversion factor (*fig 4 a,b,c&d*). This is because when the pollinators can switch resource and all pollinator growth rates are equal, all pollinator abundances would be equal if all plant competition coefficients are equal. Therefore, the higher the conversion factor, the closer plant evenness is to the maximum evenness ($Pielou=1$). The pollinator abundances are determined by the plants abundances and are therefore more even when plant frequencies are more even. The effect on plant evenness for a stable PSN is very small, and can be considered not a significant increase. However, the increase of evenness of plants with increasing conversion factor is much larger for an unstable PSN (*fig 4b*). The evenness increase for pollinators is smaller for both an unstable (*fig 4c*) and stable PSN (*fig 4d*) because the unevenness is determined by the PSN heterogeneity. The effect of increasing PSN heterogeneity on plant evenness (*fig 5b*) is a strong and significant negative effect. The larger the heterogeneity, the less even plant frequencies are. Pollinator abundances also become less even with increasing heterogeneity (*fig 5c*) but the effect is less strong than for plants (compare *fig.5b* and *fig.5c*). This is also because the PSN determines pollinator abundances. This difference could probably be smaller if pollinators and plants have on average less possible connections (a smaller network degree) was considered (not tested). Plant and pollinator evenness are also affected by increasing PSN heterogeneity when the decreased heterogeneity does not yet cause the plants to die out (compare the first 5 boxplots of *fig. 5a* with *fig. 5b* and *fig. 5c*). The effect of heterogeneity on plant and pollinator evenness is therefore independent of the number of surviving species.

Recommendations for further research

Although the conclusions are valid, further research can further investigate the effect on pollinator richness. This can be done by adding structure to the pollinator growth rates, nestedness of the PMN and the network degree of the PMN.

In the MLM the plant biomass is unknown and plants are calculated in frequencies. The model therefore produces counterintuitive results that are hard to match to the ecological processes. Therefore, it would be helpful for the interpretation of the results to calculate plants also as abundances. This could be done by plugging the frequency dependent competition network into the plant abundances calculation of Saavedra et al. (2013). To ensure the negative frequency dependence, a carrying capacity term needs to be added. This would make the pollinator dependence of plants on pollinators dependent on the abundance of pollinators (by means of the saturation function). In that case, only at low pollinator densities, plants are dependent on pollinators and is not forced by a factor c but is an emergent property of the model. At high pollinator abundances, the plant relative abundances will be determined by the PSN. A higher interaction strength might generate higher productivity. This is consistent with the observation that plants in real ecosystems become pollinator dependent when pollinator densities are low (Kaiser-Bunbury et al 2016).

Furthermore, this new model can also take into account the effect of pollinators on plant richness, that have died out because of changes in the heterogeneity. In the current MLM, the effect was only one way. So, if pollinators die out, they did not affect plant abundances because pollinator average abundances were artificially kept high because plants were calculated as abundances.

A second recommendation would be combining the model of Eppinga et al (2017) and Allensina & Levine (2012). Recent studies show that there is an eco-evolutionary feedback between plants and the soil (Bardgett & van der Putten, 2014). Some plant species adapt faster because of changes in the soil community. For example, more drought resistant species were selected by this eco-evolutionary feedback (Bardgett & van der Putten, 2014). A combination of a plant-plant network with plant-soil feedback and a plant-plant competitive network might detect how small changes in soil composition could lead to shifts in the structure of the intransitive competitive network. Such shifts to alternative stable states could then explain how soil organism enhances for example the competitive advantage of a drought resistant species.

Moreover, this new type of multi-layer modelling might give new insights for further application. Although there is recent evidence that ecological and evolutionary time scales interact (Zupping-Dingley 2014; Tilman 2014; Johansson et al. 2015; Dieckmann & Ferrière 2004) this is could not be modelled with a differential equation model so far. For now, it is only possible to model this with computational heavy individually based (Falster 2015) or physically based models (Falster 2016). There is a need for new types of models (Berger et al. 2008; Grimm & Berger 2016; Fitzpatrick & Keller 2015; Philofof). In current (mutualistic) network models, it is not possible to add adaptation because the interaction strength is static. Multilayer modelling with dynamic interaction strength might bridge the gap between these types of modelling. This would make it possible to study eco-evo dynamics in future studies.

To study the effects of intransitivities in a model more insight in the intransitive structure is needed. A model by Neutel & Thorne (2016b) gives, like the community feedback, another measure for calculating a condition for the stability of the system. Like the community feedback, this condition is a necessary but not sufficient. Further research might show if and how this condition can be converted to be applied to the plant-plant networks. Because the coefficients of σ represent effects on growth rates and not on abundances (as it is in Neutel & Thorne 2016b), the measure cannot be applied directly. If the measure can be converted, it can be tested if this condition covers the same networks as the community feedback or if this measure is a complementing condition.

A third recommendation would be to adjust the MLM for mycorrhizal networks instead of pollinator networks. This is possible because they are both mutualistic networks. Based on the results, mutualistic networks can generate negative frequency dependent feedback if the interaction strength is relative to the degree of a species (k). Further can determine or this is the case for mycorrhizal networks. A possible

candidate for a functional response, that causes the interaction strength not always to be dependent on the degree of species, could be the size of the surface of the roots. I propose that the growth of mycorrhiza and ribosomal herbivores are limited by the available space on the roots of plants. Fungi are a good candidate to start with, because they are the main drivers of decomposition. (Bardgett & van der Putten, 2014).

A way forward from there, would be splitting the PSN in direct plant-plant competition, a plant-soil food web and a mycorrhizal nested network. A better model could give better predictions of mycorrhizal productivity and thereby improve predictions of carbon sequestration. If a stronger plant-soil feedback generates a higher turnover rate a diverse developed ecosystem with stronger plant-soil feedback might sequester more carbon.

The theoretical framework of the MLM shows it is very important to know how exactly the PSN will change under future climate. It remains unsure whether changes of the mycorrhizal networks due to climate change enhances heterogeneity as represented in the model. It might be that specialists or generalist respond differently and thereby not enhance PSN heterogeneity. This could be measured more exact on real networks of mycorrhiza and their response to climate change in an experimental setting.

Conclusion

The study shows that plant richness will decrease if the plant-plant networks become increasingly unstable with changing climate. The increasingly unstable plant-plant networks might be partly stabilized by pollinator networks. This might then pose a higher dependence of the plant-pollinator network on the pollinator network structure. Furthermore, plant and pollinator abundances will become less even, which might lead to a higher risk of extinction by other factors. Therefore, soil conservation and restoration will improve plant richness and might also improve pollinator richness.

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References

- Alcántara, J. M., & Rey, P. J. (2012). Linking topological structure and dynamics in ecological networks. *The American Naturalist*, *180*(2), 186-199.
- Allesina, S., & Levine, J. M. (2011). A competitive network theory of species diversity. *Proceedings of the National Academy of Sciences*, *108*(14), 5638-5642.
- Allesina, S., & Tang, S. (2012). Stability criteria for complex ecosystems. *Nature*, *483*(7388), 205-208.
- Bardgett, R. D., & van der Putten, W. H. (2014). Belowground biodiversity and ecosystem functioning. *Nature*, *515*(7528), 505-511.
- Barnes, D. K. A., & Neutel, A. M. (2016). Severity of seabed spatial competition decreases towards the poles. *Current Biology*, *26*(8), R317-R318.
- Bascompte, J. (2009). Disentangling the web of life. *Science*, *325*(5939), 416.
- Bascompte, J., Aizen, M., Fontaine, C., Fortuna, M. A., Jordano, P., Lewinsohn, T. M., ... & Thompson, J. N. (2010). Symposium 6: mutualistic networks. *The Bulletin of the Ecological Society of America*, *91*(3), 367-370.
- Bascompte, J., Jordano, P., & Olesen, J. M. (2006). Asymmetric coevolutionary networks facilitate biodiversity maintenance. *Science*, *312*(5772), 431-433.
- Bascompte, J., Jordano, P., Melián, C. J., & Olesen, J. M. (2003). The nested assembly of plant–animal mutualistic networks. *Proceedings of the National Academy of Sciences*, *100*(16), 9383-9387.
- Bastolla, U., Fortuna, M. A., Pascual-García, A., Ferrera, A., Luque, B., & Bascompte, J. (2009). The architecture of mutualistic networks minimizes competition and increases biodiversity. *Nature*, *458*(7241), 1018-1020.
- Berger, U., Piou, C., Schiffers, K., & Grimm, V. (2008). Competition among plants: concepts, individual-based modelling approaches, and a proposal for a future research strategy. *Perspectives in Plant Ecology, Evolution and Systematics*, *9*(3), 121-135.
- Bever, J. D. (2003). Soil community feedback and the coexistence of competitors: conceptual frameworks and empirical tests. *New Phytologist*, *157*(3), 465-473.
- Burkle, L.A., Marlin, J.C. & Knight, T.M. (2013). Plant-pollinator interactions over 120 years: Loss of species, co-occurrence and function. *Science*, *339*, 1611–1615.
- Cardinale, B. J., Duffy, J. E., Gonzalez, A., Hooper, D. U., Perrings, C., Venail, P., ... & Kinzig, A. P. (2012). Biodiversity loss and its impact on humanity. *Nature*, *486*(7401), 59-67.
- Comita, L. S., Muller-Landau, H. C., Aguilar, S., & Hubbell, S. P. (2010). Asymmetric density dependence shapes species abundances in a tropical tree community. *Science*, *329*(5989), 330-332.
- Dakos, V., & Bascompte, J. (2014). Critical slowing down as early warning for the onset of collapse in mutualistic communities. *Proceedings of the National Academy of Sciences*, *111*(49), 17546-17551.
- Dieckmann, U., & Ferrière, R. (2004). Adaptive dynamics and evolving biodiversity. *Evolutionary conservation biology*, 188-224.

- Eppinga, M.B., Baudena, M., Johnson, D.J., Jiang, J., Keenan, M.L., Mack, E.S., Strands & Bever, D. (2017). Frequency-dependent feedback and plant community coexistence. *unpublished*.
- Falster, D. S., Brännström, Å., Westoby, M., & Dieckmann, U. (2015). Multi-trait eco-evolutionary dynamics explain niche diversity and evolved neutrality in forests. *BioRxiv*, 014605.
- Falster, D. S., FitzJohn, R. G., Brännström, Å., Dieckmann, U., & Westoby, M. (2016). plant: A package for modelling forest trait ecology and evolution. *Methods in Ecology and Evolution*, 7(2), 136-146.
- Fitzpatrick, M. C., & Keller, S. R. (2015). Ecological genomics meets community-level modelling of biodiversity: mapping the genomic landscape of current and future environmental adaptation. *Ecology Letters*, 18(1), 1-16.
- Fontaine, C., Guimarães, P. R., Kéfi, S., Loeuille, N., Memmott, J., van Der Putten, W. H., ... & Thébaud, E. (2011). The ecological and evolutionary implications of merging different types of networks. *Ecology Letters*, 14(11), 1170-1181.
- Gao, J., Barzel, B., & Barabási, A. L. (2016). Universal resilience patterns in complex networks. *Nature*, 530(7590), 307-312.
- Gilarranz, L. J., Hastings, A., & Bascompte, J. (2015). Inferring topology from dynamics in spatial networks. *Theoretical ecology*, 8(1), 15-21.
- Grimm, V., & Berger, U. (2016). Structural realism, emergence, and predictions in next-generation ecological modelling: Synthesis from a special issue. *Ecological Modelling*, 326, 177-187.
- Henry, M., Beguin, M., Requier, F., Rollin, O., Odoux, J. F., Aupinel, P., ... & Decourtye, A. (2012). A common pesticide decreases foraging success and survival in honey bees. *Science*, 336(6079), 348-350.
- Isbell, F. I., Losure, D. A., Yurkonis, K. A., & Wilsey, B. J. (2008). Diversity–productivity relationships in two ecologically realistic rarity–extinction scenarios. *Oikos*, 117(7), 996-1005.
- Johansson, J., Kristensen, N. P., Nilsson, J. Å., & Jonzén, N. (2015). The eco-evolutionary consequences of interspecific phenological asynchrony—a theoretical perspective. *Oikos*, 124(1), 102-112.
- Johnson, D. J., Beaulieu, W. T., Bever, J. D., & Clay, K. (2012). Conspecific negative density dependence and forest diversity. *Science*, 336(6083), 904-907.
- Jonhson, S., Domínguez-García, V., & Muñoz, M. A. (2013). Factors determining nestedness in complex networks. *PloS one*, 8(9), e74025.
- Kaiser-Bunbury, C. N., Memmott, J., & Müller, C. B. (2009). Community structure of pollination webs of Mauritian heathland habitats. *Perspectives in Plant Ecology, Evolution and Systematics*, 11(4), 241-254.
- Kaiser-Bunbury, C. N., Muff, S., Memmott, J., Müller, C. B., & Caflisch, A. (2010). The robustness of pollination networks to the loss of species and interactions: a quantitative approach incorporating pollinator behaviour. *Ecology Letters*, 13(4), 442-452.
- Kéfi, S., Berlow, E. L., Wieters, E. A., Joppa, L. N., Wood, S. A., Brose, U., & Navarrete, S. A. (2015). Network structure beyond food webs: mapping non-trophic and trophic interactions on Chilean rocky shores. *Ecology*, 96(1), 291-303.
- Klein, A. M., Vaissiere, B. E., Cane, J. H., Steffan-Dewenter, I., Cunningham, S. A., Kremen, C., & Tscharntke, T. (2007). Importance of pollinators in changing landscapes for world crops. *Proceedings of the Royal Society of London B: Biological Sciences*, 274(1608), 303-313.

- Lever, J. J., Nes, E. H., Scheffer, M., & Bascompte, J. (2014). The sudden collapse of pollinator communities. *Ecology letters*, *17*(3), 350-359.
- Mangan, S. A., Schnitzer, S. A., Herre, E. A., Mack, K. M., Valencia, M. C., Sanchez, E. I., & Bever, J. D. (2010). Negative plant-soil feedback predicts tree-species relative abundance in a tropical forest. *Nature*, *466*(7307), 752-755.
- May, R. M. (1972). Will a large complex system be stable?. *Nature*, *238*, 413-414.
- Mazzoleni, S., Bonanomi, G., Incerti, G., Chiusano, M. L., Termolino, P., Mingo, A., ... & Lanzotti, V. (2015). Inhibitory and toxic effects of extracellular self-DNA in litter: a mechanism for negative plant–soil feedbacks? *New Phytologist*, *205*(3), 1195-1210.
- Mazzoleni, S., Cartenì, F., Bonanomi, G., Senatore, M., Termolino, P., Giannino, F., ... & Chiusano, M. L. (2015). Inhibitory effects of extracellular self-DNA: a general biological process? *New Phytologist*, *206*(1), 127-132.
- Medan, D., Perazzo, R. P., Devoto, M., Burgos, E., Zimmermann, M. G., Ceva, H., & Delbue, A. M. (2007). Analysis and assembling of network structure in mutualistic systems. *Journal of theoretical biology*, *246*(3), 510-521.
- Memmott, J., Craze, P. G., Waser, N. M., & Price, M. V. (2007). Global warming and the disruption of plant–pollinator interactions. *Ecology letters*, *10*(8), 710-717.
- Nahum, J. R., Harding, B. N., & Kerr, B. (2011). Evolution of restraint in a structured rock–paper–scissors community. *Proceedings of the National Academy of Sciences*, *108*(Supplement 2), 10831-10838.
- Neutel, A. M., & Thorne, M. A. (2014). Interaction strengths in balanced carbon cycles and the absence of a relation between ecosystem complexity and stability. *Ecology letters*, *17*(6), 651-661.
- Neutel, A. M., & Thorne, M. A. (2016b). Beyond connectedness: why pairwise metrics cannot capture community stability. *Ecology and Evolution*, *6*(20), 7199-7206.
- Neutel, A. M., Heesterbeek, J. A., & de Ruiter, P. C. (2002). Stability in real food webs: weak links in long loops. *Science*, *296*(5570), 1120-1123.
- Neutel, A. M., Michael, A., & Thorne, S. (2016a). Linking saturation, stability and sustainability in food webs with observed equilibrium structure. *Theoretical Ecology*, *9*(1), 73.
- Ollerton, J., Winfree, R., & Tarrant, S. (2011). How many flowering plants are pollinated by animals?. *Oikos*, *120*(3), 321-326.
- Pielou, E. C. (1966). Species-diversity and pattern-diversity in the study of ecological succession. *Journal of theoretical biology*, *10*(2), 370-383.
- Pilosof, S., Porter, M.A., Pascual, M., & Kéfi, S. (2016). The multilayer nature of ecological networks. *arXiv preprint arXiv:1511.04453*. v2
- Potts, S. G., Biesmeijer, J. C., Kremen, C., Neumann, P., Schweiger, O., & Kunin, W. E. (2010). Global pollinator declines: trends, impacts and drivers. *Trends in ecology & evolution*, *25*(6), 345-353.
- Rafferty, N. E., CaraDonna, P. J., & Bronstein, J. L. (2015). Phenological shifts and the fate of mutualisms. *Oikos*, *124*(1), 14-21.
- Rockström, J., Steffen, W., Noone, K., Persson, Å., Chapin, F. S., Lambin, E. F., ... & Nykvist, B. (2009). A safe operating space for humanity. *Nature*, *461*(7263), 472-475.

Rohr, R. P., Saavedra, S., & Bascompte, J. (2014). On the structural stability of mutualistic systems. *Science*, 345(6195), 1253497.

Saavedra, S., Rohr, R. P., Dakos, V., & Bascompte, J. (2013). Estimating the tolerance of species to the effects of global environmental change. *Nature communications*, 4.

Saavedra, S., Rohr, R. P., Olesen, J. M., & Bascompte, J. (2016). Nested species interactions promote feasibility over stability during the assembly of a pollinator community. *Ecology and Evolution*.

Suweis, S., Grilli, J., Banavar, J. R., Allesina, S., & Maritan, A. (2015). Effect of localization on the stability of mutualistic ecological networks. *Nature communications*, 6.

Thébault, E., & Fontaine, C. (2010). Stability of ecological communities and the architecture of mutualistic and trophic networks. *Science*, 329(5993), 853-856.

Tilman, D., & Snell-Rood, E. C. (2014). Ecology: Diversity breeds complementarity. *Nature*, 515(7525), 44-45.

Zuppinge-Dingley, D., Schmid, B., Petermann, J. S., Yadav, V., De Deyn, G. B., & Flynn, D. F. (2014). Selection for niche differentiation in plant communities increases biodiversity effects. *Nature*, 515(7525), 108-111.

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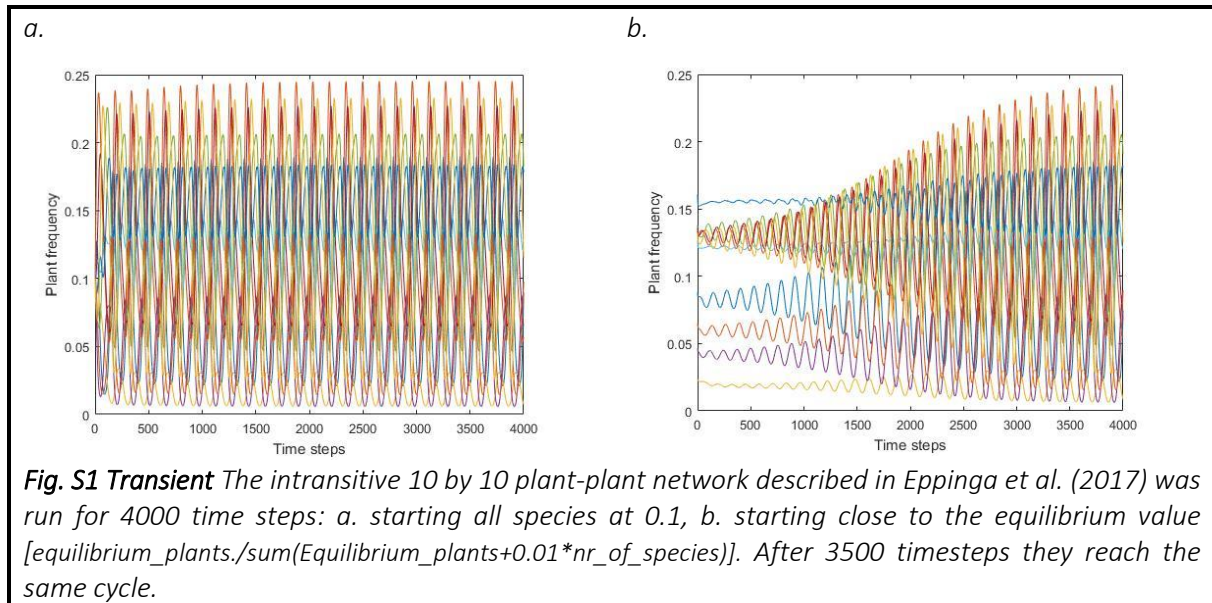
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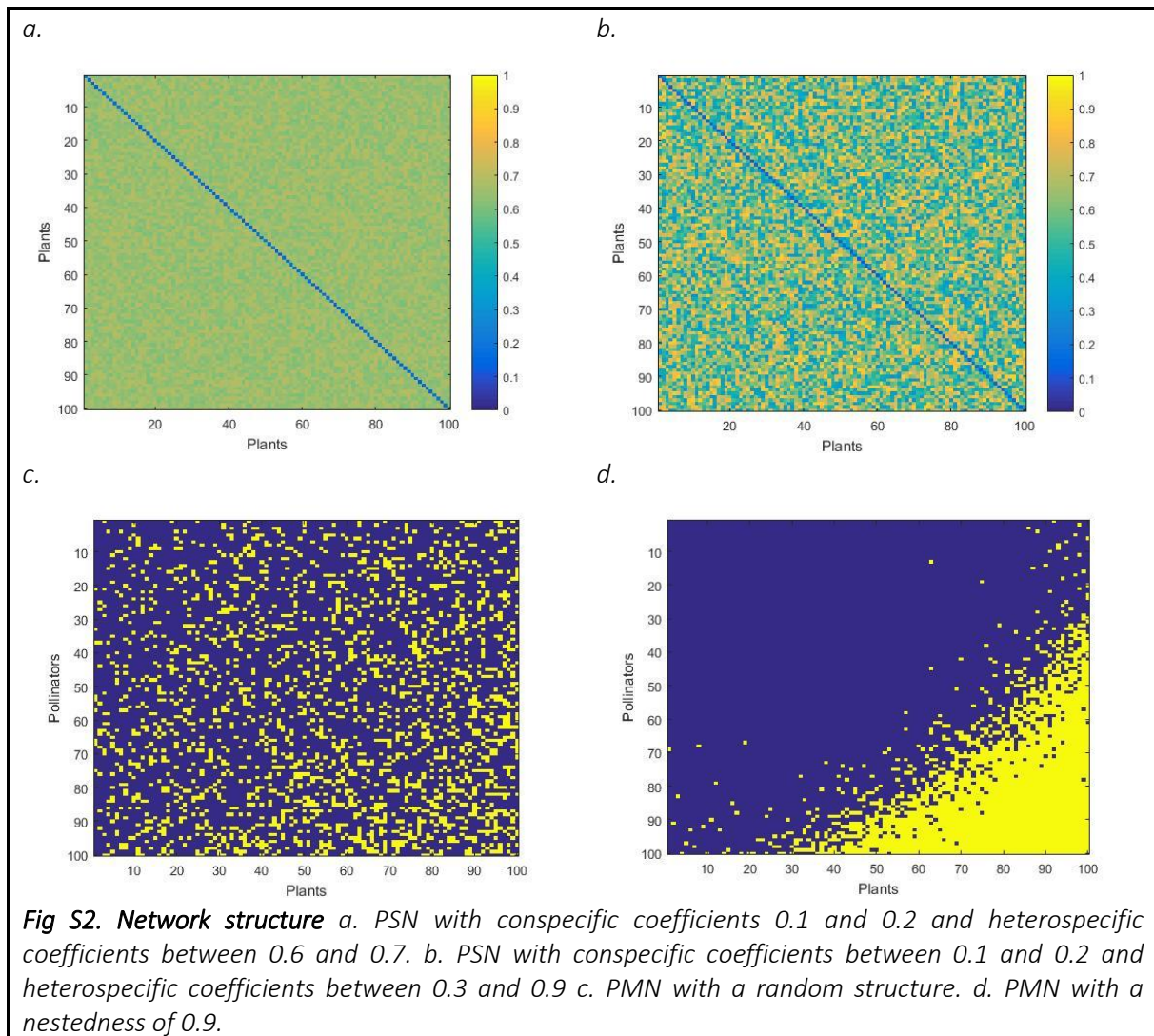
Appendix

S1 Unstable network and transient

An unstable plant-plant network goes to the same cycle, independent of the initial values, except when started exactly at the unstable equilibrium values. The closer the systems starts to the equilibrium values, the longer it takes to go to the stable cycles.



S2 Networks for analysis A2

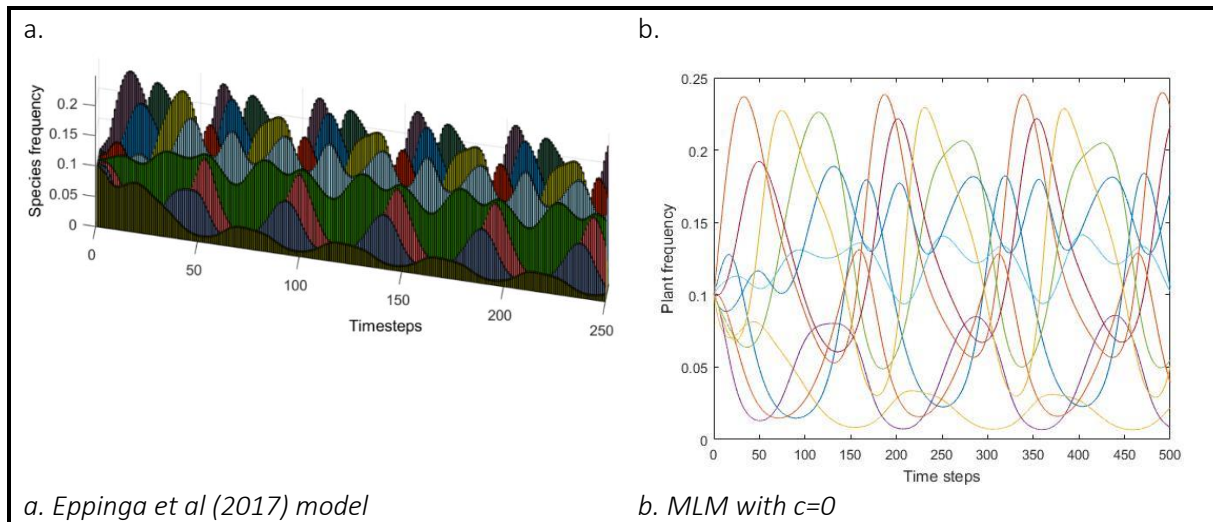


S3 Reproducing models Eppinga et al.(2017) And Saavedra et al (2013)

Reproducing Saavedra et al

The model itself works, but it was not possible to test with a PSN because the model needs to calculate a growth rate for the plants and a $\gamma^{(P)}$ depended on the plant-plant network.

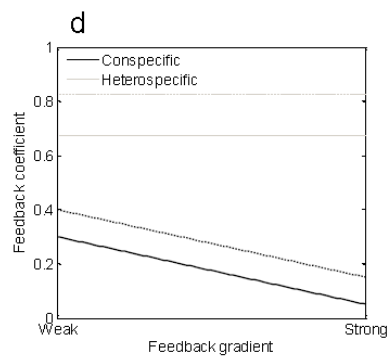
Reproducing Eppinga et al



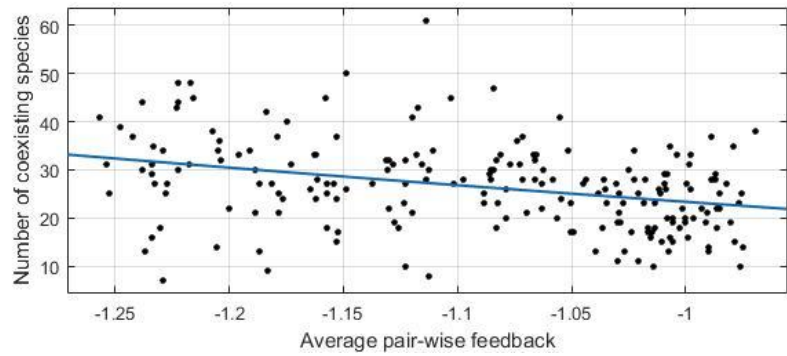
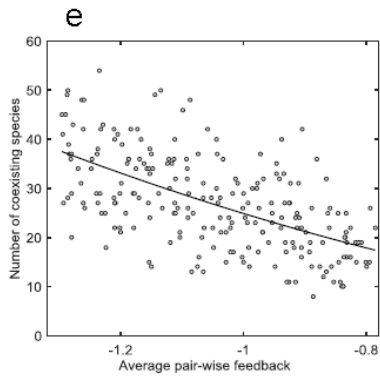
These graphs show the frequencies of plants for an unstable plant-plant network of ten species given Eppinga et al. (2017) The shape and values of the curves and the timing relative to each other is the same. The only difference is the apparent speed of the oscillations, caused by a different size of the chosen timesteps.

Comparing Number of coexisting species versus Average pair-wise feedback

Method: adding species



Feedback gradient of conspecific



Linear model Poly1:

$$f(x) = p1*x + p2$$

Coefficients (with 95% confidence bounds):

$$p1 = -36.17 \text{ } (-50.28, -22.06)$$

$$p2 = -12.9 \text{ } (-28.34, 2.536)$$

Goodness of fit:

SSE: 1.433e+04

R-square: 0.1138

Adjusted R-square: 0.1094

RMSE: 8.487

General model:

$$f(x) = a*x^2+b*x$$

Coefficients (with 95% confidence bounds):

$$a = 10.12 \text{ } (-2.546, 22.79)$$

$$b = -13.24 \text{ } (-27.27, 0.7832)$$

Goodness of fit:

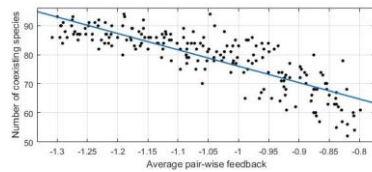
SSE: 1.435e+04

R-square: 0.1128

Adjusted R-square: 0.1083

RMSE: 8.492

method 2 adding species with 50 tries for adding a new species



Linear fit

Linear model Poly1:

$$f(x) = p1*x + p2$$

Coefficients (with 95% confidence bounds):

$$p1 = -56.45 \text{ } (-61.66, -51.25)$$

$$p2 = 19.58 \text{ } (14.04, 25.11)$$

Goodness of fit:

SSE: 5743

R-square: 0.6967

Adjusted R-square: 0.6951

RMSE: 5.372

General model:

$$f(x) = a*x^2+(b*x)$$

Coefficients (with 95% confidence bounds):

$$a = -19.65 \text{ } (-24.55, -14.75)$$

$$b = -96.16 \text{ } (-101.6, -90.77)$$

Goodness of fit:

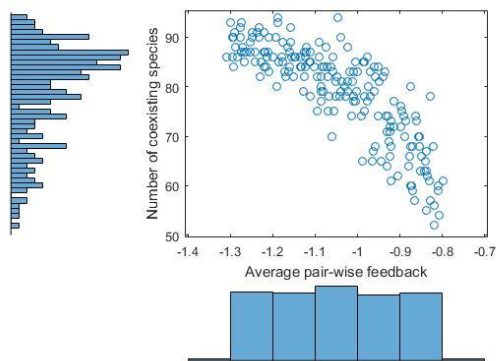
SSE: 5437

R-square: 0.7128

Adjusted R-square: 0.7114

RMSE: 5.227

Tail distribution number of coexisting species



This histogram shows the frequencies of the average pair-wise feedback and number of coexisting species. There is a tail distribution for the nr. of coexisting species with a peak of high frequencies between 80 and 90 species of coexisting species.

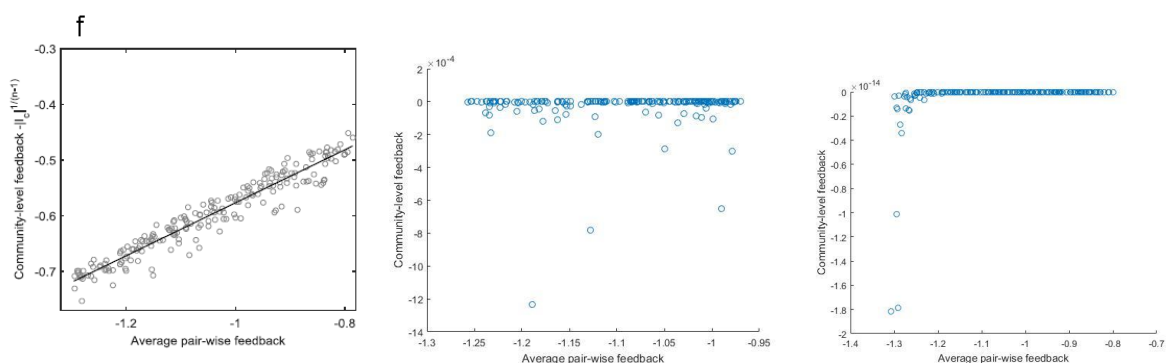
Range size conspecifics

With a small conspecific range the network average pair-wise feedback splits in groups.

Heterospecific range: 0.5-0.7 Conspecific range 0.01-0.01

Comparing Community level feedback versus Average pair-wise feedback

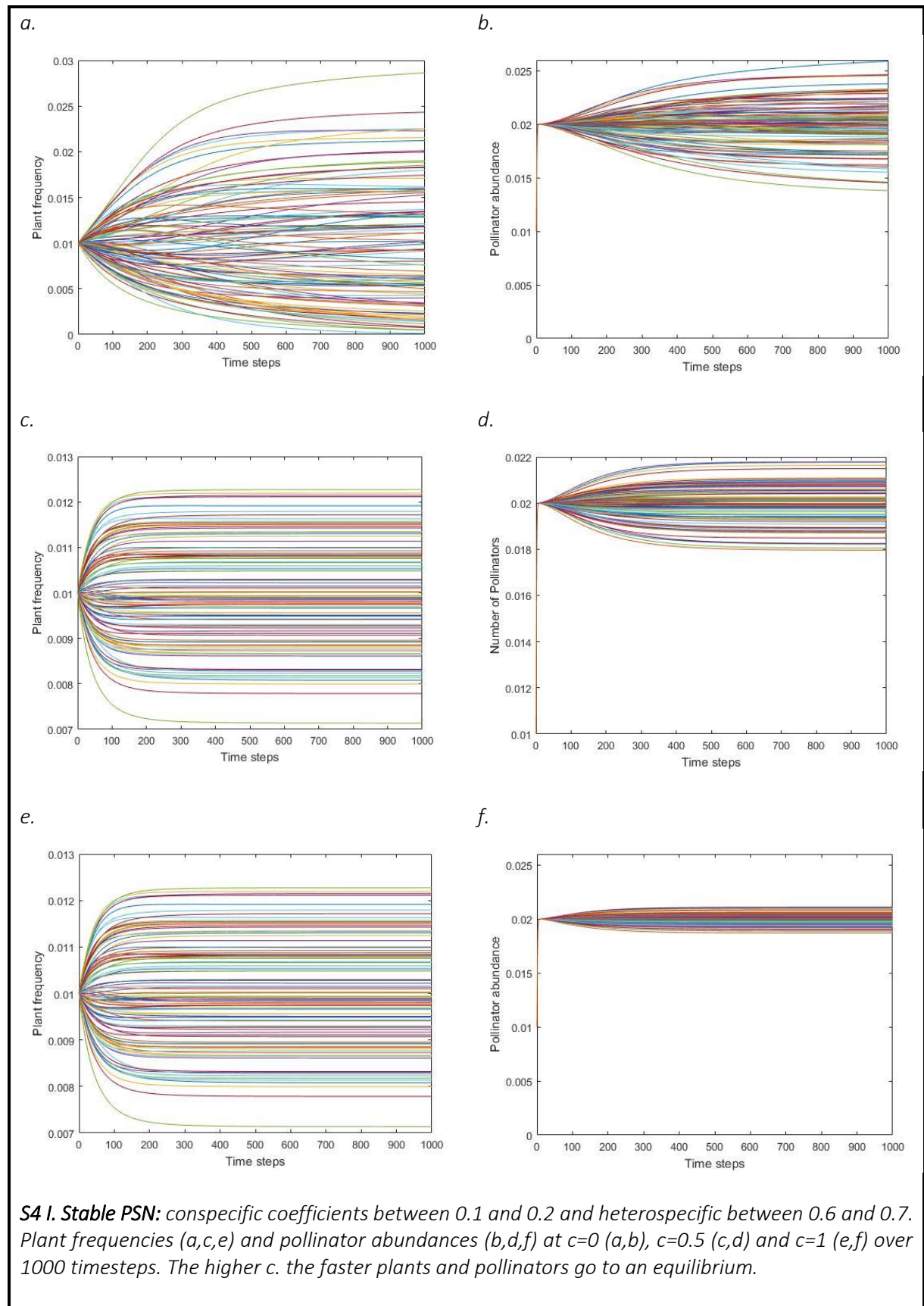
Without a correction for nr of species ($-|I_c|^{1/(n-1)}$, see S7a) there is no correlation between I_c and average pair-wise feedback when using the assembly method. At the highest possible nr of species for a given parameter setting I_c becomes close to zero (order of magnitude 10^{-14}). When adding a new species I_c becomes negative. This becomes even more clear when using the 2nd method. When using several tries for finding an extra species that would be possible to add because the random effect of choosing a species that does not fit while there are species left that do fit becomes much smaller. The correlation of S7a is due to the strong correlation between Average pair-wise feedback and nr of coexisting species (See S3 & S4).



S7 a: Figure of Epping et al. Community level feedback adjusted for nr. of species with: $-|I_c|^{1/(n-1)}$

b: Method 1: Adding species until 1 species would make the plant-plant network unstable. c: Method 2: Adding species with several tries for adding a new species.

S4 Time plots



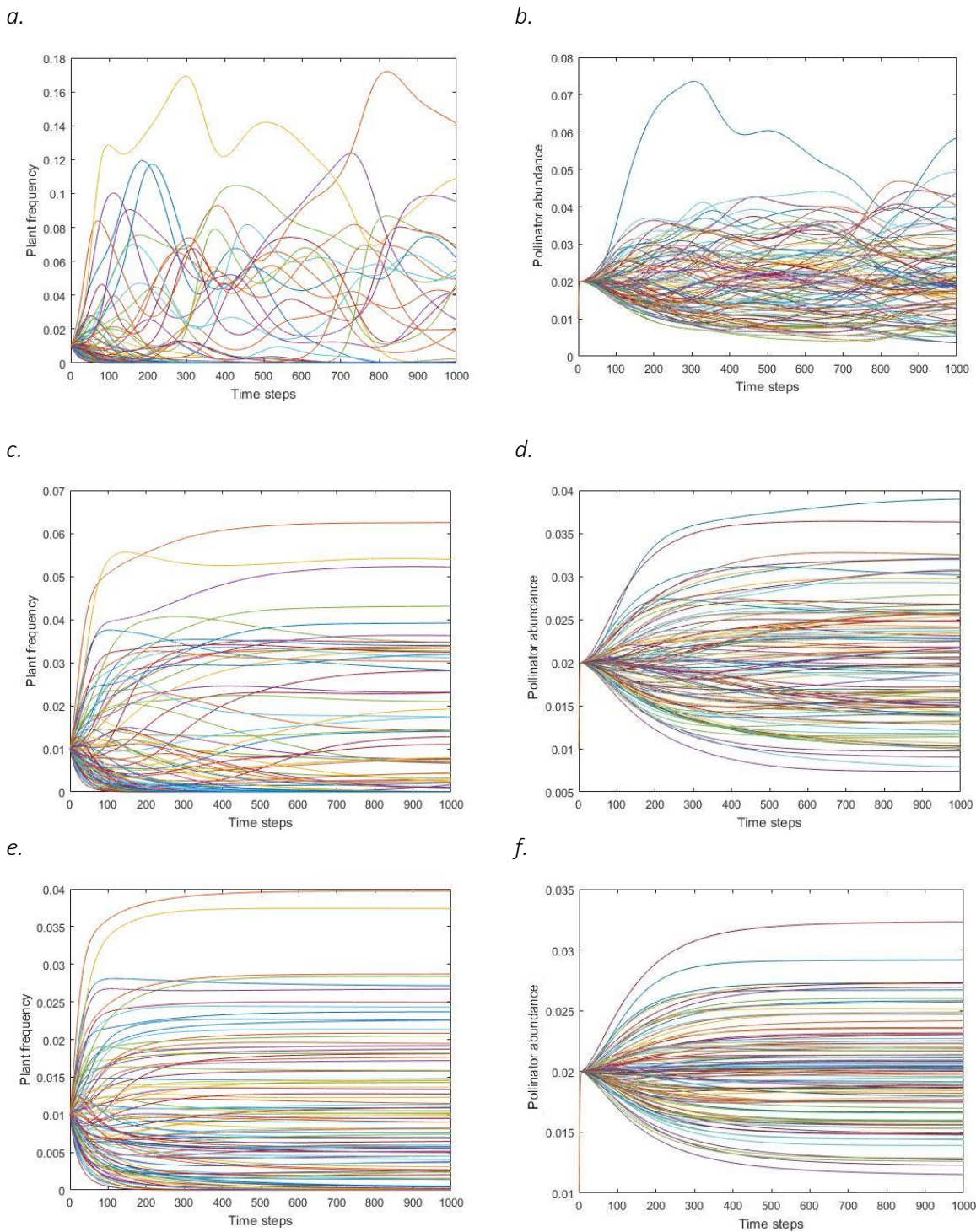
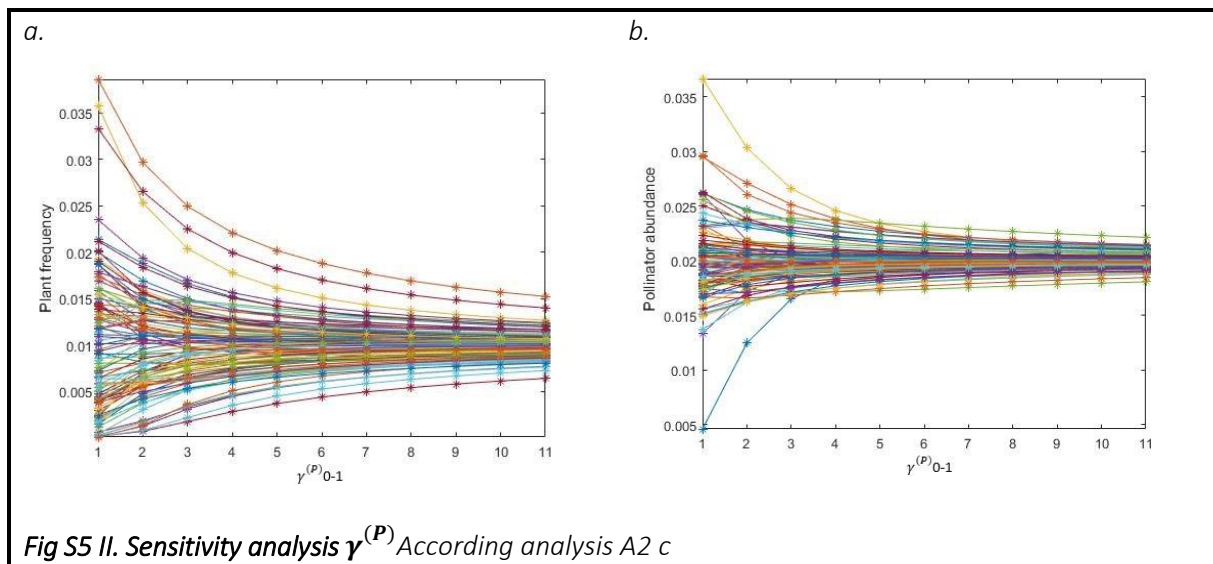
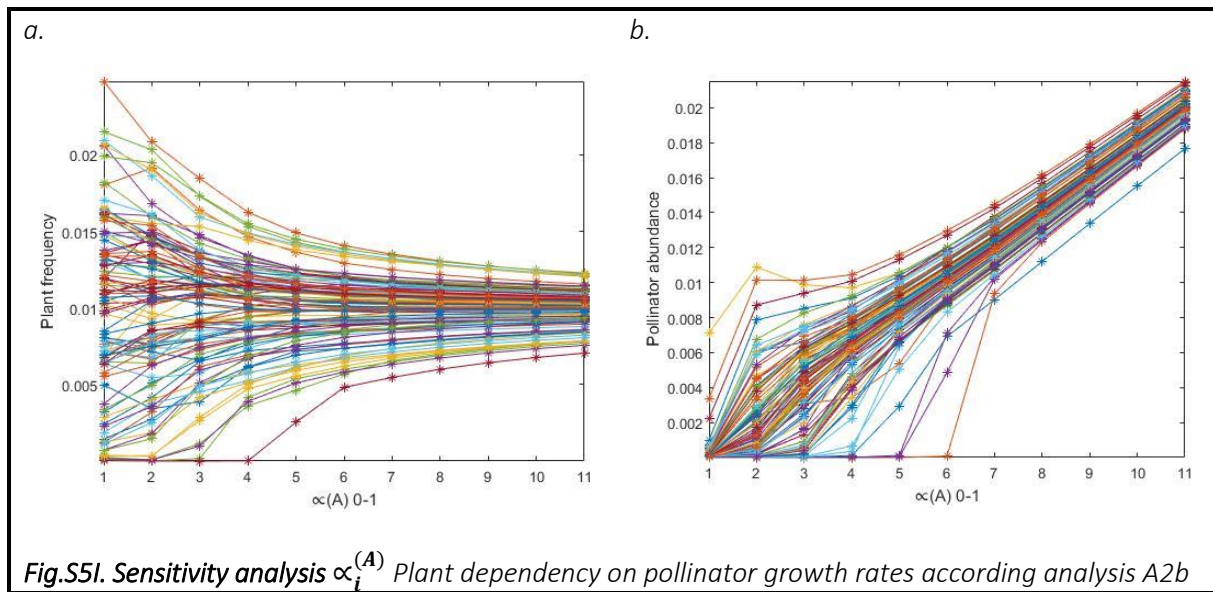
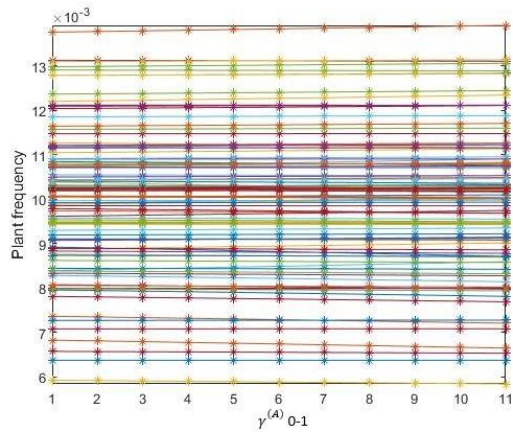


Fig. S4 II. Unstable PSN: conspecific coefficients between 0.1 and 0.2 and heterospecific between 0.3 and 0.9. Plant frequencies (a,c,e) and pollinator abundances (b,d,f) at $c=0$ (a,b), $c=0.5$ (c,d) and $c=1$ (e,f) over 1000 timesteps. The higher c , the faster plants and pollinators go to an equilibrium.

S5 Sensitivity analyses



a.



b.

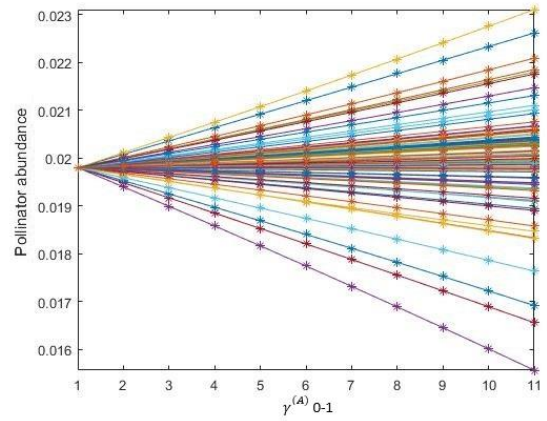
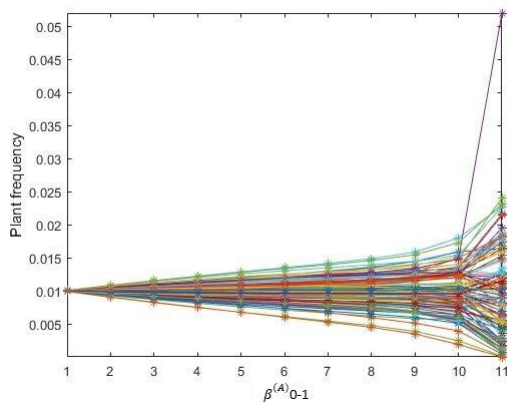


Fig S5 III Sensitivity analysis $\gamma^{(A)}$ According analysis A2d

a.



b.

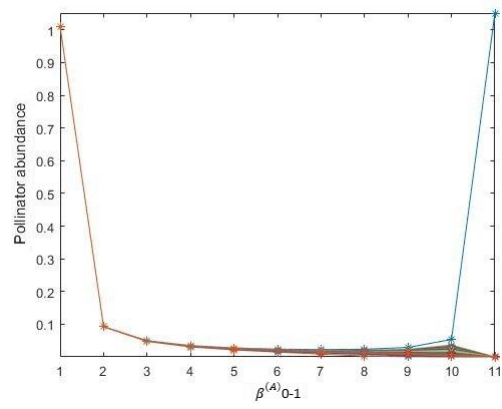


Fig S5 IV Sensitivity analysis $\beta^{(A)}$ According analysis A2e

