Article Title: Incorporating traits into consumer-resource models for a mechanistic trait ecology

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Abstract

Traits provide a powerful way to infer community assembly processes, responses to environmental perturbations, and coexistence mechanisms, although most work has focused on plants and has not incorporated the role of trophic interactions. Here, we briefly review the main goals of trait-based ecology and highlight recent examples that use traits to study insect communities, specifically focusing on multitrophic communities and interactions between plants and insect herbivores. We then introduce a mechanistic multi-species consumer-resource model that incorporates traits involved in trophic interactions (i.e., leaf toughness and mandible strength) to outline mechanistic hypotheses for how interactions structure communities. Models show that different ways in which plants and herbivores interact through their traits, trait-matching vs. strong mandibles, substantially changes community coexistence patterns. Furthermore, we simulate interactions across a productivity gradient to generate predictions for how community composition changes across gradients, given a mechanistic hypothesis. Finally, we evaluate these patterns through the lens of community trait metrics and Modern Coexistence Theory. The modeling output highlights that, even under one mechanistic structure (i.e., trait matching between plants and herbivores), community composition patterns and the relative strength of equalizing and stabilizing mechanisms change strongly across environmental gradients. Our review provides an avenue for future research that combines functional traits and mechanistic models to provide a richer understanding of the processes that structure and maintain diversity in insect communities.

Highlights (3-5)

- Traits can be used to infer how trophic interactions shape communities
- Mechanistic models parameterized with trait information predict community patterns
- Relative strength of equalizing and stabilizing mechanisms changes across gradients

Introduction

Understanding the factors that drive patterns of species diversity and community assembly across space is a central goal in ecology. Traditionally, research has focused on how community composition of a single trophic level (i.e., taxonomic richness or diversity) changes across environmental gradients [1,2]. However, it has been established that environmental variation can simultaneously affect multiple trophic levels, for example, herbivore diversity can be affected either directly by abiotic factors like climate or indirectly via changes in plant diversity [3,4]. Studies of diversity patterns across trophic levels have typically found positive relationships, where diversity at one trophic level is correlated with diversity at an adjacent level [5,6]. While it is generally recognized that taxonomic diversity can be linked to resource differentiation, the processes that mechanistically link co-variation in structure across trophic levels remain poorly understood.

Functional traits to infer assembly patterns

Trait-based ecology is well suited to elucidate mechanisms shaping communities at more than one trophic level because it focuses on how functional properties beyond their taxonomic identities shape interactions with the abiotic and biotic environment [7,8]. Functional traits are broadly defined as characteristics (morphological, physiological, or phenological) of an organism that influence its performance and fitness [9]. Over the last two decades, trait-based approaches have successfully revealed mechanisms that structure plant communities [7,10,11]. For example, functional traits have been used to show that plant communities shift from slower growing species with conservative resource-use strategies to species characterized by rapid growth and resource acquisition along gradients of increasing resource availability [12,13]. Traits associated with plant resource acquisition strategies also alter plant susceptibility to herbivores as articulated in the resource availability hypothesis from plant defense theory [14]. Slow growing plants occurring in low-resource environments tend to be better defended and less palatable to herbivores, whereas faster growing plants in high-resource environments tend to have few defenses and be more palatable to herbivores [14,15]. However, most functional trait research to date has focused primarily on plants, and it has only recently been applied to community processes at other trophic levels [16,17]. Very few studies have investigated functional traits related to plant-herbivore trophic interactions and how they might contribute to structuring communities [18–21] despite the potential to identify which plant or herbivore traits may lead to shifts in community composition.

One popular use of functional traits is to inference drivers of community assembly, specifically differentiating between environmental filtering and competition [22]. Communities strongly structured by inter-specific competition would exhibit trait overdispersion as a result of niche differentiation, making them more likely to coexist, whereas species with similar traits would most likely outcome one another. In contrast, environmental filtering is expected to select strongly for certain functional traits that are necessary for establishment and persistence within a community, resulting in trait underdispersion, or clustering. Interpreting trait dispersion patterns from observational data, particularly environmental filtering [23], is difficult unless combined with two additional steps [16,24]. First, the degree of clustering/dispersion must be shown to correlate with the hypothesized environmental driver. This step would show that the environmental variable is the likely driver of trait dispersion patterns. The final step is relating functional traits to abundance or performance across an environmental gradient [16,24]. This last point connects traits directly to environmental drivers. For insects, grasshoppers with long wings (i.e., greater dispersal potential) tended to be more abundant after prescribed fires as indicated by greater community weighted mean wing length, suggesting that dispersal ability is important for structuring communities responding to recent fire [21]. In contrast, if competition structures communities, trait patterns would not correlate with environmental variables. Previous studies have documented correlations between plant variables (i.e., richness, habitat type) and insect herbivore communities. Therefore, established theory coupled with functional traits is well poised to address important and unanswered questions regarding how trophic interactions structure communities.

Trait-matching to explain assembly of multi-trophic communities

Recent observational trait-based studies of insect communities have demonstrated the roles of species interactions in structuring community composition (e.g., competition, pollination, predation [25,26]), identifying how insect communities response to environmental change [27–30], and how herbivores impact ecosystem functioning [31,32]. Additionally, traits may provide insight on functional linkages between plants and consumers (i.e., trait matching; [33]). “Trait matching” refers to traits that specifically enable trophic interactions among species [33]. The most well-known examples include plant-pollinator interactions (matching proboscis length with corolla depth; [34]. When there is a mismatch in traits, such as proboscides or bills that are shorter than flower tubes, this creates an interaction barrier [35]. However, trait matching is also important for plant-herbivore interactions and can provide insights on how insect communities are structured [36] as well as how insects influence plant communities and ecosystem function. For example, plant communities dominated by species with tough leaves tend to support grasshopper species with strong mandibles [36]. In response, herbivore communities dominated by large-bodied species or species with powerful mandibles can have larger impacts on plant communities than small-bodied, weak-jawed species [18,19]. Thus, linking plant and herbivore traits is likely to provide mechanistic information beyond the taxonomic diversity approaches of most previous studies (e.g., correlating plant and consumer richness). While there is robust and comprehensive framework for describing and identifying “trait matching” [33], there is still a lack of model-based predictions for how trait matching through plant-herbivore interactions may influence structure of communities at both trophic levels.

Building functional traits into mechanistic models

To provide general predictions for how functional traits may influence community patterns, we modified the classic MacArthur consumer-resource model [37–39] that describes the dynamics of a plant–herbivore system. This mechanistic model has biologically informed parameters compared to phenomenological models, such as Lotka-Volterra, and therefore is desirable for its interpretability [38,40,41]. In this model, plant populations grow at a rate of R_i and are regulated by density-dependence (i.e., intra-specific competition; C_i; note that interspecific competition coefficients can also be added: C_{ik}), as well as by being consumed by herbivores. Herbivore populations are regulated by mortality (M_j) and the availability of their preferred host plants, which they forage on in a density (or frequency) dependent manner (i.e., Type I or II functional response). Herbivores do not compete directly, but rather indirectly by suppressing resources [38,41]. Parameter values are taken from McPeek ([39], pg. 116) with slight modifications (Table 1). For simplicity, several model parameters are set to zero (i.e., inter-specific plant competition meaning plant species only compete through shared herbivores via apparent competition [42] and handling time which specifies a Type I functional response).

The basic model can be formally written as:

Plant dynamics: $\frac{dP_i}{dt} = P_i \left[R_i - \sum_k C_{ik} P_k - \sum_j \frac{A_{ij} H_j}{1 + \sum_k A_{ij} L_{ij} H_j} \right]$

Herbivore dynamics: $\frac{dH_j}{dt} = H_j \left[\frac{\sum_i E_{ij} A_{ij} P_i}{1 + \sum_i A_{ij} L_{ij} P_i} - M_j \right]$

Table 1. Model parameters descriptions. Interactions are denoted by matrices (*ik* for plant-plant or *ij* for plant-herbivore).

Parameter	Description	Units	Trait(s)	Value(s)
P_i	Plant biomass	g m^{-2}		
H_i	Herbivore density	# m^{-2}		
R_i	Intrinsic growth rate of plant i	g m^{-2} day^{-1}	Could add traits	2
C_{ik}	Competition between plant i and k	m^{2} g^{-1}	Could add traits	0.04 (intra), 0 (inter)
A_{ij}	Attack rate of herbivore j on plant i	m^{2} #$^{-1}$ day^{-1}	Mandible strength~ Leaf toughness	max = 0.4; calculated via trait matching
E_{ij}	Conversion efficiency of plant i to herbivore j	g g^{-1}	Could link traits	0.1
L_{ij}	Handling time modifier	day g^{-1}	Could link traits	0
M_j	Herbivore mortality rate	day^{-1}	Could add traits	1

These mechanistic models can also incorporate plant and herbivore functional traits by allowing trait values to modify the attack rates or other parameters of herbivores on different plant species

[43]. Previous examples have examined how herbivores with different body sizes can coexist by linking body size to conversion efficiencies and encounter rates [44]. Feng and DeAngelis [43] incorporated toxicity into the Type II functional response in a two-plant, one-herbivore system.

We incorporated traits by allowing the attack rate matrix, A_{ij}, to change as a function of the trait similarity (normalized Gaussian-shaped function, similar to [33]) between mandible strength and leaf toughness ("Trait matching hypothesis"): $A_{ij}=\exp\left(-\beta\left(\frac{m_j/\bar{m}}{t_i/\bar{t}}-1\right)^2\right)$ where mj and ti are mandible strength and leaf LDMC, respectively, for herbivore j and plant i, and β controls the spread of the trait matching ($\beta = 10$ in this case), columns are then normalized so that $\sum A_{ij} = 0.5$ (Appendix A, Fig. A1A). Trait matching between mandible strength and leaf toughness (specifically, leaf dry matter content, LDMC) has been empirically linked in several previous studies with plants and grasshoppers [19,21,36,45]. We used hypothetical values based on the ranges of LDMC and mandible strength from Grosdidier et al. [21]. An alternative hypothesis is that stronger mandibles are always better, which we incorporated into a second model ("Strong mandibles hypothesis"), assuming that weak-mandible species would experience a "trait-barrier" when trying to consume tough leaved plants [33]. We used a monotonic relationship such that stronger mandible herbivores had greater attack rates across the board and low LDMC are preferred by all herbivores: $A_{ij} = \alpha_0 * \frac{m_j/\bar{m}}{t_i/\bar{t}}$ where α_0 is a base attack rate (0.04; Fig. A1B). Both models contained 10 plant and herbivore species, with increasing mandible strengths (H1 <…< H10) and leaf toughness (i.e., LDMC, P1 <…< P10). All other parameters were as in Table 1. We focus specifically on attack rate, Aij, because these traits should impact the probability of an herbivore consuming a plant, although other traits could be added to affect other model parameters, based on the mechanism (Table 1).

The results of our model showed that the two most abundant herbivore species in the "trait matching" model had the most dissimilar traits (H1 and H10) and all 10 species persisted through 100 time points (Fig. 1A). The two most abundant species in the "strong mandibles" model, not surprisingly, had the strongest mandibles (H10 and H9) and most other species went extinct (Fig. 1B).

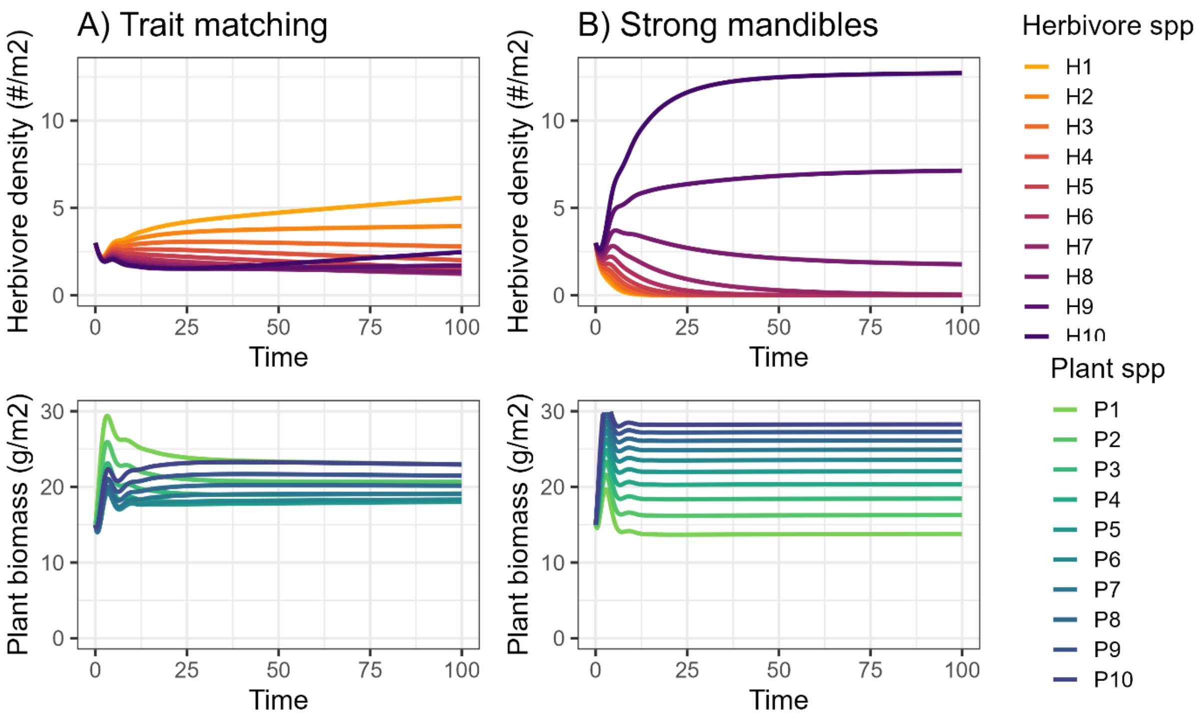

Fig. 1. A) Abundances of 10 herbivore (top) and 10 plant (bottom) species over 100 iterations assuming trait-matching between leaf toughness and mandible strength based on normalized (%) similarity of traits and B) assuming stronger mandibles are better for consuming plants. Traits of the plant and herbivore species are ordered from low (P1, H1) to high (P10, H10).

Mechanistic models to predict functional trait dispersion across gradients

We further modified the above models to develop alternative hypotheses for how interactions should influence communities across environmental gradients. We simulated an environmental gradient of plant community LDMC by varying the growth rates of all plant species systematically across 20 growth rate values. In these simulations, average growth rate of the plant community was held constant at $R = 2$, such that if $R1 = 1$ then $R10 = 3$, and so forth (see McPeek [39], pg. 100-118). Without herbivores present, this creates a gradient from low to high community weighted LDMC (Appendix B).

Next, we added herbivores, assuming the “trait matching” scenario described above. In this scenario, the plant community follows the same general pattern of increasing community LDMC, although herbivory does dampen this pattern to some degree (Fig. 2A). Herbivore abundance also changes substantially across this gradient, with the weakest-mandibled species strongly decreasing and the strongest-mandibled species increasing, as expected, with all species coexisting at intermediate levels of the gradient (Fig. 2B).

At the community level, weighted mean (CWM) mandible strength of the herbivore community increased along the LDMC gradient (Fig. 2C). Interestingly, mandible trait diversity, measured as Rao’s entropy, peaked at the center of the LDMC gradient, likely because plant community traits were most even, and therefore provided even and diverse resources for the herbivores. Although the mechanism structuring herbivore communities is bottom-up environmental filtering, driven by the traits of the plant community, the standardized effect sizes shifted strongly across the LDMC gradient (Fig. 2E). However, at low and high CWM LDMC values, herbivore mandible traits were strongly underdispersed, which appropriately detected the environmental filtering. However, at intermediate values of CWM LDMC, herbivore mandible traits were strongly overdispersed, which is typically an indicator of strong competition. However, in this case, the trait overdispersion resulted from the high evenness of the plant traits (Fig. 2A). Although herbivores are competing indirectly for resources by depressing plant abundance (compared Fig. 2A to Fig. B1 in Appendix B), herbivore species are only excluded at the extremes of the LDMC gradient, where trait matching is most intense.

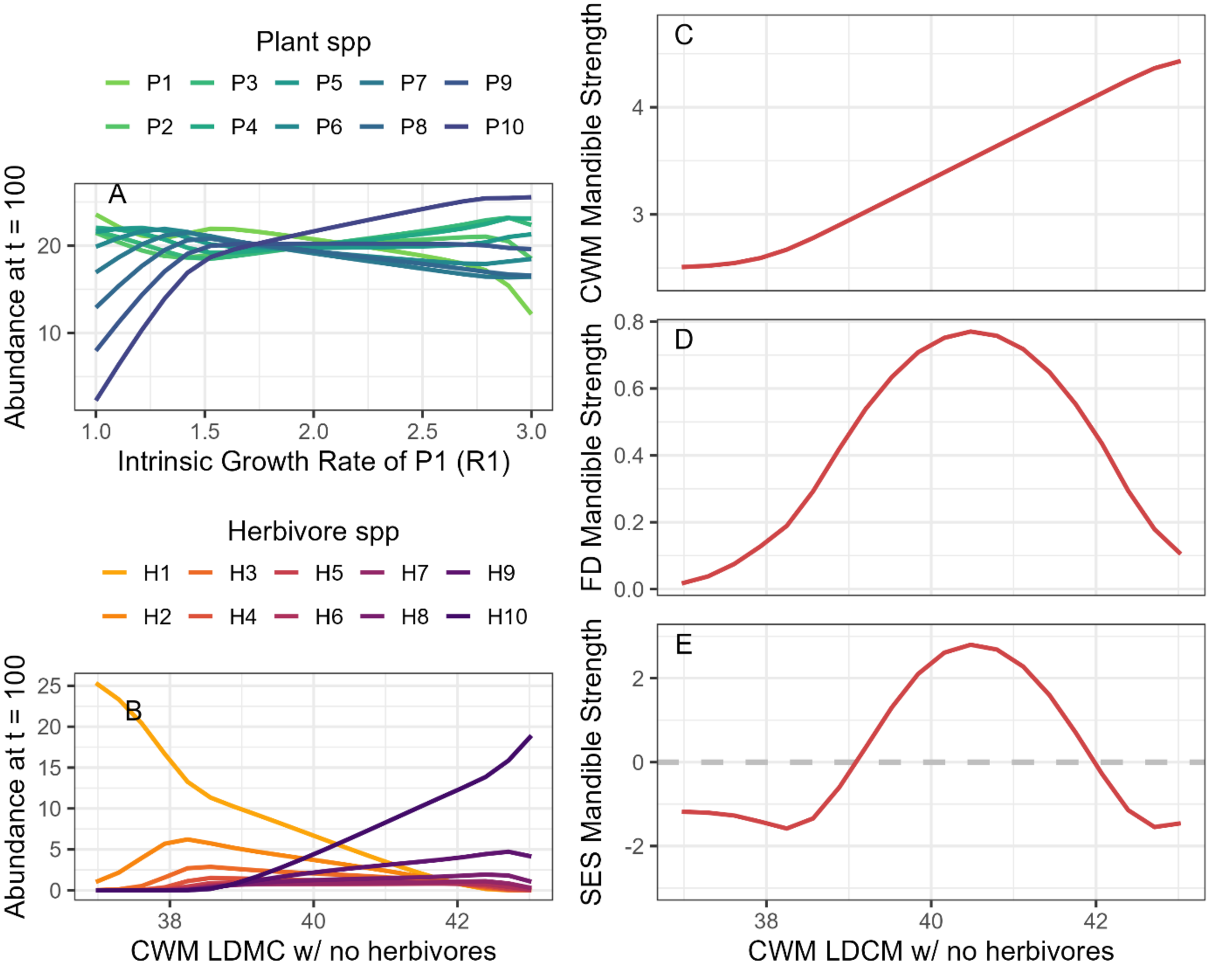

Fig. 2. A) Abundances of 10 plant species simulated across 20 different growths rates that were systematically varied across all 20 plant species. Herbivores are present in this model, depressing plant abundances (see Appendix for no-herbivore model). Shown on the x-axis is the growth rate of plant species 1 (*R1*). B) Abundances of 10 herbivore species across the simulated gradient of plant LDMC. Responses of herbivore community mandible metrics across the LDMC gradient are shown, C) community weight mean, D) Rao's entry as a measure of functional dispersion, and E) standardized effect sizes, where negative values represent trait underdispersion and positive values represent trait overdispersion. x-axis in B-E is the CWM LDMC from the no-herbivore model in Appendix.

Linking to modern coexistence theory

Modern coexistence theory centers on stabilizing and equalizing mechanisms to explain how species coexist in diverse communities despite competing for shared resources [46]. Stabilizing mechanisms, or niche differences, occur when species possess different traits that allow them to exploit different resources, thereby minimizing interspecific competition relative to intraspecific competition. Equalizing mechanisms, or fitness differences, reduce competitive disparities by minimizing differences in intrinsic growth rates or fecundities, preventing consistent advantages of one species [47]. Mechanistic model offer a powerful way to connect functional traits to coexistence outcomes because they can be parameterized with functional traits data and contain the elements necessary to calculate niche and fitness differences, and therefore coexistence criteria [48–50].

New definitions of niche and fitness differences now account for a broader range of interactions, from competition to facilitation, making it possible to test higher-order interactions beyond simple pairwise relationships [51–53]. This $\mathcal{N}$-$\mathcal{F}$ mapping framework has several advantages over traditional metrics, mainly that estimates are made at the species level (i.e., whether it suppresses itself more than it is suppressed by the community) rather than only pairwise comparisons and can accommodate multiple trophic levels simultaneously [54,55]. For three scenarios across the LDMC gradient described above for the trait-matching hypothesis, we estimated niche and fitness differences across a range of parameter values. In the "null" community, where all plant species have the same growth rate ($R = 2$), niche differences are large enough overcome fitness differences, stabilizing coexistence for most species (Figure 3). However, in the "soft" community, the three herbivore species that are best matched to the plant community (i.e., H1-H3 with the weakest mandibles) persist while the others are excluded. The "tough" community is in between, with most species persisting especially the ones best matched to the plant community (e.g., H9-10).

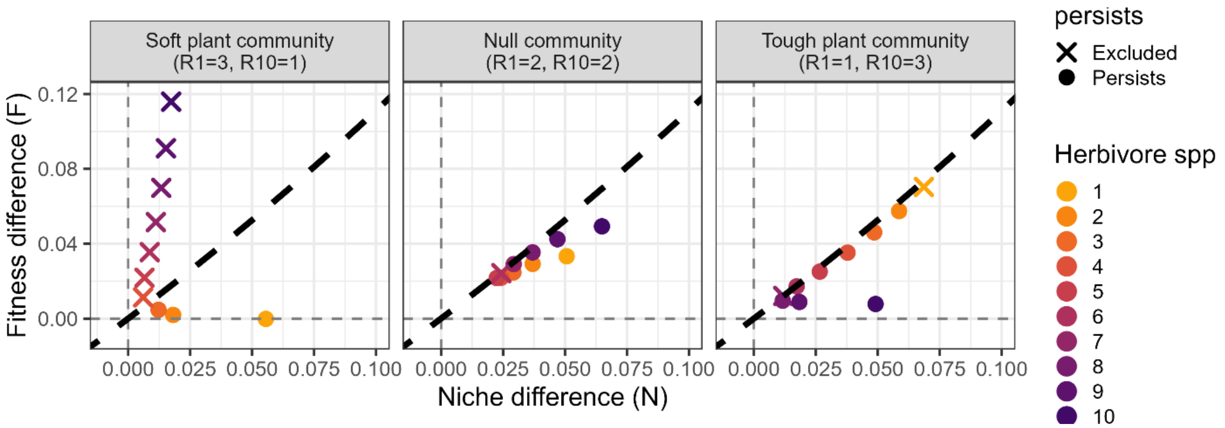

Fig. 3. Three scenarios with plant communities simulated across a gradient of CWM LDMC assuming the "Trait-matching" hypothesis. Points show each herbivore species mapped into Niche and Fitness difference space (Spaak et al. 2021). Thick diagonal dashed line is a 1:1 line that indicates $N = F$, where a species will be excluded left of line ($N < F$) or persist right of line ($N > F$) (see Spaak et al. 2021).

Future directions

There is growing evidence that ecological assemblages can be interpreted using trait-based approaches though the lens of stabilizing and equalizing mechanisms. Theoretical models are a valuable tool for advancing this understanding and can be used to generate predictions across a range of scenarios, including various trophic levels and abiotic conditions. Mechanistic models in particular are particularly powerful because they incorporate rich biological information [38,48,50] and can generate predictions for a range of scenarios, including for multiple traits, incorporating predators or mutualists [39,56]. They are also highly flexible, and can accommodate various functional responses that may better capture ecological dynamics with different outcomes for coexistence [57], including capturing indirect effect like apparent competition [42] as well as incorporating more traits for multidimensional inference [58].

An additional important source of variation that should be considered when generating future scenarios is intraspecific trait variation, as it represents the breadth of a species' niche and has been shown to alter stabilizing and equalizing dynamics under different abiotic conditions [59–61]. As with most trait-based interactions across trophic levels and overall communities, the effects of individual trait variation on species fitness and competitive advantage remain largely unknown. Finally, it is critical to consider that, as ecological scenarios become more complex, multiple processes can result in similar patterns and trait metrics should be chosen carefully to investigate specific underlying processes [62].

Acknowledgements
PGH was funded by NSF (IOS-2226881) and USDA-NIFA McIntire-Stennis (FLA-ENY-006721).

Author Contributions

Philip Hahn: Conceptualization, Methodology, Formal analysis, Writing – Original Draft, Visualization, Funding acquisition. **Lucia Navia:** Methodology, Writing – Review and Editing. **Antonia Millet:** Methodology, Writing – Review and Editing. **Robert Holt:** Formal analysis. **Carolina Baruzzi:** Conceptualization, Methodology, Writing – Review and Editing.

Data availability statement

No data were used in this article. R code for the models is available on github: https://github.com/hahnp13/Hahn_COIS2026_MCR.git

Declaration of interests: none.

Declaration of generative AI and AI-assisted technologies in the manuscript preparation process:

During the preparation of this work, the lead author used Claude Sonnet 4.6 ran on the University of Florida's NaviGator Chat to generate R code. Prompts were written to be very detailed for specific purposes. The conversation was built as a retrieval automated generation (RAG) so that the model had access to published resources and R scripts written by the lead author that were uploaded into the chat session. All code produced by the model was reviewed and revised by the lead author.

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Appendix A

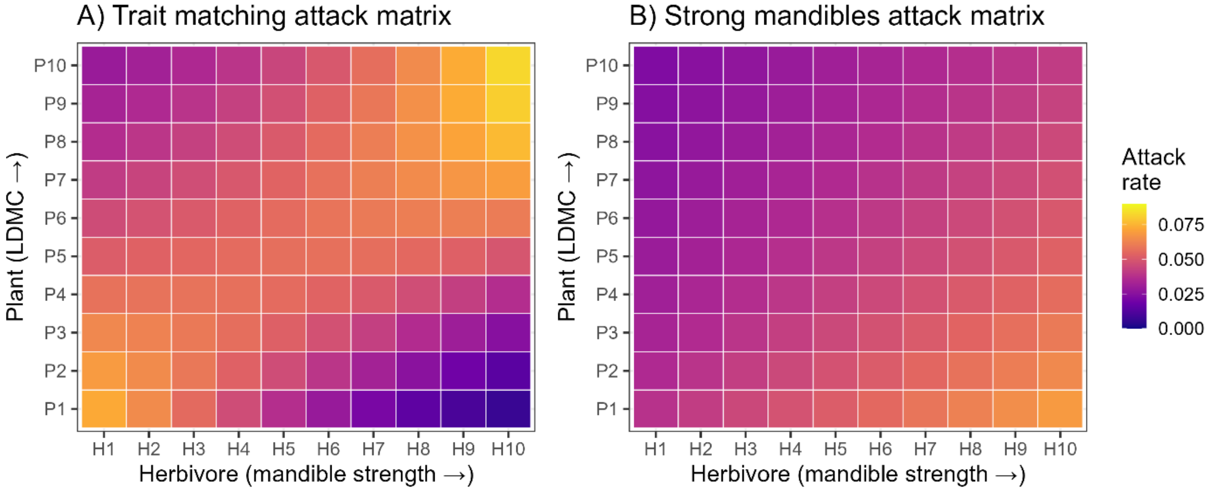

Figure A1. Attack rate matrices for A) trait matching and B) strong mandibles hypotheses.

Appendix B

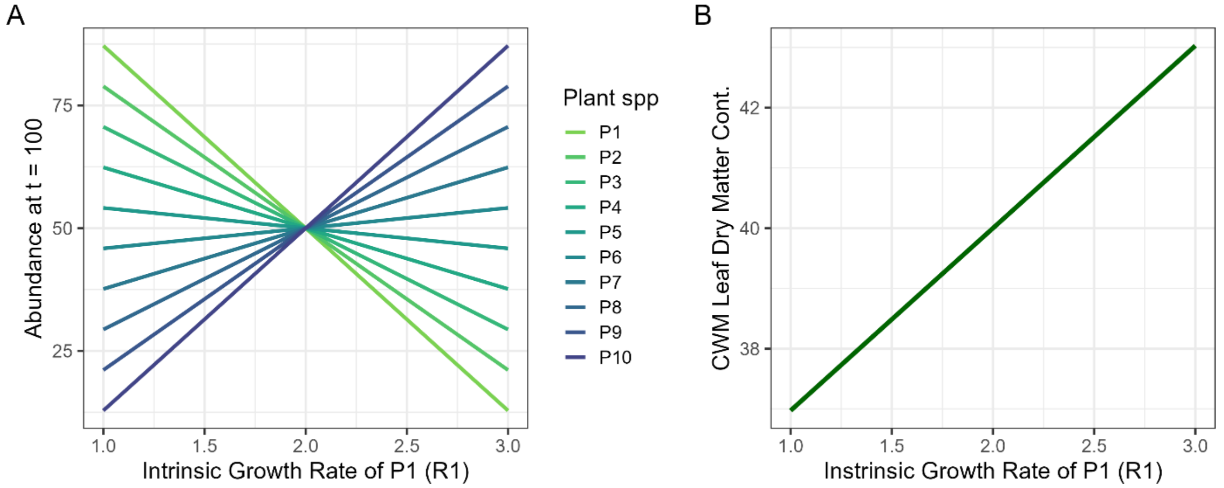

Figure B1. A) Abundances of the 10 plant species simulated across 20 different growth rates that systematically varied the growth rates (i.e., productivity) of all species. In these simulations, average growth rate of the community was held constant at $R = 2$, such that if $R1 = 1$ then $R10 = 3$, and so forth. Shown on the x-axis is the growth rate of plant species 1 ($R1$). Since the plant species increase in leaf dry matter content (LDMC), the simulations created B) a gradient of community weighted mean (CWM) LDMC. The CWM values were calculated from the abundances of the 10 plant species at time 100 for each of R values. No herbivores are present in these simulations.