Time-dependent Interaction Modification Generated from Plant-soil Feedback

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Abstract

Pairwise interactions between species can be modified by other community members, leading to emergent dynamics that are contingent on the composition of a community. Despite the prevalence of such higher-order interactions, little is known about how they are linked to the timing and order of species' arrival. Yet, these temporal patterns typically affect their pairwise interactions (i.e., priority effects) and thus could also modify higher-order interactions in multispecies communities. Here, we first develop a general framework of time-dependent interaction modifications by building on pairwise priority effects. By applying this framework to data generated by a mechanistic plant-soil feedback model, we show that how pairwise interactions are modified by a third plant depends on the relative sequence and spacing of plants' germination phenology. This time-dependence of interaction modifications emerges from concurrent changes in plant and microbe populations and they become stronger with a higher overlap between plants' associated microbiomes. We discuss how processes in the plant-soil feedback model represent a wide range of mechanisms applicable in other systems from which similar time-dependent interaction modifications can emerge. Our results highlight the need to integrate temporal shifts of species interactions to predict the emergent dynamics of natural communities.

Introduction

A key challenge in predicting the dynamics of complex ecological communities is the potential for higher-order interactions to occur (Levine *et al.* 2017). Higher-order interactions are common among ecosystems and arise when the presence of a third species affects the interactions between two species (Billick & Case 1994; Werner & Peacor 2003; Wootton 1994). However, when exploring higher-order interactions, ecologists have traditionally overlooked the temporal dimension of community structure. Recent studies indicate that outcomes of pairwise interactions strongly depend on the relative timing of species' life history events, i.e., phenology (Fukami 2015; Rudolf 2019; Zou & Rudolf 2023a). In a multispecies community, a pairwise interaction can, therefore, be affected by the presence of other species and the timing of all constituents. Yet, recent advances in modeling higher-order interactions do not consider the temporal changes in interaction strengths (Kleinhesselink *et al.* 2022; Lai *et al.* 2022; Letten & Stouffer 2019; Mayfield & Stouffer 2017), and theory studying the effects of variation in arrival sequence still focuses on pairwise interactions (Song *et al.* 2020; Zou & Rudolf 2023b) despite numerous experiments conducted in multispecies communities (Dickie *et al.* 2012; Drake 1991; Pu & Jiang 2015; Song *et al.* 2021b; Uricchio *et al.* 2019). As species-rich communities in nature face widespread reshuffling in phenology and timing of interactions (Kharouba *et al.* 2018; Parmesan 2006), we need a general framework for higher-order interactions that includes this temporal dimension of community structure.

In pairwise systems, the shift in species interactions and community states with changes in species arrival times is well described by the framework of priority effects. Documented in systems from microbes and plants to crustaceans and amphibians (Blackford *et al.* 2020; Fragata *et al.* 2022; Grainger *et al.* 2019; Rudolf 2018; Shorrocks & Bingley 1994), priority effects are

generated by either positive frequency dependence or temporal changes in species traits (Zou & Rudolf 2023a). For example, early-colonizing bacteria may grow to higher abundance and exclude late arrivers (Grainger *et al.* 2019), and plants can be affected by the chemical composition or microbiomes in soil previously occupied by other species (Kardol *et al.* 2007). Because these changes in relative abundances or traits are not instantaneous but develop over time, the relative arrival time between two species directly modifies their interaction strengths. Similarly, in multispecies systems, how a third species affects a pairwise interaction (interaction modification) can depend on its arrival time, which can change its density, traits, or both, and that of other community members. For instance, increasing the coverage of barnacles decreases bird predation of limpets in intertidal communities (Wootton 1993). If the coverage (*density*) of barnacles depends on the length they colonized the patch before limpets arrive, then this change in coverage over time could lead to a temporal change in the strength of interaction modification. In an aquatic predator-prey system, morphological changes of snails induced by the presence of a first predator increased its risk towards a second predator (Hoverman & Relyea 2008). Because changes in morphological *traits* are not instantaneous, the length of the acclimation period with the first predator could affect the amount of increased predation risk. These temporal changes in interaction modification are the higher-order equivalent of priority effects, and we term them "time-dependent interaction modification." This term includes all forms of higher-order interactions that can change with species' arrival times.

In plant communities, such time-dependent interaction modification could arise from plant-soil feedback. Early-arriving plants modify the soil environment, e.g. via allelopathy, changes in the microbiome, and litter addition from previous residents, which reduces the fitness of the later arriving plant (Inderjit & van der Putten 2010; van der Putten *et al.* 2016; Suding & Goldberg

1999). However, the strength of the plant-soil feedback often depends on how long the plant conditions the soil (Ke *et al.* 2021; Lepinay *et al.* 2018). Furthermore, plant-plant interactions can also be mediated by soil microbiome cultivated by a third species arriving before them (Zhang *et al.* 2020). These studies indicate the potential of time-dependent interaction modification in plant communities, but this relationship is still unknown.

To fill this conceptual gap, we explore how time-dependent interaction modifications can arise in nature in a community with plant-soil feedback. We first mathematically define time-dependent interaction modifications. Then, we apply this framework to data generated by a mechanistic plant-soil feedback model that focuses on the interaction between plants and their microbiomes to reveal the relationship between the temporal structure of communities and their higher-order interactions.

Methods

Time-Dependent Interaction Modification

Here, we first present the mathematical definition of time-dependent interaction modification using a three-species community that assembles over time (Figure 1A). Consider a system where the change in density (*N*) of a species between time steps can be characterized by a pairwise Ricker model:

$$\frac{N_i(t+1)}{N_i(t)} = \lambda_i \exp\left(-\alpha_{ii}N_i(t) - \alpha_{ij}N_j(t) - \alpha_{ik}N_k(t)\right) \text{ (Eqn. 1)},$$

where λ_i is the intrinsic growth rate of species i, and α_{ij} is the per-capita effect from species j to i. In a pairwise system with priority effects (Figure 1B), the per-capita interaction from species j to i can depend on the difference between their arrival times (phenology) within a year, $p_j - p_i$, i.e., their phenological difference Δp_{ij} (Rudolf 2019; Zou & Rudolf 2023a) (Figure 1B):

$$\alpha_{ij} = f_{ij}(\mathrm{p_i}, \mathrm{p_j}) = f_{ij}(\Delta p_{ij}) \text{ (Eqn. 2).}$$

Higher-order interactions in this three-species system can be modeled by the following variant of the Ricker model (Kleinhesselink *et al.* 2022):

$$\frac{N_i(t+1)}{N_i(t)} = \lambda_\mathrm{i} \exp\left(-\alpha_{ii}N_i(t) - \alpha_\mathrm{ij}\mathrm{N_j(t)} - \alpha_\mathrm{ik}\mathrm{N_k(t)} - \beta_{i(jk)}N_j(t)N_k(t)\right) \text{ (Eqn. 3),}$$

where $\beta_{i(jk)}$ quantifies the strength of the higher order interaction (HOI), i.e., how densities of species j and k modify each other's effect on species i non-additively (Letten & Stouffer 2019). For simplicity, we only consider one HOI coefficient here. If phenological differences between species can affect the strengths of both pairwise and higher-order interactions by changing the corresponding per-capita coefficients (Figure 1C), Eqn. 3 can be written as:

$$\frac{N_i(t+1)}{N_i(t)} = \lambda_i\, exp\left(-\alpha_{ii}N_i(t) - \mathrm{f_{ij}}(\Delta\mathrm{p_{ij}})\mathrm{N_j(t)} - \mathrm{f_{ik}}(\Delta\mathrm{p_{ik}})\mathrm{N_k(t)} - f_{i(jk)}{}'(p_j, p_k)N_j(t)N_k(t)\right)$$

$$\text{(Eqn. 4),}$$

where $f_{i(jk)}{}'(p_j, p_k)$ defines how the HOI coefficient, $\beta_{i(jk)}$, depends on the phenology of both species j and k. If we consider species i and j as the "focal pair" and fix their phenology while shifting species k's phenology, then $f_{ij}(\Delta p_{ij})$ and p_j become constants, and $\beta_{i(jk)}$ only depends on p_k. We maintain this assumption to simplify our analyses of three-species communities.

To detect time-dependent interaction modification, we compare $\beta_{i(jk)}$ values fitted from population dynamics with different phenology of species k (p_k). If interaction modifications are absent, $\beta_{i(jk)}$ should be close to 0; if $\beta_{i(jk)}$ is nonzero but constant for all p_k, then the interaction modification does not depend on time. This definition does not consider time-dependent interaction modification via temporal changes in species density, which is beyond our scope. Alternatively, one can quantify time-dependent interaction modifications by fitting pairwise models between focal species i and j with and without species k, then examine how the

difference of the two pairwise interaction coefficients change with the phenology of species k (p_k). Under this definition, the time-dependent interaction modification combines the effects of both the density and phenology of species k. This approach is mathematically linked to the definition outlined in Eqn. 3-4 (Appendix II). In practice, it simplifies the experimental design but carries stronger assumptions on the community with and without the third species k. We discuss these pros and cons in Appendix II, but focus here on the first approach (Eqn. 3-4) to facilitate direct comparison to previous studies (Kleinhesselink *et al.* 2022; Letten & Stouffer 2019). In both approaches, the interpretation of fitted higher-order interactions depends on the specific system and its biological processes, and the statistical power of the phenomenological model structure (Kleinhesselink *et al.* 2022; Letten & Stouffer 2019).

Plant-soil Feedback Model

We simulate population dynamics of annual plants using a mechanistic, discrete-time model of plant-soil feedback to explore how time-dependent interaction modifications can arise in natural communities. Each year has T time steps. We use τ to represent each specific time step within the year, and each plant species germinates at a specific time step $\tau = p_i$. Note that a "year" defines the suitable growing season for plants and microbiomes, which may be a few months per calendar year. After germination, each plant cultivates its associated microbiome which affects mortality rates of all plants (Bever *et al.* 1997). Here, we focus on the role of soil pathogens only and assume that microbiomes increase the mortality within the year in addition to a baseline density-dependent mortality, although our methods can be readily extended to mutualistic and mixed microbiomes. To highlight the effect of plant-soil feedback, we assume that all interspecific interactions are mediated by changes in microbiomes (Figure 2A) rather

than resource competition, which represents a natural scenario where each species is limited by different resources (Tilman 1982). At the end of their life cycles, plants reproduce and senesce, and their dormant seeds germinate in the next year without additional mortality. All plants finish their life cycles within a year, regardless of their germination phenology. We assume that life cycles of all plants have identical lengths of l time steps. This implies that the plant germinating earliest will also reproduce and senesce earliest in the year.

Within the life cycles, the mortality of plant x depends on its density ($\mathrm{N_x}(\tau)$) and the accumulated effects from all microbiomes ($\sum_{\mathrm{y}} \mathrm{m_{xy}}\, \mathrm{S_y}$; Suding *et al.* 2013), where $\mathrm{d_x}$ is the mortality rate, and $\mathrm{m_{xy}}$ denotes the effect of microbiome associated with plant y on plant x (Eqn. 5). At the end of their life cycle, plants produce seeds with fecundity λ_{x} (Eqn. 6). For plants,

$$\mathrm{N_x}(\tau+1) = \mathrm{N_x}(\tau)\left(1 - \mathrm{d_x}\mathrm{N_x}(\tau) + \sum_{\mathrm{y}} \mathrm{m_{xy}}\, \mathrm{S_y}(\tau)\right) \text{ when } \tau < l \text{ (Eqn. 5);}$$

$$\mathrm{N_x}(\tau+1) = \lambda_{\mathrm{x}}\mathrm{N_x}(\tau) \text{ when } \tau = l \text{ (Eqn. 6).}$$

Within the year, the population of microbiomes ($\mathrm{S_x}(\tau)$) increases proportionally with plant density at the rate $\mathrm{v_{xy}N_y}$ once the plants emerge, where $\mathrm{v_{xy}}$ is the rate of cultivation by plant y, and is limited by a density-dependent mortality $\mu_{\mathrm{x}}\mathrm{S_x}(\tau)$ (Eqn. 7). This models the natural decay of the microbiome after the removal of the host plant (Esch & Kobe 2021). We assume a constant proportion (μ_{year}) of each microbiome does not carry over to the next year (Eqn. 8). For microbiomes,

$$S_x(\tau+1) = S_x(\tau)\left(1 + \sum_y v_{xy}\, N_y(\tau) - \mu_x S_x(\tau)\right) \text{ when } \tau < T \text{ (Eqn. 7);}$$

$$\mathrm{S_x}(\tau+1) = \left(1 - \mu_{\mathrm{year}}\right)\mathrm{S_x}(\tau) \text{ when } \tau = T \text{ (Eqn. 8).}$$

In nature, plants can share pathogenic or mutualistic microbes (Crawford *et al.* 2019; Gilbert & Webb 2007; Sedio & Ostling 2013; Spear & Broders 2021), which can be cultivated by

multiple plants in the same community. We simulate this "interspecific cultivation" by allowing for the plant x to cultivate not only its associated microbiome but also those associated with other plants ($\mathrm{v_{yx}} \neq 0$ for all $x \neq y$). Empirically, interspecific cultivation may range from absent (no interspecific cultivation, meaning that the microbiome is specific to each plant species) to strong (microbiomes of plants greatly overlap; Figure 2A). We assume each plant's total capacity of cultivation ($V_x = v_{xx} + \sum_y v_{yx}$ for all $x \neq y$) is constant, reflecting a finite pool of resources plants can provide to microbiomes. To simulate different levels of shared microbiomes among plants, we partition each plant's cultivation rate to simulate three scenarios: no overlap ($\sum_y v_{yx} = 0V_x$), low overlap ($\sum_y v_{yx} = 0.2V_x$), and high overlap in microbiomes ($\sum_y v_{yx} = 0.8V_x$). The strength of interspecific cultivation is equally split between microbiomes associated with other plants and therefore depends on the number of plant species.

Simulation and Detection of Time-dependent Interaction Modification

We specify that the length of plant life cycles (l) is shorter than the length of the year (T). In our simulations, we use $T = 12$ and $l = 6$; therefore, the earliest germination phenology is 1 (the beginning of the year), and the latest 6. This range ensures enough time for species interaction while allowing for a proper gradient of phenological differences between plants. We first run the model for 50 years (600 time steps) to examine long-term community dynamics; the duration ensures that all populations reach equilibrium. We choose identical fecundity λ and effects of microbiomes m_{xy} (Table 1) for all plants, such that any differences in population dynamics would arise from phenological differences between plant species and different overlaps of microbiomes. We further test the robustness of our results by drawing the total capacity of cultivation V and m_{xy} from a uniform distribution (Table 1).

To obtain interaction coefficients, we used a response surface design (commonly used in empirical studies; Inouye 2001; Kleinhesselink *et al*. 2022) with 6 densities of each plant species, yielding 36 and 216 combinations of initial densities for two-plant and three-plant communities, respectively. We ran all response surface simulations for one year, representing the typical duration of plant experiments (increasing the duration does not qualitatively change our results; Appendix I). We then repeated each set of simulations along a phenological gradient. In two-plant communities, we set population of plant k and its microbiome to 0 and simulated population dynamics of this two-plant community with a gradient of 11 phenological differences from $\Delta p_{ij} = p_j - p_i = -5$ (species j early by 5 time steps) to $\Delta p_{ij} = 5$ (species i early by 5 time steps). In three-plant communities, when a third plant is added to the focal pair, it could arrive either before (scenario I), between (scenario II), or after the focal species pair (scenario III; Figure 3). For simplicity, we examined scenarios I and III by fixing the phenology of the focal pair (i and j) both at the latest (time 6; scenario I) or at the earliest (time 1; scenario III) and changed the phenology of the third plant p_k ranging from 1 to 6. Note that this allows all plants to germinate simultaneously in some cases. To explore the case where plant k germinates between the focal pair, we let plant i arrive at the earliest (time 1) and j at the latest (time 6) and again let $1 \leq p_k \leq 6$.

To quantify interaction modifications, we fitted a discrete-time Ricker model containing all higher-order interaction terms to plant population at the end of the year (i.e., seeds):

$$\frac{N_i(t+1)}{N_i(t)} = \lambda_i \exp\Big(-\alpha_{ii}N_i(t) - \alpha_{ij}N_j(t) - \alpha_{ik}N_k(t) - \beta_{i(ij)}N_{i(t)}N_{j(t)} - \beta_{i(ik)}N_i(t)N_k(t) - \beta_{i(jk)}N_j(t)N_k(t)\Big) \text{ (Eqn. 9).}$$

The Ricker model structure fits our simulated data best among several other discrete-time population models (Hart *et al.* 2018) based on Akaike Information Criterion (AIC; results not

shown). To evaluate whether a model with higher-order coefficients indeed significantly improves model performance, we fitted three-plant population dynamics to pairwise Ricker models (Eqn. 1) with either plants i or j as the focal species, then compared both the root-mean-squared error (RMSE) and the AIC values of the pairwise (Eqn. 1) and higher-order Ricker model (Eqn. 9) at different p_k. Finally, to test the sensitivity to model parameters, we randomly drew 100 sets of feedback rate (m) and cultivation rate (V) from a uniform distribution that ensures a finite, positive plant population after the first year (Table 1), and fitted Eqn. 9 to obtain a distribution of higher-order coefficients.

We conducted all simulations in R 4.2.1 (R Core Team 2022) and fitted models using the function *nlsLM()* in the R package *minpack.lm* (Elzhov *et al.* 2016). The code is available at github.com/hengxingzou/Zou2023bioRXiv.

Results

Two-plant Communities

We first examine two-plant communities to analyze causes and consequences of priority effects. Under otherwise equal parameterization, the late arriving plant always has a lower population, and this disadvantage is smaller with an overlap of microbiomes between plants (Figure 2B). With no overlap in the microbiomes across plants, the density of the microbiome associated with the early plant grows faster and reaches a higher maximum within a year because the plant does not divert its resources to other microbiomes, but it also declines faster because after its host senesces, it cannot be cultivated by the later arriving plant (Figure 2B). With overlap in microbiomes, the fixed total capacity of cultivation reduces growth rates of the plant's primary microbiome, leading to a smaller peak density of the early arriver's microbiome, but a

higher density of the late arriver's microbiome (Figure 2B). Together, these temporal dynamics lead to approximately the same densities of microbiomes with different levels of overlap. When the overlap in the microbiome is less than 50% (i.e., $0 \leq v_{ji} < v_{ii}$), the microbiome associated with the early plant reaches higher density; the reverse is true when $v_{ji} > v_{ii}$ because the early plant now cultivates the late plant's microbiome more (Figure 2B). Population dynamics of plants and microbiomes are quantitatively different with different v_{ii} and v_{ji} values (Figure S1A).

The fitted interaction coefficients between the early and the late plants correspond to these observations: the effect of the early plant on the late plant increases when it germinates earlier. Changes of α_{ij} and α_{ji} with differences in germination phenology Δp_{ij} for both plants are symmetrical (Figure 2C) and correspond to nonlinear shapes observed in empirical studies (Blackford *et al*. 2020; Rudolf 2018; Shorrocks & Bingley 1994). Note that when one plant arrives very late ($|\Delta p_{ij}| \geq 4$), its effect on the early plant is negligible because the temporal overlap between the two plants is too short, and the effect it experiences from the early plant slightly decreases because the early plant's microbiome declines without its host. Despite these shared patterns, interactions are generally weaker without overlap in microbiomes because the late plant experiences less feedback from the early plant's microbiome compared to scenarios with higher overlap in the microbiomes within the first year (Figure 2B). Interaction-phenology functions with small and large overlaps are the same because population dynamics of plants are identical in this scenario but can be quantitatively different with alternative v_{ii} and v_{ji} values (Figure S1B).

Three-plant Communities: Population Dynamics

We examine patterns of equilibrium population density following three scenarios of plant phenology (plant k germinates before, between, or after the focal pair; Figure 3). The equilibrium population density of plants was contingent on the relative arrival time of all species. In general, the earlier a plant germinates relative to its competitors, the higher its equilibrium population (Figure 3). However, when all three species arrive at different times (scenario II), both the earliest and the last arriving species benefit from delaying the arrival of the intermediate species, while only the intermediated species itself is negatively affected. This alternating pattern indicates a time-dependent interaction chain, which can be explained by concurrent changes in densities of plants and microbiomes. When plant k arrives later than plant i (scenario II), plant i experiences lower total microbiome densities and reaches a higher equilibrium population. Because plant k arrives later it has also less time to cultivate its microbiome. This combination of reduced density and cultivation time of the intermediate arriving plant (k) results in a decline in total density of the microbiome, which benefits the last arriving plant j (Figure S2). All above patterns are consistent across different levels of overlap in microbiomes, but larger overlaps (higher inter- vs. intraspecific cultivation) lead to higher equilibrium populations because plants with earlier phenology devote less in cultivating their microbiomes, leading to a slower increase of microbiomes before the late plants germinate and subsequently a lower overall density of microbiomes. (Figure S2, S3).

Time-Dependent Interaction Modifications

We examine patterns of time-dependent interaction modifications using the higher-order coefficient associated with densities of all three plants ($\beta_{i(jk)}$ for plant i, $\beta_{j(ik)}$ for plant j, and $\beta_{k(ij)}$ for plant k) following the same scenarios of plant phenology (Figure 4). In general, all

higher-order interaction coefficients depend on the phenology of plant k, and the plant that germinates first experiences the weakest higher-order interaction. However, the specific pattern and magnitude of higher-order interactions also depend on the level of overlap in associated microbiomes (Figure 4). When plant k germinates before both plants i and j (scenario I), earlier germination phenology of plant k decreases the strengths of higher-order interactions experienced by late arriving plants i and j ($\beta_{i(jk)}$ and $\beta_{j(ik)}$) without overlap, increases then decreases them with low overlap, and decreases them nonlinearly with high overlap of microbiomes. Without overlap in microbiome, early germination of plant k leads to negative $\beta_{i(jk)}$ and $\beta_{j(ik)}$ values. Because we assume higher-order interactions are additive terms (Eqn. 9), these negative values indicate that time-dependent interaction modifications weaken the *overall* interactions experienced by plants i and j due to a smaller temporal overlap with plant k (Figure 4).

When plant k germinates between plants i and j (Scenario II), the first arriver (plant i) always experiences the weakest higher-order interaction while the last arriver (plant j) always experiences the strongest higher-order interaction. This higher-order effect on the late arriver follows from the cascading effect observed in population dynamics (Figure 3). The cascading effect is more evident when we let plant k germinate before plant i in scenario II (Figure S4). Without any overlap in microbiomes, $\beta_{j(ik)}$ and $\beta_{k(ij)}$ are negative when plant k germinates later, indicating that the two plants experience weaker interactions.

When plant k germinates after both plants i and j (scenario III), higher-order interactions experienced by plants i and j $\beta_{i(jk)}$ and $\beta_{j(ik)}$ generally decrease with later phenology of plant k because its effect on the microbiomes associated with the focal pair diminishes, while the higher-

order effect of the early plants on the late germinating plant k ($\beta_{k(ij)}$) generally increases because the effects from the focal pair get stronger when they germinate relatively earlier.

All the other higher-order terms among the three plants in Eqn. 9 also change with the phenology of plant k (Figure S5) and their general patterns shift along a continuum with increasing overlap in microbiomes. Randomly drawn feedback and cultivation rates change the strengths but not patterns of time-dependent interaction modifications (Figure S6, S7), indicating that these patterns are robust and not specific to parameter choices. Evaluating model performance, we found that models that include higher-order interaction terms almost always fit best, except when fitted higher-order coefficients are close to 0, despite additional parameters (Figure S8, S9). These results support the observed time-dependent interaction modifications quantified by our methods.

Discussion

To understand the present and future of ecological communities, we need to first understand their history (Fukami 2015; Gause 1934). Here, we bring this temporal perspective to multispecies communities with higher-order interactions. Using a mechanistic model of plant-soil feedback, we show that the timing of arrival of a third plant determines how it modifies interaction between other plants. The strength of this interaction modification depends on the overlap in associated microbiomes between all plants which control indirect interaction effects in this system. Together, these results highlight the time-dependence of higher-order interactions in complex communities and provide a road map to further exploring the temporal dimension of species interactions in diverse communities.

Our framework puts higher-order interactions in a temporal context. In our model, the accumulation of microbiomes over time affects the strength of plant-plant interactions. The germination phenology of a third plant marks the starting point of its microbiome cultivation, subsequently the total microbiome densities of the community and their effects on plants. Importantly, the interaction modification changes with phenological differences because the underlying biological process is not instantaneous, despite models of community dynamics that often assume otherwise. Non-instantaneous processes in real ecosystems can lead to time lags between different populations, especially when their life cycles are of similar time scales (e.g. the hare-lynx cycle; Nisbet 1997; Stenseth *et al.* 1998; Adler *et al.* 2008). The ubiquity of these temporal processes implies that all higher-order interactions have the potential to be time-dependent.

Higher-order interactions can arise from various ecological mechanisms. When one species alters the environment, the modification can often affect how other species interact, leading to higher-order interactions (Wootton 1993; Zhang *et al.* 2020). When these environmental modifications progress with time, they can also lead to priority effects (Chappell *et al.* 2022). The temporal process of environmental modification is therefore a potential source of time-dependent interaction modification in complex communities. In our model, the cultivation of microbiomes by plants modifies the fitness of other plants, and the different germination phenology affects the temporal extent of these environmental modifications, leading to time-dependent interaction modifications. Similarly, one species can alter the traits of other species, which can also progress with time, leading to time-dependent interaction modifications (Hoverman & Relyea 2008; O'Keeffe *et al.* 2021; Werner & Peacor 2003). Theoretical studies often mechanistically model individual species' demographic parameters or traits that give rise to

higher-order interactions, such as growth rates (Kleinhesselink *et al.* 2022; Lai *et al*. 2022), fecundity (Mayfield & Stouffer 2017), and size (Levine *et al*. 2017). Since these traits often change with species' arrival times (Blackford *et al.* 2020; Rasmussen *et al*. 2014) the strengths of resulting higher-order interactions should also be time-dependent. Incorporating time-dependence in these traits is essential to understand changes in higher-order interactions over time in complex communities.

In our model, multiple plants interact with a group of microbiomes that exert uniform negative impacts on plants, leading to indirect interactions among plants (Sotomayor & Lortie 2015). The overlap in microbiomes among plants represents a generalist-specialist gradient: without any overlap, each plant only cultivates the portion of microbial community it associates with; with total overlap, all plants can cultivate all microbiomes. Therefore, microbiomes that are more general lead to tighter coupling between plants and subsequently stronger higher-order interactions. Our results support that the composition of generalist vs. specialist shapes dynamics across communities, especially via indirect interactions in predator-prey or host-pathogen systems (Garzon-Lopez *et al*. 2015; Holt & Lawton 1993; Jiao & Cortez 2022; Snyder & Ives 2001). Although the temporal aspect of these indirect interactions is studied in the context of pairwise priority effects (Clay *et al.* 2019; Jiao & Cortez 2022), future studies need to consider the role of time-dependent interaction modifications in these intrinsically complex communities (e.g., O'Keeffe *et al.* 2021).

In nature, plants often share mutualists or pathogens, especially among those more phylogenetically related (Davison *et al*. 2015; Gilbert & Webb 2007; Põlme *et al.* 2018), and the sharing is often assumed in studies that explicitly model mutualists and pathogens (Abbott *et al.* 2021; Jiang *et al.* 2020). Although the net antagonistic effect of soil microbes can be common

(and assumed in our model; Lekberg *et al.* 2018), mutualistic effects from microbiomes can change niche or fitness differences between plants (Kandlikar *et al.* 2019; Ke & Wan 2020; Yan *et al.* 2022), affecting population dynamics and fitted interaction coefficients. The pathogenic vs. mutualistic roles of microbiomes can further interact with the generalist-specialist gradient in our model (Semchenko *et al.* 2022). For instance, specialist mutualists can amplify fitness differences between plants and promote exclusion or positive frequency dependence (Xi *et al.* 2021); more abundant plants can be more exposed to their specialist pathogens, leading to conspecific negative density dependence that favors biodiversity (Hülsmann *et al.* 2021; Liang *et al.* 2016; Sedio & Ostling 2013). Studying the specific roles of microbiomes will greatly improve our understanding of pairwise and higher-order interactions between plants and mechanisms of coexistence in highly diverse communities.

Increasing evidence suggests that the plant-soil feedback is a highly dynamic process, challenging the classic assumption that microbial dynamics are much faster than plant dynamics such that feedback between plant and microbiome is instantaneous (the "separation of time scales"; Eppinga *et al.* 2018; Kandlikar *et al.* 2019; Mack *et al.* 2019; Ke & Wan 2020). We model the change of microbial community compositions over the same time scale as plants and the decay of plant-associated microbiomes after the senescence of the host. In nature, these common processes can lead to rich dynamics of microbiomes and strongly affect strengths of plant-soil feedback (Chung 2023; Dombrowski *et al.* 2017; Esch & Kobe 2021; Hannula *et al.* 2019, 2021; Ke *et al.* 2021; Ke & Levine 2021; Lepinay *et al.* 2018; Tan *et al.* 2021), and in our model, they lead to temporal changes in pairwise and higher-order interactions between plants.

Life histories of plants and soil microbes vary greatly across ecosystems. In our model, we make several biologically realistic assumptions, which may only apply to certain communities.

We model large differences in germination phenology, which represents systems where native and invasive species respond differently to environmental cues (Cleland *et al.* 2015; Wainwright & Cleland 2013). In some annual plant communities where germination is highly synchronized (e.g., California annual grassland; Chiariello 1989; Bart *et al.* 2017), the potential for priority effects and time-dependent interaction modifications may be reduced. Likewise, we assume fixed lengths of life cycles among plants because allowing for all plants to live until the end of the year would lead to unintentional disadvantages (overall higher mortality) for early-arriving plants in our model. In nature, life history strategies are often contingent on environmental factors, such as water availability or temperature. This plasticity could lead to novel tradeoffs between species, affecting the presence and strengths of higher-order interactions (Kleinhesselink *et al.* 2022; Levine *et al.* 2022). Finally, we assume that all microbiomes are present at the same density before plants germinate. This fixed baseline does not consider the potential differences in the life cycles and phenology of soil microbiomes (Rudgers *et al.* 2020) or the potential for early-germinating plants to associate preferentially with early microbes. Nevertheless, our model provides an important baseline for future empirical and theoretical works on the temporal dynamics of complex plant communities.

Our framework of time-dependent interaction modification lays the groundwork for quantifying temporal changes pairwise and higher-order interactions in multispecies communities, advancing the understanding of their assembly over time (Song *et al.* 2020, 2021b, a). An important next step is to test how time-dependent interaction modifications affect species coexistence. Higher-order interactions are often considered to promote coexistence (Bairey *et al.* 2016; Grilli *et al.* 2016), but a recent study also found a more nuanced connection (Gibbs *et al.* 2022). Resolving higher-order interactions along the temporal axis reveals new processes that

could stabilize or destabilize communities, such as fluctuations of arrival times (phenological variations) over years (Carter *et al.* 2018; Rudolf 2019; Theobald *et al.* 2017; Zou & Rudolf 2023b), further contributing to the context-dependency of the complexity-stability relationship. The concept of time-dependent interaction modification combines the two burgeoning fields, higher-order interactions, and time-explicit ecology. This temporal layer of realism is essential to understanding the processes shaping complex communities in nature, and to predicting how they will change as climate change continues to reshuffle species phenology worldwide.

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Figures and Tables

Table 1. Parameters used for simulations. All values except for phenology are not plant-specific and follows the general notations in Eqn. 5-8.

Definition	Symbol	Values
Initial density of plants	$N(0)$	1
Initial and baseline density of microbiomes	$S(0)$	0.1
Length of the year	T	12
Length of plants' life cycle	l	6
Plant mortality rate within the life cycle	d	0.1
Microbiome mortality rate within the year	μ	0.1
Microbiome mortality at the end of the year	μ_{year}	0.7
Plant fecundity	λ	3
Total capacity of cultivation (plants to microbiomes)	V	0.3; or drawn from uniform distribution $(0.1, 0.3)$
Cultivation rate from plant x to its associated microbiome	v_{xx}	V_x if no overlap, $0.8V_x$ if small overlap, $0.2V_x$ if high overlap
Cultivation rate from plant x to other plants' associated microbiome	v_{yx} for all plants $x \neq$ y	0 if no overlap, $0.2V_x/n$ if small overlap, $0.8V_x/n$ if high overlap; n is the number of plant species other than itself
Effects of microbiomes on plants	m_{xy} for all plants x and y	-0.3; or drawn from uniform distribution $(-0.5, -0.1)$
Phenology of plants i, j and k	p_i, p_j, p_k	1 (earliest) to 6 (latest)
Phenological difference between the focal pair i and j	Δp_{ij}	-5 to 5

Figure 1. Conceptual figure of time-dependent interaction modification. A. In a three-species module, each species arrives at a certain time, leading to three distinctive relative arrival times, Δp_{ij}, Δp_{jk}, and Δp_{ik}. B. In a pairwise system (i and j), trait-dependent priority effects occur when the per-capita interaction from j to i (α_{ij}) is determined by the relative arrival time between j and i (Δp_{ij}), i.e., the interaction-phenology function $f_{ij}(\Delta p_{ij})$. C. In a system with non-pairwise interactions, the presence and arrival time of a third species (here k) can determine the interaction between the other two species ($\beta_{i(jk)} = f_{i(jk)}{}'(\Delta p_{ij}, p_k)$), leading to time-dependent interaction modification.

Figure 2. Conceptual figure of two-plant communities and results. A. With no overlap of associated microbiomes between plants, each plant can cultivate only its associated microbiome (v_{ii} and v_{jj}), which in turn affects both plant species (m_{ii}, m_{ij}, m_{ji}, and m_{jj}). With overlap in microbiomes, cultivation, each plant species can also cultivate the microbiome associated with the other plant species (v_{ij} and v_{ji}, black arrows); higher overlap leads to higher interspecific cultivation rates. B. Population dynamics of two-plant communities showing a clear early-arriver advantage. Densities of plants and microbiomes are in solid and dashed lines. Equilibrium densities (after 50 years) of plants (in seeds) and microbiomes at the end of the year are shown in solid and empty dots. Plants senesce and convert to dormant seeds after completing their life cycles; densities of plants are therefore 0 after senescence. Dynamics of seeds are not shown. The plant population dynamics of low and high overlap are identical while the microbiome population dynamics are reversed because the cultivation rate from plant i to its microbiome with low overlap ($v_{ii} = 0.8V_i$) is equal to its cultivation rate to the microbiome associated with plant j with high overlap ($v_{ji} = 0.8V_i$). C. Fitted interspecific interaction coefficients between

plants i and j along a temporal gradient of relative arrival times Δp_{ij}, with different levels of overlap. A $\Delta p_{ij} < 0$ means that j arrives early, $\Delta p_{ij} > 0$ means that i arrives early.

Figure 3. Equilibrium population (after 50 years) of three plant species in three-plant communities by cases. Scenario I shows plant k arriving before the focal pair i and j, Scenario II shows k arriving between the focal pair, and Scenario III shows k arriving after the focal pair. When species arrive at the same time, their equilibrium population is identical; points and lines of each plant are jittered for visibility.

Figure 4. Time-dependent interaction modification in three-plant communities by cases. The higher-order interaction coefficients $\beta_{i(jk)}$ and $\beta_{j(ik)}$ are fitted according to Eqn. 9. Scenario I shows plant k arriving before the focal pair i and j, Scenario II shows k arriving between the focal pair, and Scenario III shows k arriving after the focal pair. When the focal pair arrives at the same time (Scenarios I and III), the two plants are equivalent and higher-order interaction coefficients $\beta_{i(jk)}$ and $\beta_{j(ik)}$ are identical; points and lines of each coefficient are jittered for visibility.

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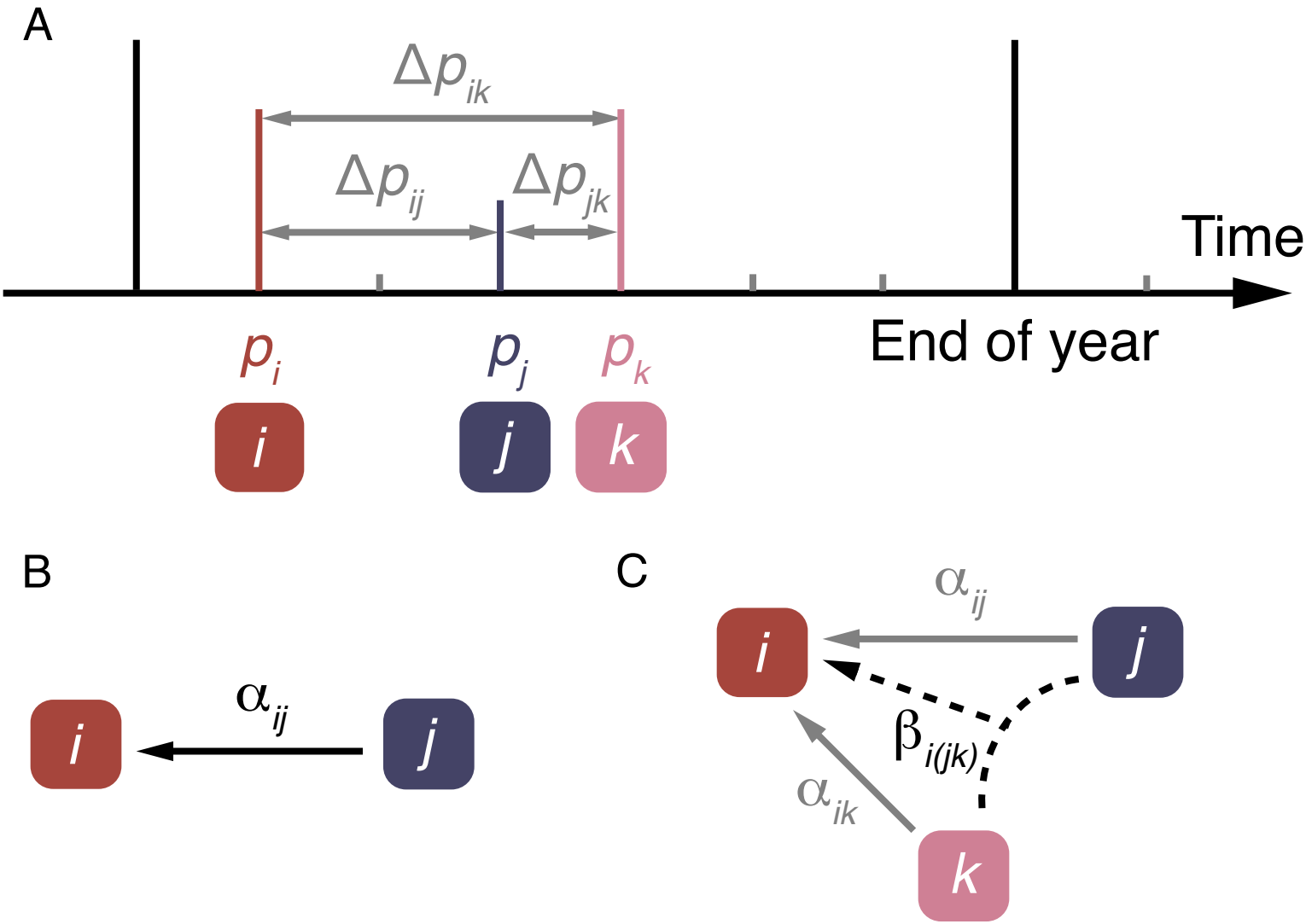
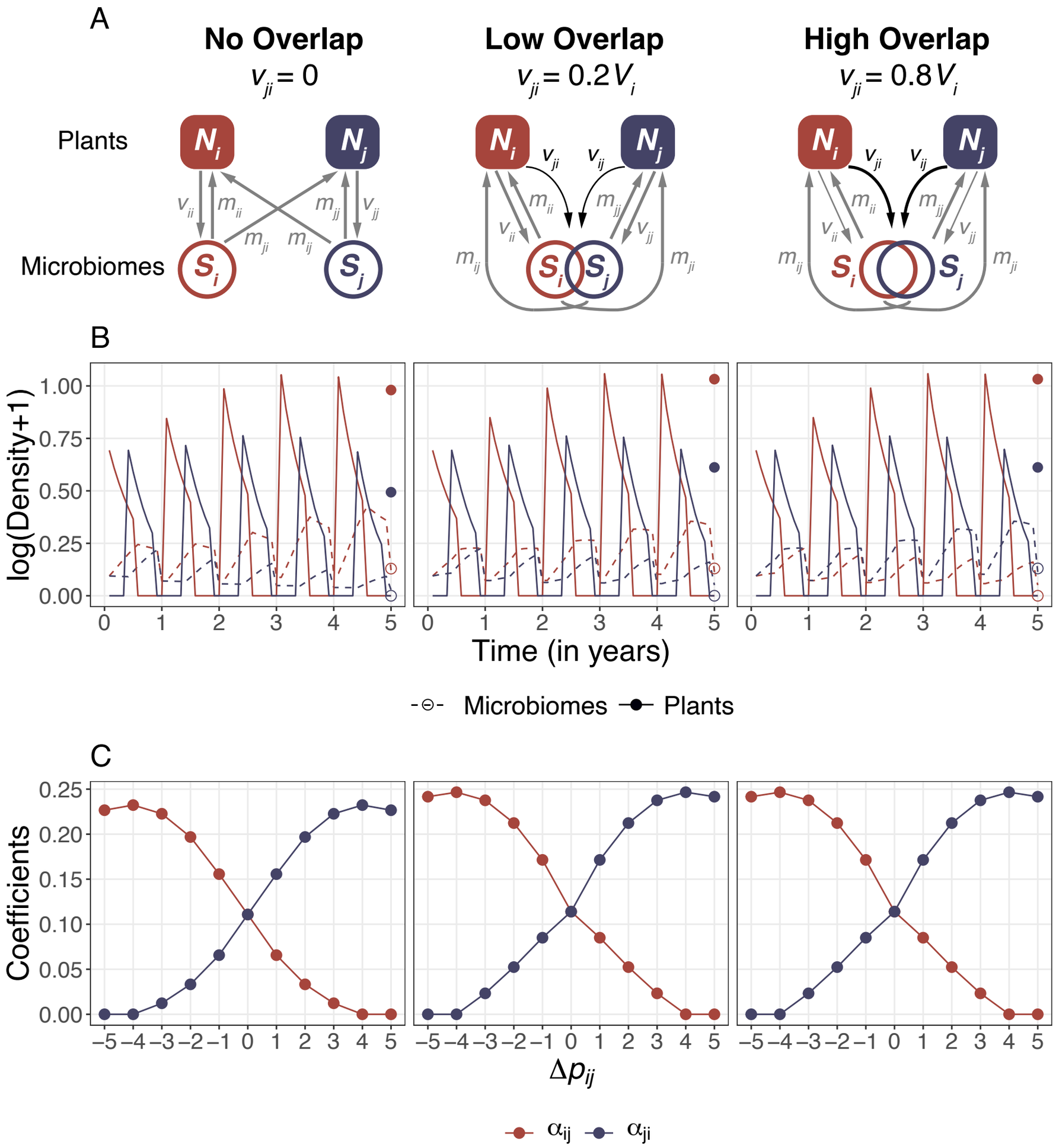


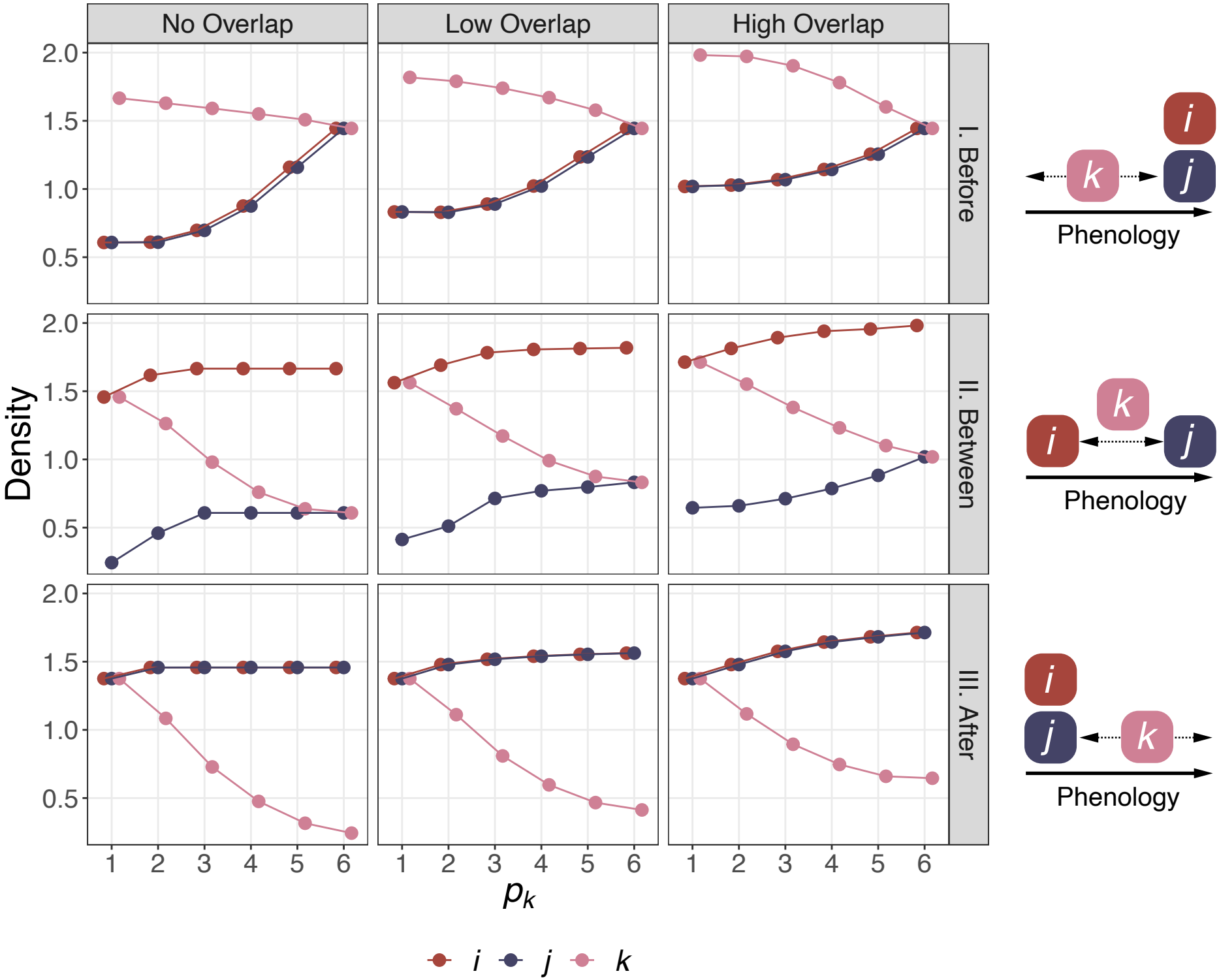
$$\alpha_{ij} = f_{ij}(p_i, p_j)$$
$$= (\Delta p_{ij})$$

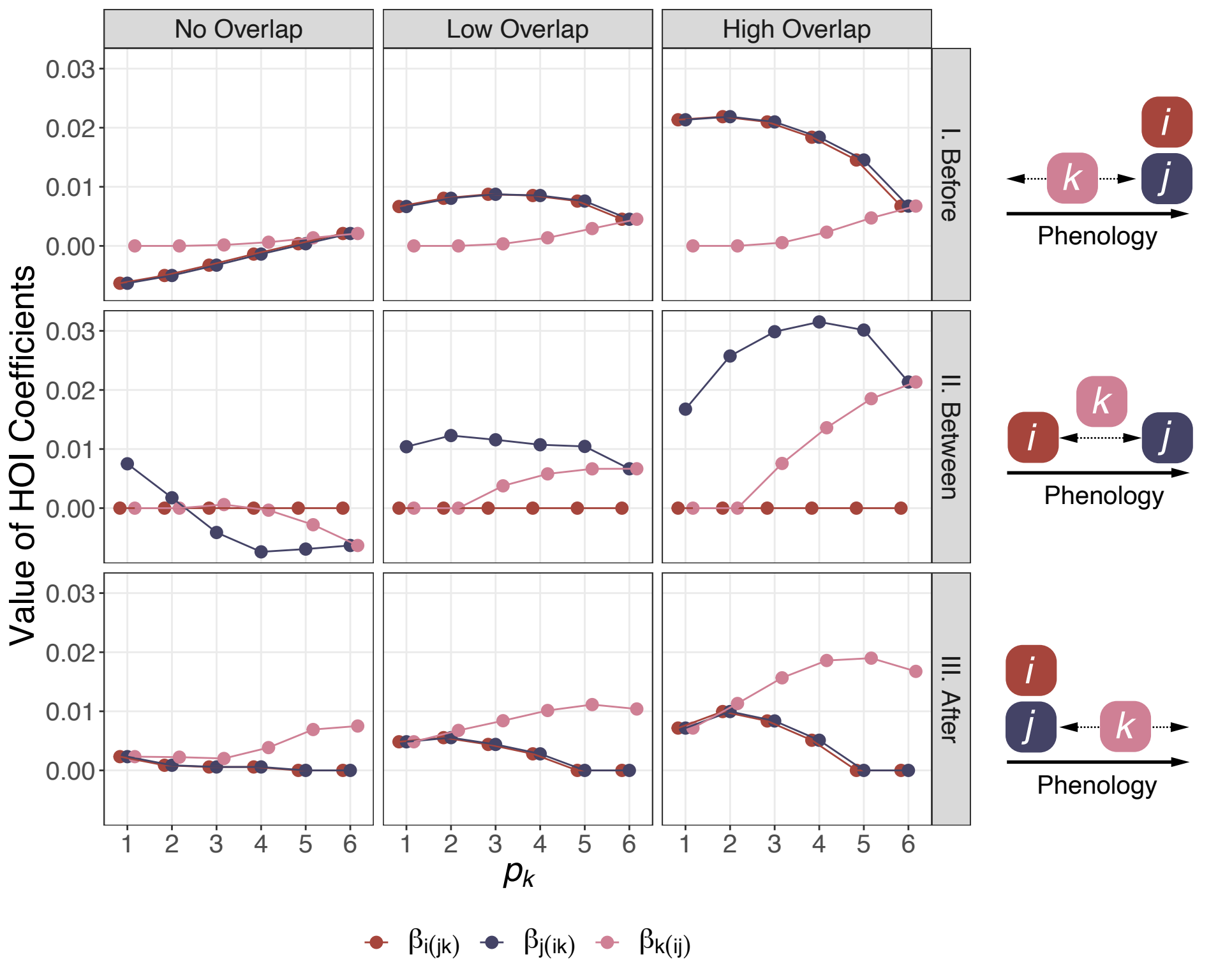
Pairwise Priority Effects

$$\alpha_{ij} = f_{ij}(\Delta p_{ij}),\ \alpha_{ik} = f_{ik}(\Delta p_{ik})$$
$$\beta_{i(jk)} = f'_{i(jk)}(p_j, p_k)$$

Pairwise Priority Effects and Time-dependentInteraction Modification


A
No Overlap
$v_{ji} = 0$
Low Overlap
$v_{ji} = 0.2V_i$
High Overlap
$v_{ji} = 0.8V_i$
Plants
Microbiomes
N_i
N_j
S_i
S_j
v_{ii}
m_{ii}
m_{jj}
v_{jj}
m_{ji}
m_{ij}
v_{ji}
v_{ij}
B
log(Density+1)
1.00
0.75
0.50
0.25
0.00
0
1
2
3
4
5
Time (in years)
Microbiomes
Plants
C
Coefficients
0.25
0.20
0.15
0.10
0.05
0.00
−5 −4 −3 −2 −1 0 1 2 3 4 5
Δp_{ij}
α_{ij}
α_{ji}


No Overlap
Low Overlap
High Overlap
I. Before
II. Between
III. After
Density
2.0
1.5
1.0
0.5
1
2
3
4
5
6
p_k
i
j
k
Phenology
i
j
k
Phenology
i
j
k
Phenology
i
j
k


No Overlap
Low Overlap
High Overlap
I. Before
II. Between
III. After
Value of HOI Coefficients
0.03
0.02
0.01
0.00
1
2
3
4
5
6
p_k
i
j
k
Phenology
$\beta_{i(jk)}$
$\beta_{j(ik)}$
$\beta_{k(ij)}$