The role of higher-order biotic interactions on tropical tree growth

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Abstract

Growth in individual size or biomass is a key demographic component in population models, with wide-ranging applications from quantifying species performance across abiotic or biotic conditions to assessing landscape-level dynamics under global change. In forest ecology, the responses of tree growth to biotic interactions are widely held to be crucial for understanding forest diversity, function, and structure. To date, most studies on plant–plant interaction only examine the direct competitive or facilitative interactions between species pairs; however, there is increasing evidence of indirect, higher-order interactions (HOIs) impacting species demographic rates. When HOIs are present, the dynamics of a multi-species community cannot be fully understood or accurately predicted solely from pairwise outcomes because of how additional

species “interfere” with the direct, pairwise interactions. Such HOIs should be particularly prevalent where species show nonlinear functional responses to resource availability and resource-acquisition traits themselves are density dependent. With this in mind, we used data from a tropical secondary forest—a system that fulfills both of these conditions—to build a ontogenetic diameter-growth model for individuals across ten woody-plant species. We allowed both direct and indirect interactions within communities to influence the species-specific growth parameters in a generalized Lotka–Volterra model. Specifically, indirect interactions entered the model as higher-order quadratic terms, i.e. non-additive effects of conspecific and heterospecific neighbour size on the focal individual’s growth. For the whole community and for four out of ten focal species, the model that included HOIs had more statistical support than the model that included only direct interactions, despite the former containing a far greater number of parameters. HOIs had comparable effect sizes to direct interactions, and tend to further reduce the diameter growth rates of most species beyond what direct interactions had already reduced. In a simulation of successional stand dynamics, we show that such a further reduction in diameter growth by HOIs is important in reducing size asymmetry—and potentially less competitive exclusion due to shading—in a highly light-competitive forest. Our study highlights the potential role of higher-order interactions in stabilising communities in diverse forests.

Keywords

Non-additivity, Coexistence, Indirect interaction, Competition, Facilitation, Diameter growth, Secondary succession, Light limitation

Introduction

A key pursuit in ecology is to understand the processes that maintain biodiversity (Sutherland et al. 2013). In species-rich systems such as tropical forests, many studies aim to determine how it is possible for hundreds of species to coexist within a small spatial extent. Species co-occurring

in close proximity should compete intensely for limiting resources, so what are the ecological processes that contribute to species coexistence? In the framework of modern coexistence theory (Chesson 2000; Adler, HilleRisLambers, and Levine 2007; HilleRisLambers et al. 2012), species coexistence is determined by equalising and stabilising mechanisms. On the one hand, equalising mechanisms are processes that reduce the fitness differences between species thereby preventing the dominance of one species over another. On the other hand, stabilising mechanisms reduce niche overlap thereby slowing or preventing competitive exclusion when strong fitness differences exist between species. In a two-species system, long-term coexistence requires stabilising niche differences to be large enough to overcome fitness differences (Chesson 2018). This has led to numerous studies searching for stabilising processes that arise from ecological differences in resource use or relevant traits between species pairs (e.g. Lasky et al. 2014; Kraft, Godoy, and Levine 2015; Kunstler et al. 2016; Ousterhout et al. 2019), even when more than two species are involved in a community.

These "species pair" approaches assume that a focal species is simply influenced by the sum of all pairwise interactions between itself and its direct neighbours, although such an additive assumption has been long recognised to likely be a major oversimplification. Indirect interactions with another intermediary species outside of the isolated pair, for instance, are thought to be able to non-additively impact a focal species as well (Abrams 1983; Adler and Morris 1994; Billick and Case 1994; Wootton 1994). Non-additivity arises when the intermediary species does not only directly interact with the focal species, but also induces behavioural or plastic changes in the direct-neighbour species, thereby modifying the direct-interaction strength or direction between the focal pair (Abrams 1983; Wootton 1994). This means that the whole biotic effect that a focal species experiences can be more than the sum of all direct effects from both the direct- and intermediary-neighbour species. Regardless of their mechanistic basis (which we discuss in the next paragraph), signals of this non-additivity can be statistically detected by fitting quadratic or interaction terms in a phenomenological model (Letten and Stouffer 2019). Recently, Mayfield and Stouffer (2017) presented an analytical framework to quantify and compare direct, pairwise

interactions to indirect HOIs through an extension of the phenomenological Lotka–Volterra competition model. The basis of this framework is a regression model that (i) fits the performance of focal species as an additive response to pairwise-interaction effects from direct neighbours and (ii) also includes higher-order quadratic terms to allow the strength of these pairwise interactions to be moderated by species outside of or within the focal pair (i.e. introduces density-dependence to the pairwise-interaction coefficients). Testing if these higher-order quadratic terms are non-zero without sacrificing model parsimony therefore allows us to determine whether or not observed community dynamics can be sufficiently described by pairwise interactions alone.

Various biological mechanisms have been proposed as to how intermediary species may modify the interaction between a focal pair, as well as the conditions under which HOIs should be most prevalent. In multi-trophic systems, for example, the mere presence of a top predator may induce behavioural change in a meso-predator thus modifying the latter's predation rate on its prey (Adler and Morris 1994). In single-trophic plant–plant interactions, an intermediary species may indirectly influence the focal species by causing plastic change in the direct competitor of the focal species. For instance, the presence of a deep-rooted intermediary species may cause a direct-competitor species to produce shallower roots and hence compete more intensely with a shallow-rooted focal species (Levine et al. 2017). Similarly in a light-limiting forest, an intermediary species just outside of a focal species' light-interception radius may shade the focal species' direct neighbours, thereby preventing (or delaying) the direct neighbours from attaining a taller canopy position to shade the focal species. These indirect mechanisms between the intermediary and focal species will manifest phenomenologically as non-negligible HOIs, and are expected to be common in systems where resource-acquisition traits such as size are themselves density dependent (Kleinhesselink, Kraft, and Levine 2019). This is because the intermediary species depletes more resources from the focal pair while simultaneously altering the focal pair's size growth. This double impact shifts the focal pair's ability to acquire and deplete each other's resources thereby modifying their pairwise interaction strength. In addition, HOIs also emerge when species have nonlinear functional responses to resource availability (Letten and Stouffer

2019). Consider, for example, a saturating functional response such as the size growth–light availability relationship in many plants (Rüger et al. 2011; Poorter et al. 2019): at low neighbour density, light resource is plentiful; a small increase in neighbour density thus depletes light at the plateau of the focal's light-response curve, where the competitive impact on size growth is minimal. However, the impact on size growth becomes greater when subsequent increases in neighbour density deplete light toward the steeper region of the focal's light-response curve. Importantly, such a non-constant density dependence can happen to the focal pair even without an interaction-modifying third, intermediary species (Kleinhesselink, Kraft, and Levine 2019; Letten and Stouffer 2019).

Tropical tree communities naturally meet these conditions under which HOIs are predicted to prevail, yet studies that test for HOIs remain scarce in this system. Tropical forests are known for their high primary productivity (Gillman et al. 2015) and biomass accumulation rate during succession (Poorter et al. 2016), which lead to rapid canopy closure that imposes strong light limitation to the understorey (van Breugel et al. 2013; Yee et al. 2019). While HOIs can already arise from the nonlinear size-growth response of tree individuals to light extinction due to increasing neighbour densities, the fact that size itself also determines how much light is depleted through shading allows even more room for intermediary species to modify pairwise interactions and give rise to HOIs. Moreover, the relative longevity of perennial trees provides more time for these indirect biotic effects to build up and manifest as detectable HOI signals. In this study, we therefore examine if HOIs are important descriptors of the diameter growth of ten interacting tree species in a tropical secondary forest system. Although there are many tropical forest studies on density dependency (e.g. Harms et al. 2000; Uriarte et al. 2004; Comita et al. 2010; Kunstler et al. 2016), the vast majority of them consider only direct, not higher-order, interactions (but see Li et al. 2020). With increasing empirical evidence showing pronounced effects of HOIs on multi-species dynamics (e.g. Weigelt et al. 2007; Mayfield and Stouffer 2017; Li et al. 2020; Xiao et al. 2020), it is becoming important to assess the ubiquity of non-negligible HOIs across natural systems. If HOIs are widespread and emerge easily under a wide range of conditions

(Kleinhesselink, Kraft, and Levine 2019; Letten and Stouffer 2019), their effects need to be captured by community models in order to accurately predict the outcome of multi-species interactions both quantitatively (e.g. abundance and size distributions) and qualitatively (e.g. coexistence vs. competitive exclusion; Levine et al. 2017). We expect HOIs to emerge in our tropical forest site and if so, adds to the growing empirical evidence for HOIs in annual and perennial plant communities (Mayfield and Stouffer 2017; Li et al. 2020; Xiao et al. 2020).

Methods

Data collection

The community data originated from Yee et al. (2019) who surveyed a secondary lowland tropical forests in the Central Catchment Nature Reserve, Republic of Singapore (known locally as the 'Mandai forest'; 1°24.8′N, 103°47.5′E). Regenerating for at least 80 years, the Mandai forest is a mixture of young and old secondary forest patches characterised by both early- and late-successional native plant species (Yee et al. 2016). The climate is tropical with annual precipitation of 1,300–2,700 mm yr^{-1} and mean daily temperatures of 26–29°C across the study period. Yee et al. (2019) originally designed the study to track the recovery of woody plant communities from a windstorm disturbance on 11 February 2011. Within 3 months following the windstorm, forty 10×10 m^2 plots were established randomly in blowdown areas delimited by the National Parks Board of Singapore from an aerial survey with a minimum 40 m distance between plots. Five annual censuses were conducted between April and August in 2011–2015, during which we counted, identified and measured the diameter-at-breast-height (DBH, cm) of all woody stems ≥ 1 cm DBH in each plot.

For this study, we selected the 10 focal tree species that were the most common species by abundance and provided sufficient data for the analyses that follow. These species naturally span a range of slow-to-fast diameter growth and included *Archidendron clypearia* (Jack) I. C. Nielsen, *Calophyllum wallichianum* Planch. & Triana var. *incrassatum*, *Elaeocarpus mastersii* King,

Garcinia parvifolia Miq., *Gironniera nervosa* Planch., *Macaranga bancana* (Miq.) Mull. Arg., *Palaquium obovatum* (Griff.) Engl., *Prunus polystachya* (Hook. f.) Kalkm., *Syzygium borneense* (Miq.) Miq., and *Timonius wallichianus* (Korth.) Valeton. Total abundances of each focal species range from 75 to 687 (median = 213) giving a total of 2,481 observations (see Table S1 in Supplementary Information).

Analyses

We calculated the absolute growth rate, $G_{m_i,p,q}$ (cm yr^{-1}) of focal individual m in species i observed in plot p and year q as the increment in diameter, D (cm) between the census intervals (yr): $G_{m_i,p,q} = \frac{D_{m_i,p,q+1} - D_{m_i,p,q}}{t_{q+1} - t_q}$, and then modelled growth as a function of diameter using the size-decline growth equation (Zeide 1993, see also Chong et al. 2017),

$$G_{m_i,p,q} = aD^b_{m_i,p,q} e^{-cD_{m_i,p,q}} \,. \tag{1}$$

In Equation 1, parameter a mainly determines the initial growth rate at small diameters; b influences is the 'size expansion' component of diameter growth and describes the power relationship between absolute growth rate and size; and c describes the exponential decline in absolute growth rate with size due to various ecological limitations. As all of a, b, and c are expected to be positive and non-zero, Equation 1 qualitatively predicts absolute growth rate to increase with diameter at smaller sizes followed by a decline as size increases. This results in the hump-shaped growth–diameter relationship commonly observed in many tree species and forest systems (e.g. Kunstler et al. 2016) including ours.

The diameter–growth relationship given by Equation 1 was originally intended to be fit to data from a single species. To accommodate our community data pooled across multiple species, we expanded Equation 1 under the multilevel modelling framework such that each of the growth parameters (a, b, and c) are partitioned into population-level estimates ('fixed effects') and multiple species-specific estimates ('random effects'). First, we assumed the absolute growth rate, $G_{m_i,p,q}$ to follow a lognormal distribution with mean $\mu_{m_i,p,q}$ and variance σ_i^2, which reflects the

natural constraints and hence skewness of growth data:

$$
\begin{aligned}
G_{m_i,p,q} &\sim \text{lognormal}(\mu_{m_i,p,q}, \sigma_i^2) \\
\mu_{m_i,p,q} &= f(D_{m_i,p,q}) \\
&= \log a + b \log D_{m_i,p,q} - c D_{m_i,p,q} \qquad (2) \\
&= a' + b \log D_{m_i,p,q} - c D_{m_i,p,q}\,. \qquad (3)
\end{aligned}
$$

Note that we reparameterised Equation 2 to 3 by defining the logarithmic initial growth rate at small diameters, $a' = \log a$, so that the three growth parameters a', b, and c had more similar scales which assisted model convergence.

In our multilevel model, a', b, and c are then estimated to respectively be a'_0, b_0, and c_0 on average while varying by a'_i, b_i, and c_i for species i. To further account for spatiotemporal variations in diameter growth, we included both plot-specific and year-specific effects—a'_p and a'_q—on the average logarithmic growth rate a', such that:

$$
\begin{aligned}
a' &= a'_0 + a'_i + a'_p + a'_q \\
b &= b_0 + b_i \\
c &= c_0 + c_i\,.
\end{aligned}
$$

Incorporating plot 'random' effects also helps to account for differences in edge effects in our spatially-implicit model, and together with the year 'random' effect they account for the residual effects of other rarer non-focal species. Equation 3 hence becomes:

$$
f(D_{m_i,p,q}) = (a'_0 + a'_i + a'_p + a'_q) + (b_0 + b_i) \log D_{m_i,p,q} - (c_0 + c_i) D_{m_i,p,q}\,. \qquad (4)
$$

To incorporate biotic interactions amongst the ten focal species into the diameter–growth equation, we first modified Equation 4 to include the cumulative effect of direct interactions with neighbouring species, $g(A_{j,p,q})$ on $G_{m_i,p,q}$ in a generalised Lotka–Volterra fashion:

$$
\begin{aligned}
\mu_{m_i,p,q} &= f(D_{m_i,p,q}) + g(A_{j,p,q}) \qquad (5) \\
g(A_{j,p,q}) &= -\sum_{j=1}^{10} \alpha_{ij} A_{j,p,q},
\end{aligned}
$$

where $A_{j,p,q}$ is the total basal area (cm^2) of neighbour species j in plot p and year q, and α_{ij} are

pairwise interaction coefficients that quantify the per-basal-area direct effects of species j on growth of the focal species i. We generalised the Lotka–Volterra form in Equation 5 such that α_{ij} can be positive or negative to encompass both competitive and facilitative interactions. The cumulative effect of direct interactions on focal species i is then the sum of $\alpha_{ij}A_{j,p,q}$ across the ten neighbour species. Note that when $i = j$, $\alpha_{ij} = \alpha_{ii}$ is the measure of intraspecific direct interaction.

We next incorporated cumulative effects of indirect, higher-order interactions (HOIs) amongst species into Equation 5 following Mayfield and Stouffer (2017):

$$\mu_{m_i,p,q} = f(D_{m_i,p,q}) + g(A_{j,p,q}) + h_{\text{intra}}(A_{j,p,q}) + h_{\text{inter}}(A_{j,p,q}) \tag{6}$$

$$h_{\text{intra}}(A_{j,p,q}) = -\sum_{j=1}^{10} \beta_{ijj} A_{j,p,q}^2 \tag{7}$$

$$h_{\text{inter}}(A_{j,p,q}) = -\sum_{j=1}^{10} \sum_{k=j+1}^{10} \beta_{ijk} A_{j,p,q} A_{k,p,q}\,. \tag{8}$$

where β_{ijj} captures the higher-order (i.e. quadratic) effect of neighbour j on the direct interaction between species j and focal species i, and is hereafter coined ‘intraspecific HOI’ (after Mayfield and Stouffer 2017) as this higher-order term takes place between conspecifics of species j. On the other hand, β_{ijk} captures the higher-order effect of a heterospecific neighbour k’s total basal area, $A_{k,p,q}$ on the direct interaction between neighbour species j and focal species i, and is hereafter coined ‘interspecific HOI’. In Kleinhesselink, Kraft, and Levine (2019), the intraspecific HOI terms, β_{ijj}, were referred to as ‘soft HOIs’ since they still only involve the directly interacting species pair. This also helps distinguish them from the interspecific ‘hard’ HOI interactions, β_{ijk}, that involve a third species that could modify how the first two species interact in a multi-species community. In this study, we include both soft and hard HOIs in the HOI-inclusive model as they all capture non-additivities in any neighbour species’ biotic influence over the focal species. Alternatively, Equation 7 and 8 can be equivalently written as:

$$h_{\text{intra}}(A_{j,p,q}) = -\beta_{iii}A_i^2 - \sum_{j\neq i}^{10} \beta_{ijj}A_j^2$$

$$h_{\text{inter}}(A_{j,p,q}) = -\frac{1}{2}\sum_{j\neq i}^{10} \beta_{iij}A_iA_j - \frac{1}{2}\sum_{j\neq i}^{10} \beta_{iji}A_jA_i - \sum_{j\neq i}^{10}\sum_{k=j+1}^{10} \beta_{ijk}A_jA_k$$

so that the intra- and interspecific direct interaction coefficients can each be compared to their HOI counterparts: namely, (i) α_{ii} with β_{iii} and $\frac{1}{2}\beta_{iij}$ and (ii) α_{ij} with $\frac{1}{2}\beta_{iji}$, β_{ijj}, and β_{ijk}.

Model fitting

Prior to analysis, zero and negative growth data were removed (15% and 9% of observations, respectively) because the lognormal diameter–growth model only allows for non-zero, positive growth. We discuss a few caveats related to such data filtering in the *Discussion* section. Prior to model fitting and to assist model convergence, we standardised D to unit standard deviation and also normalised and standardised A to a mean of zero and unit standard deviation. We fit three models in total (Equations 4, 5, and 6) and estimated the parameters through Bayesian inference by fitting non-linear hierarchical models via `Stan` (Stan Development Team 2018) using the `brm` function in the `brms` package (Bürkner 2017) in `R`. For the population-level 'fixed' parameters, we used a weakly informative Normal(0, 10) prior for a_0' and Halfnormal(0, 10) priors for both b_0 and c_0. For the standard deviations of group-level 'random' parameters (i.e. all parameters with subscript i, p, or q, including α and β), we used a weakly informative Student-t prior with 3 degrees of freedom, zero mean and one standard deviation. The parameter posterior distributions were obtained after four chains of 3,000 Hamiltonian Monte Carlo (HMC) warmup iterations followed by 1,000 HMC sampling iterations. We considered models as converged when the $\hat{R}$ value of all parameters across chains were < 1.05 (Vehtari et al. 2019).

Model comparison

To assess if the inclusion of direct and/or higher-order interaction terms are necessary for a parsimonious explanation of diameter growth, we compared the null, direct-interaction-only, and HOI-inclusive models using three goodness-of-fit measures: Bayes R^2, Widely Applicable

Information Criteria (*WAIC*), and 10-fold Cross Validation Information Criteria (*CVIC*). These goodness-of-fit measures were chosen to complement one another: Bayes R^2 quantifies the expected fit or variance explained by a model; both *WAIC* and *CVIC* also measure the expected fit of a model, but *WAIC* penalises a model with a greater number of effective parameters, whereas *CVIC* penalises a model that overfits the training dataset and hence predicting poorly on the test dataset. Bayes R^2, *WAIC*, and *CVIC* were computed for the whole dataset, as well as for each focal species separately. Because both *WAIC* and *CVIC* are sums across observations, they need to be standardised to a fixed number of observations so they can be fairly compared among focal species that varied in sample size. Therefore, for each species we additionally bootstrapped its observations with replacement to $n = 75$, which is the lowest number of observations among the 10 focal species. We performed this resampling 1,000 times and obtained the median *WAIC* and *CVIC* with distribution percentiles at $n = 75$. For the 10-fold cross validation, each model was refit 10 times each leaving out one-tenth of the original data.

Simulation

The above analysis examines variation in instantaneous annual diameter growth rate. We additionally want to explore how the exclusion or inclusion of HOI in modelling would influence predicted forest-stand structure and community dynamics over a longer timeframe. To do so, we used both the direct-interaction-only and HOI-inclusive models to numerically simulate the temporal change in diameter for each focal species growing under three recruitment scenarios (described in more detail below). All simulations were assumed to take place under an average spatiotemporal condition, so both plot and year effects (a_p and a_q) were set to zero in each time step.

To have a realistic initial neighbourhood composition, we used a joint species distribution model previously published from the same study site (Lai et al. 2020) to predict the recruitment of each focal species in a given plot under fully-open canopy and other environmental variables at their averages in the first census since wind disturbance. We specifically compared ‘low’,

‘median’, and ‘high’ initial recruitment scenarios, which correspond to the 5th, 50th, and 95th percentiles of predicted recruitments. Because the Lai et al. (2020) model also predicts that recruitment of other non-focal species would constitute roughly half (50.9%) of the total recruitment across species in a plot, we replaced these non-focal recruits with our focal recruits by doubling the predicted focal recruitments to obtain the focal species’ initial abundances; this resulted in 16, 26, and 46 initial stems for the ‘low’, ‘median’, and ‘high’ initial recruitment scenarios, respectively (Table S2). We assumed all recruits to begin at DBH = 1 cm and then calculated both A_j and A_k as the initial neighbourhood densities. We then used parameters inferred from both the ‘direct-interaction-only’ model (Equation 5) and the ‘HOI-inclusive’ model (Equation 6) to simulate individual diameter growth of focal species under the three recruitment scenarios at daily timesteps over two years—the time taken for canopy closure in our study site (Yee et al. 2019).

Results

Compared to both the null and direct-interaction-only models, the HOI-inclusive model had a greater predictive accuracy across the pooled or species-specific observations, as judged by Bayes R^2 (Fig. 1a). A greater R^2 is not surprising given that the HOI-inclusive model has approximately 83 more effective parameters. Nevertheless, the HOI-inclusive model was still judged by both *WAIC* and 10-fold cross validation (*CVIC*) as a far better model for the pooled data (Figs 1b and 1c). When *WAIC* and *CVIC* were resampled and calculated for each species separately, the HOI-inclusive model performed better than both the null and direct-interaction-only models ($\Delta WAIC < -2$ and $\Delta CVIC < -2$) for four out of the ten focal species as well as for all species combined, but performed as well or worse for the other six focal species.

The standardised HOI coefficients (β’s) have magnitudes that are comparable to those of direct interactions (α’s; Fig. 2). Almost all (90%) direct-interaction coefficients between conspecifics (α_{ii}’s) are positive (i.e. competitive); their corresponding HOI coefficients are mostly

positive (69%) but roughly one-third (31%) have the opposite sign (Fig. 2a). In contrast, both the interspecific direct interactions (α_{ij}'s) and their corresponding HOI coefficients are more equally spread across the positive and negative domains (54%–46% and 61%–39%, respectively; Fig. 2b).

In combination with the observed range of neighbour basal areas, these direct interactions and HOIs cumulatively reduced focal species' annual diameter growth rates by varying magnitudes (Figs 3 and 4). Under the average neighbour basal areas, HOIs tend to further reduce the diameter growth rates of most species beyond what direct interactions had already reduced (Fig. 3). In the observed data, the median cumulative effects of intraspecific direct interaction, $e^{-\alpha_{ii}A_i}$ ranged between 0.80–1.00 across focal species (i.e. observed growth rate was reduced to 80% of its maximum value or not changed by direct interaction; X axis in Fig. 4a), whereas the median cumulative effects of the HOIs, $e^{-\beta_{iii}A_i^2-\frac{1}{2}\sum_{j\neq i}^{10}\beta_{iij}A_iA_j}$, which modify intraspecific direct interactions had a narrower range between 0.93–1.00 (Y axis in Fig. 4a). On the other hand, the median cumulative effects of interspecific direct interaction, $e^{-\sum_{j\neq i}^{10}\alpha_{ij}A_j}$ had a narrower range (0.96–1.03) than their corresponding interaction modifiers, $e^{-\sum_{j\neq i}^{10}\beta_{ijj}A_j^2-\frac{1}{2}\sum_{j\neq i}^{10}\beta_{iji}A_jA_i-\sum_{j\neq i}^{10}\sum_{k=j+1}^{10}\beta_{ijk}A_jA_k}$ that lied between 0.86–1.02 (Fig. 4b). Combined, there is a weak negative association between the median cumulative effect of all HOIs, $e^{h_{\text{intra}}(A_j)+h_{\text{inter}}(A_j)}$ (ranged 0.79–1.00) and that of all direct interactions, $e^{g(A_j)}$ (ranged 0.70–1.01)—though this seems to be mainly driven by focal species with the HOI-inclusive model as best-supported by *WAIC*—resulting in most focal individuals having their observed diameter growth fall between half of and equal to their average potential growth rates due to all biotic interactions in combination (0.62–1.01; Fig. 4c).

In addition to the aforementioned *instantaneous* effect of HOIs on focal species' diameter growth, we examined the *short-term* effect of HOIs by simulating the ten focal species growing together over two years under low, median, and high recruitment scenarios, and then compared the community size structures resulting from the direct-interaction-only and the HOI-inclusive models (Fig. 5). Between the two models, we found that differences in community size structure at the end of the second year became more apparent as initial recruitment increased. Especially in

the high-recruitment scenario, species that grew largest as predicted by the direct-interaction-only model (Fig. 5a) experienced disproportionally greater growth reductions when HOIs were taken into account (Figs 5b and c). On the other hand, species that reached smaller sizes seemed to be less impacted by model choice (Fig. 5c). The inclusion of HOIs thus resulted in less size asymmetry among individuals, and this was especially true for denser communities (bottom panel in Fig. 5b). As a result of the growth reductions that realised under HOIs, rank swaps in the final diameter between models occurred more frequently and with greater magnitudes as the initial recruitment increased, even for the focal species whose HOI-inclusive model was not the best model as judged by either *WAIC* or *CVIC* (Fig. S2). Across recruitment scenarios, simulations that included HOIs also showed earlier signs of plateauing in diameter increment at about 1.5 years into the simulation (Fig. 5b), compared to the direct-interation-only simulation which proceeded without clear signs of growth slowing down (Fig. 5a).

Discussion

Building on early literature that questioned the consequences of ignoring non-additive biotic interactions (e.g. Neill 1974; Abrams 1980; Wootton 1994), recent empirical works have provided evidence for non-negligible higher-order interactions (HOIs) in various natural systems (e.g. Weigelt et al. 2007; Mayfield and Stouffer 2017; Li et al. 2020; Xiao et al. 2020) and prompted theoretical research into the conditions under which HOIs should be expected to emerge (Kleinhesselink, Kraft, and Levine 2019; Letten and Stouffer 2019). Tropical forests meet two of the proposed conditions for emergent HOIs: resource acquisition traits, such as size, that are themselves density-dependent and growth in size that responds non-linearly to resource availability. Using a tropical secondary forest dataset from Singapore, we examined how the size–growth relationships of ten interacting tree species changed additively with direct interactions and non-additively with HOIs. We found that HOIs have comparable standardised effect sizes to direct interactions, and are non-negligible at the community level and important for

at least four out of ten focal tree species at the species level in this dataset. Across these species, HOIs tend to further reduce their instantaneous diameter growth rates beyond what direct interactions had already reduced. Even for the other focal species that were less sensitive to the instantaneous effect of HOIs, HOIs could still influence their diameter growth rate by suppressing their competitors' or facilitators' size over a longer period of time (as discussed below).

The primary role of HOIs in our study system seems to be reducing the size discrepancy or asymmetry among species during succession in forest gaps. As basal area builds up in a community, the strength of biotic interactions intensifies with accelerating rates due to non-additive HOIs, quickly preventing fast-growing species from attaining disproportionately large sizes and shading their smaller neighbours. By preventing or delaying competitive exclusion through shading in light-limited environments, HOIs hint at a suite of stabilising mechanisms that are crucial to diversity maintenance (Grilli et al. 2017; Levine et al. 2017). Although our phenomenological model does not mechanistically point out what the exact stabilising processes are and how they operate, it adds to the accumulating empirical support for HOIs in plant communities by demonstrating the presence of non-additive biotic interactions in perennial plant systems. While the next step is obviously the search for mechanisms, we can already conclude that an accurate understanding of diameter growth across life stages not only requires the specific information of a tree's direct neighbours (e.g. Uriarte et al. 2004; Comita et al. 2010; Kunstler et al. 2016), but also that of other indirectly interacting intermediary species. Our results suggest that ignoring such non-additivities tend to overestimate the rate of structural development, which can be more prone to happen during the early stages of succession (especially in regions with higher productivity, greater propagule pressure, and/or more diverse species pool), when light depletion happens more rapidly and the nonlinear size-growth responses of tree species constantly regulate the interaction strengths among themselves. Such an overestimation can also propagate when projected over a longer period or summed across a spatial extent that is much larger than the size of our study plots.

At the species level, the HOI-inclusive model provided a better predictive accuracy for four

out of ten focal species, was only marginally better than the null or direct-interaction-only model for three other focal species, and was worse than or had no improvement over the null model for the remaining three focal species. Though this may seem to indicate that most species are insensitive to HOIs, we argue that HOIs should not be considered unimportant for these species in a community-wide context. For observational data, the results for any given focal species can depend as much on what that species is as with which neighbours it happens to be observed. As a result, there are contexts in which a species that is more sensitive to direct than higher-order interactions can still be affected by HOIs: for example, when it is directly responding to an HOI-sensitive direct neighbour. This could be especially prevalent when this type of neighbour species is locally common or attains large sizes. In our short-term simulation, for example, *Macaranga bancana* (labelled MACABA) was a focal species with the direct-interaction-only model performing better than the HOI-inclusive model. When HOIs were taken into account during simulation, *M. bancana* was less impacted thus maintaining its top size rank unlike the HOI-sensitive species *Prunus polystachya* (labelled PRUNPO). Nonetheless, individuals of *M. bancana* still exhibited some degrees of growth reduction as they responded to changes in the size of their HOI-sensitive neighbours. Furthermore, seemingly weak HOI-effects on the *instantaneous* diameter growth rates of HOI-insensitive species can accumulate and become long-lasting when *integrated* over the longer lifecycle of perennial plant species (as demonstrated in our simulations), as well as over larger spatial extents encompassing whole populations. Future studies should be aware that HOIs—as well as direct interactions—may be common but are simply too weak to be detected (Abrams 1983; Billick and Case 1994; Kleinhesselink, Kraft, and Levine 2019), especially over very short time-scales or if HOIs are only important at a certain life stage.

The context-dependence of HOIs begs the question "what is the right scale to test for HOIs?" Over very short time-scales, HOIs emerge when an intermediary species instantaneously modifies the interaction strength between a focal pair. Even if HOIs have minimal instantaneous effects, over a longer timeframe a focal species could still experience indirect interactions when the biotic

effects of intermediary species domino through the direct neighbours via an interaction chain. Although HOIs and interaction chains have been treated as distinct phenomena resulting from indirect interactions (e.g. Billick and Case 1994), our perennial-plant system presents a case for HOIs and interaction chains representing two ends of a temporal scale (Levine et al. 2017; Letten and Stouffer 2019). Given that negligible HOIs do not preclude non-additivity due to interaction chains, it follows that the *neighbours' response to* biotic interactions can be just as important as the focal's response, because the former continuously determines the neighbours' size and hence their cumulative *effects on* the focal species. Indirect interactions therefore challenge how we conceptualise a focal individual's biotic milieu or interaction radius: does it extend from a single spatial point as in many pairwise-interaction studies (e.g. Uriarte et al. 2004; Adler, Ellner, and Levine 2010; Comita et al. 2010) or should it be a larger area that includes the neighbours' neighbours and their decaying yet percolating effects on the focal individual?

Due to limited data, we only examined one of the many vital rates impacting perennial plants: size growth. We also lack the data to examine how the effects of biotic interactions on such a single vital rate carry over to influence the final reproductive fitness and hence per capita population growth—the key variable of modern coexistence theory. Other vital rates (e.g. survival and reproduction) that contribute unequally to per capita population growth (Moll and Brown 2008; Adler et al. 2014; Visser et al. 2016) can offset the strong biotic effects on size growth and provide stabilising niche differences through their unequal contributions to overall performance (Broekman et al. 2019). Some of the negative or zero diameter growth rates that were omitted from analysis could be early signs of a focal individual experiencing fatal biotic interactions (Bigler et al. 2004). A stronger test of coexistence demands the quantification of the relative contribution of direct and higher-order interactions to multiple vital rates across life stages, and then the estimation of net effects of these biotic interactions on per capita population growth using tools such as population integral projection models (e.g. Chu and Adler 2015). Knowing species' responses to neighbourhood density in terms of other vital rates will also allow us to improve our diameter–growth simulation (or any other simulation of community dynamics) by

incorporating mortality and recruitment.

As the size growth of perennial plants is not only density dependent but also size dependent, another approach is to allow biotic interactions to not only influence the initial diameter growth rate (i.e. the parameter a as in this study) but also the ontogenetic effect of size on growth (i.e. the parameter c in Equation 1). The latter allows one to test if larger-sized individuals are less sensitive to biotic interactions, and if such a size-conferred storage effect is important in stabilising size-structured communities (Warner and Chesson 1985; Kohyama 1993). Doing so, however, not only further increases the number of parameters in a model that is already data-hungry, but also demands more data collection from larger individuals that are inherently rare in the field (Needham et al. 2018). Facing the dilemma between trying to fully capture the interplay between size-dependence and density-dependence while keeping the question statistically and logistically tractable, a solution may be to select only a few interaction coefficients that are non-zero with different statistical approaches and biological foresight. In this and many previous studies (including those that lumped species into conspecifics versus heterospecifics), the decision to include or not HOIs has been treated as an "all or none" question, tantamount to assuming that HOIs from all neighbour species are either equally important or equally unimportant. Although there have been attempts to identify important neighbour species by fitting numerous nested models varying in the identity and number of neighbour species (e.g. Mayfield and Stouffer 2017), implementing this in the Bayesian framework can be computationally impractical. The advancing field of Bayesian variable or model selection (Tenan et al. 2014) can be a good place to start looking for a solution to relax this biologically irrational "all or none" assumption.

Conclusion

We showed that HOIs are a non-negligible phenomenon at the community level in a tropical forest and an important predictor of diameter growth for a subset of focal tree species. Our study represents one of the early attempts to search for HOIs' ubiquity in perennial plant systems. With

a high number of HOI parameters that increase exponentially with species number, we expected the effects of most HOIs to be small if not undetectable. Yet we detected the presence of HOIs even with a relatively small dataset, suggesting that many larger datasets can reveal more conclusively the true prevalence and magnitude of HOIs. Though our small dataset limited us to a handful of focal species, the fact that these focal species are all common implies that HOIs are necessarily a widespread phenomenon experienced by many tree *individuals* across the landscape, even if HOIs turn out to be "unimportant" to a large number of rarer species. Last but not least, the empirical quantification of HOIs can only inform us so much about the where and when of biological non-additivity. Much is left to be discovered about the mechanistic why and how of this emergent phenomenon in multi-species communities.

Author contributions

HRL and DBS conceived of the research idea; HRL and KYC collected the data; HRL analysed the data and led the writing; HRL, KYC, MMM, and DBS discussed the results and commented on the manuscript.

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Data availability

Our data will be archived on GitHub upon acceptance.

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Supporting information

Table S1: Focal species information.

Table S2: Focal species initial recruitment at the beginning of diameter-growth simulation.

Figure S1: Diameter rank swap across focal species during growth simulation.

Figures

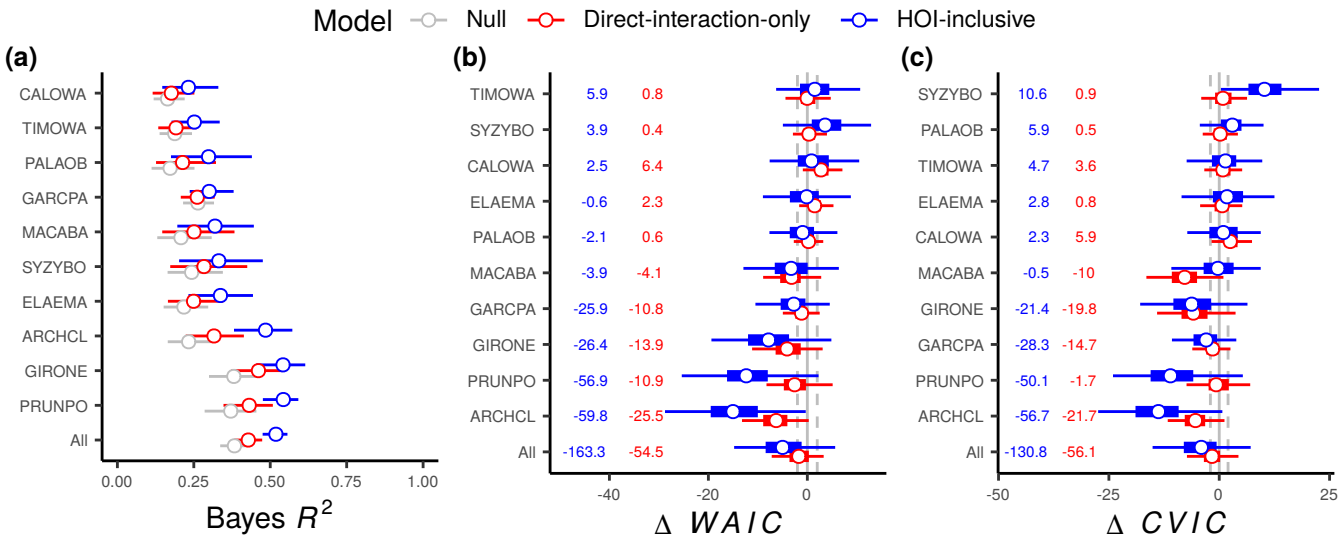

Figure 1: Comparing the goodness-of-fit among the null model (grey), direct-interaction-only model (red), and HOI-inclusive model (blue) in terms of **(a)** Bayes R^2, **(b)** difference in *WAIC*, and **(b)** difference in 10-fold cross-validation information criteria (*CVIC*) for each focal species or all combined. In **(a)**, circles and horizontal bars denote the median and 95% credible intervals of Bayes R^2, respectively. In **(b)** and **(c)** respectively, circles, thick and thin horizontal bars denote the median, 50% and 95%-tile intervals of the resampled $\Delta WAIC$ and $\Delta CVIC$ to $n = 75$ of both direct-interaction-only (red) and HOI-inclusive models (blue) compared to the null model, while vertical dashed lines denote ± 2 $\Delta WAIC$ or $\Delta CVIC$ from zero. The numbers adjacent to each species are the actual $\Delta WAIC$ or $\Delta CVIC$ summed across all observations without resampling.

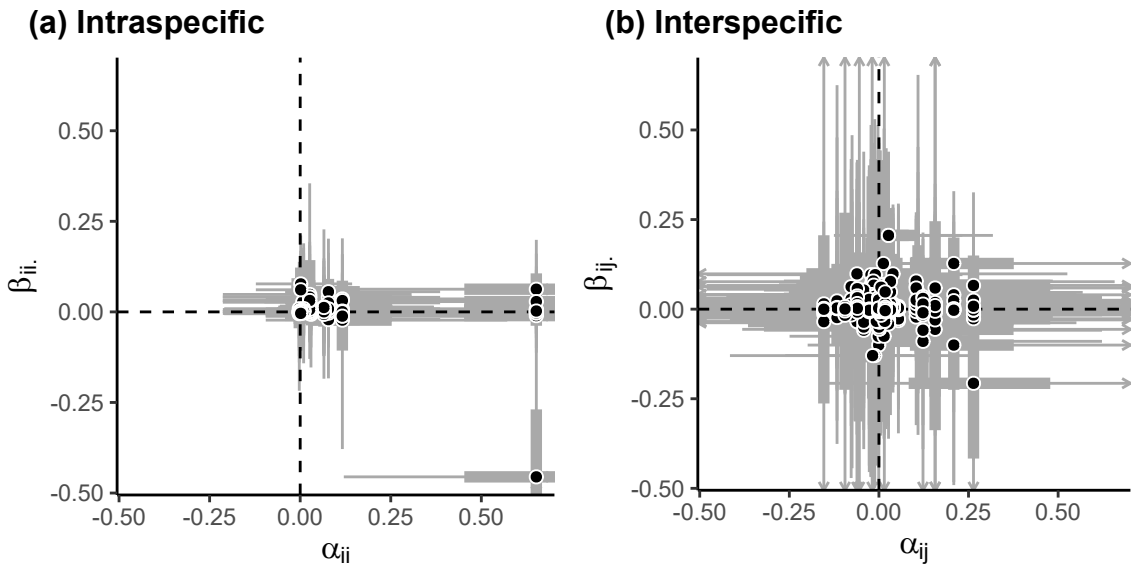

Figure 2: The relationship between direct-interaction coefficients (α's) and HOI coefficients (β's). Both axes are standardised coefficients that have comparable magnitudes. In **(a)**, intraspecific direct-interaction coefficients (α_{ii}) are plotted with their corresponding HOI coefficients (β_{iii} or $\frac{1}{2}\beta_{iij}$, together denoted $\beta_{ii.}$). Similarly in **(b)**, interspecific direct-interaction coefficients (α_{ij}) are plotted with their corresponding HOI coefficients ($\frac{1}{2}\beta_{iji}$, β_{ijj} or β_{ijk}, together denoted $\beta_{ij.}$). Points are median estimates with 50% and 95%-tile intervals across the posteriors (thick and thin bars; arrows denote 95%-tile intervals that extend beyond the plot limits).

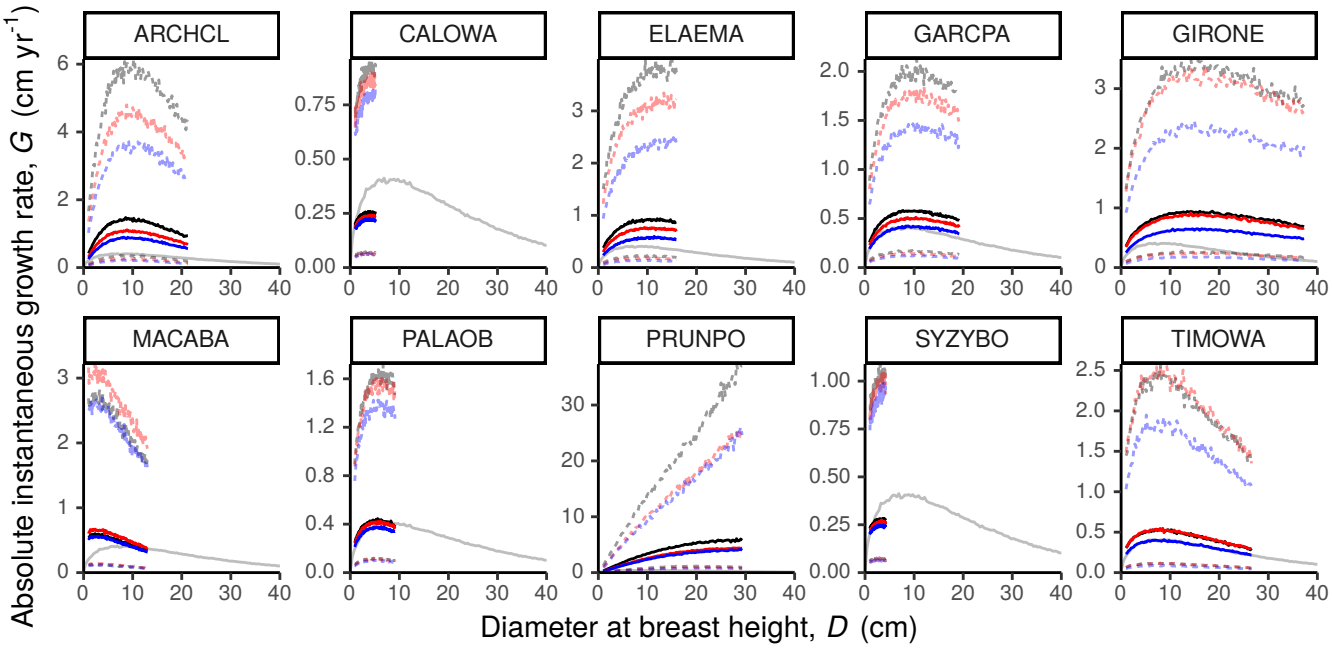

Figure 3: Predicted absolute instantaneous growth rate of focal species with increasing diameter-at-breast-height (DBH, *D*; cm) under three combinations of biotic interaction terms: no biotic interaction (black curves), direct interactions only (red), and all biotic interactions including HOIs (blue). For the two latter scenarios, predictions were made with all neighbours set at their average total basal areas at any space and time. Solid lines are the median predictions, whereas semi-transparent dotted lines below and above the median are lower and upper bounds of the 95% credible intervals. For a baseline for comparison, grey curves show the absolute growth rate of an 'average' species (prediction without species-specific 'random' effects) when all types of biotic interaction are taken into account. Note the different scales on the Y axes.

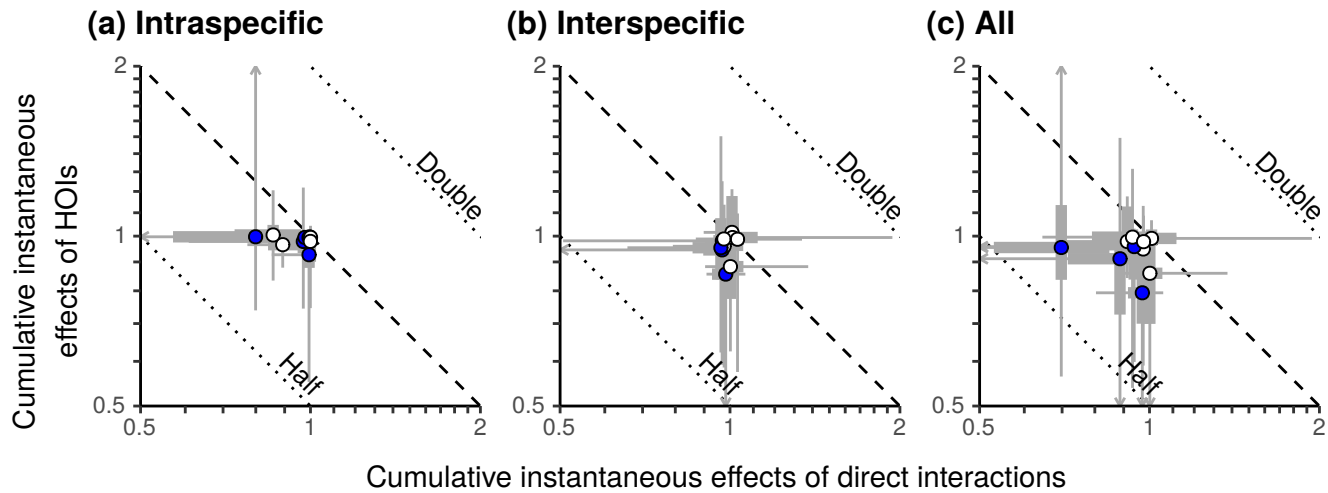

Figure 4: Comparing the observed cumulative effects of direct-interaction and HOI on the absolute instantaneous growth rate of focal species. In **(a)**, the cumulative effects of intraspecific direct interactions, $e^{-\alpha_{ii}A_i}$, are compared against their corresponding cumulative HOI effects, $e^{-\beta_{iii}A_i^2-\frac{1}{2}\sum_{j\neq i}^{10}\beta_{iij}A_iA_j}$. In **(b)**, the cumulative effects of interspecific direct interactions, $e^{-\sum_{j\neq i}^{10}\alpha_{ij}A_j}$, are compared against their corresponding cumulative HOI effects, $e^{-\sum_{j\neq i}^{10}\beta_{ijj}A_j^2-\frac{1}{2}\sum_{j\neq i}^{10}\beta_{iji}A_jA_i-\sum_{j\neq i}^{10}\sum_{k=j+1}^{10}\beta_{ijk}A_jA_k}$. In **(c)**, the cumulative effects of all direct interactions, $e^{g(A_j)}$ are compared against the cumulative effects of all HOIs, $e^{h_{\text{intra}}(A_j)+h_{\text{inter}}(A_j)}$. Both axes represent the proportional change in the average absolute diameter growth rate of a focal species: a focal species experiences decreased in growth rate when $0 <$ cumulative effects < 1 ('competitive effect') but increases in growth rate when cumulative effects > 1 ('facilitative effect'). Each circle represents a focal species' median with 50% and 95%-tile intervals across individuals (thick and thin bars; arrows denote 95%-tile intervals that extend beyond the plot limits). Blue filled circles are the four focal species with HOI-inclusive model as the best supported as judged by *WAIC* (see Fig. 1b). The dashed diagonal line denotes an isocline where there is no *total* proportional change in the absolute growth rate due to the total cumulative effect of both axes cancelling each other out, i.e. values of both axes multiply to 1. The lower and upper dotted diagonal lines denote a total cumulative effect that halves and doubles the absolute growth rate, respectively. Note the log-scale on both axes.

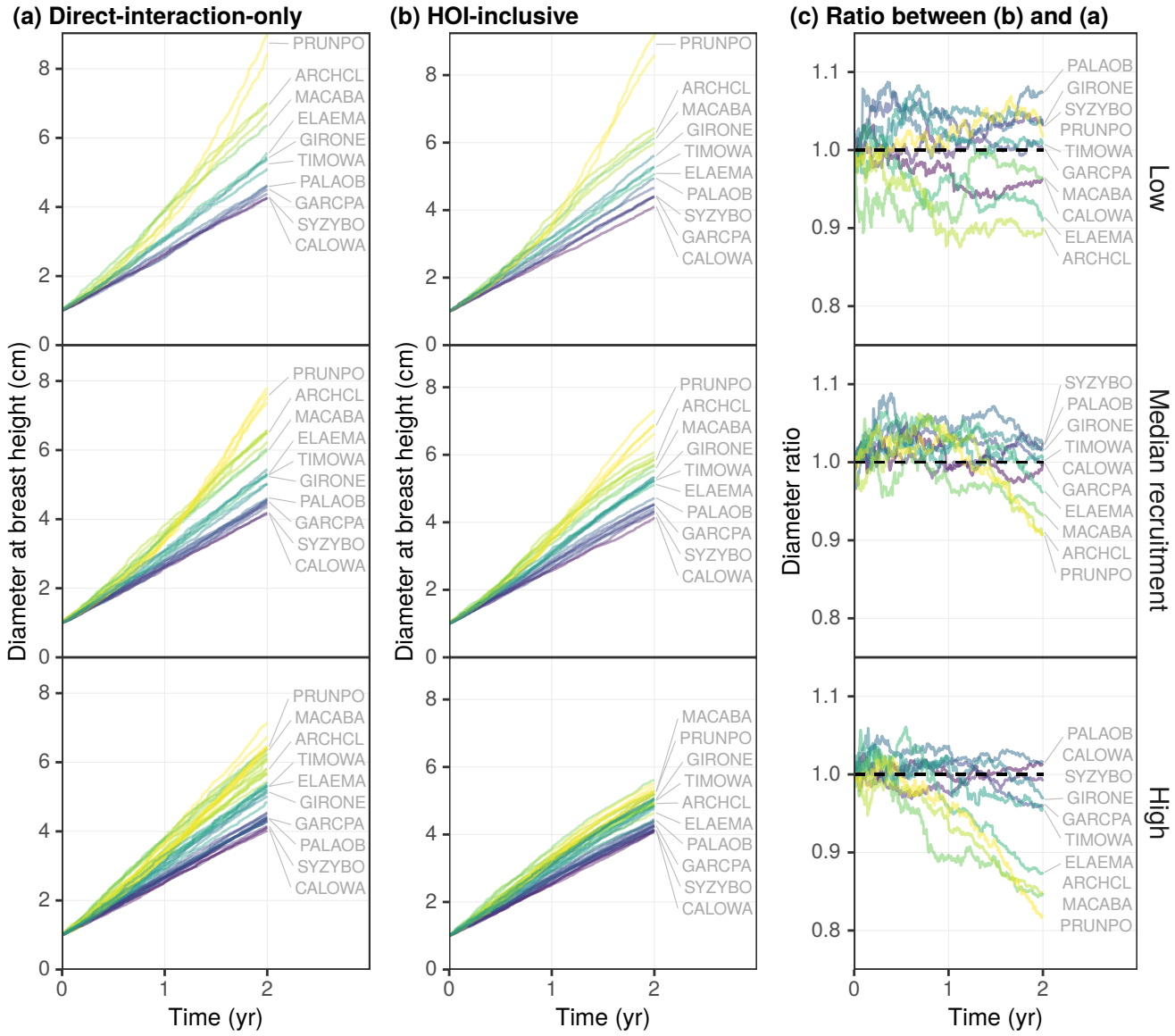

Figure 5: Two-year diameter-growth simulations of the ten focal species growing under low, median, and high recruitment scenarios: **(a)** predictions from the direct-interaction-only, **(b)** predictions from the HOI-inclusive model, and **(c)** the species-median ratio of simulated diameter between HOI-inclusive and direct-interaction-only models. In **(a)** and **(b)**, each line represent an individual tree colour-coded by species, according to their median final diameter under the median recruitment scenario. Species labels on the right mark the median value of each species. In **(c)**, each line is the median across all individuals per species for visual clarity.