

# Environmental gradients modify biotic interactions among tree species in temperate rain forest

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## Abstract

The realised niche is jointly shaped by both abiotic and biotic processes. Moreover, the strength and direction of biotic interactions may vary across abiotic conditions and generate non-additivities that, if ignored, could lead to inaccurate predictions of species responses to changes in environment and composition. We tested this idea by analysing nationwide forest inventory data that span broad environmental gradients throughout New Zealand. The use of Bayesian shrinkage priors enabled our conclusion that the most complex model—featuring biotic interactions that changed with vapour pressure deficit and higher-order interactions with intermediary species—had the highest predictive accuracy of tree diameter growth. That is, pairwise competition became pairwise facilitation, or vice versa, depending on atmospheric moisture and/or the density of a third species. Our study highlights the importance of the interplay between abiotic and biotic processes when predicting how biotic interactions may structure communities under global change.

## Introduction

The nature of the interplay between biotic interactions and the abiotic environment has been debated since the early conceptualisation of the ecological niche (Hutchinson 1957). Uncontrolled, observational field data usually reflect a species' *realised* niche jointly driven by both biotic and abiotic influences, rather than the fundamental niche shaped solely by abiotic influences (Kraft *et al.* 2015). Although the environmental dependence of biotic interactions is widely acknowledged by theoretical (Welden & Slauson 1986; Callaway & Walker 1997; Chesson 2000; Lam & Chisholm 2020; Koffel *et al.* 2021) and multitrophic empirical studies (Tylianakis *et al.* 2008; Chamberlain *et al.* 2014; Lanuza *et al.* 2018), biotic interactions between plant species have often been empirically treated as constants or implicit averages across environments (but see Soliveres *et al.* 2015; Bimler *et al.* 2018; Wainwright *et al.* 2019). If the strength or direction of biotic interactions between plant species change along environmental gradients and so are non-transferable across sites, we will be limited in our ability to predict how biotic interactions may structure communities under global change (Adler *et al.* 2012; Coomes *et al.* 2014; Copenhaver-Parry & Cannon 2016). The motivation for assuming abiotic independence may have its root in a sequential view of classical assembly rules (Diamond 1975), which depicts environmental filtering as a selection process that happens before, not concurrent with, biotic interaction (Kraft *et al.* 2015; Cadotte & Tucker 2017). Under this paradigm, abiotic factors would only determine which species are available to interact locally, but not *how* they interact (Dunson & Travis 1991).

Many proposed mechanisms of environmentally-dependent biotic interactions centre on non-additivity arising from indirect effects of environment on competition (Kleinhesselink & Adler 2015). The environment can indirectly influence a species' competitive ability by directly affecting its vital rates or its behaviour. For example, environmental conditions that promote faster growth of a competitor also cause the competitor to deplete shared resources more rapidly, thereby increasing its subsequent competitive impact on its neighbours (Tilman 1982). Environmental variability could also modify how individuals interact by inducing plastic changes in biomass, such as root expansion or leaf senescence during drought (Levine *et al.* 2017). Such indirect environmental effects are ignored in statistical discrete-time models that assume neighbour densities remain constant between sampling events (Billick & Case 1994; Kleinhesselink *et al.* 2019). In these models, the strength of competition is typically estimated by regressing current species performance against neighbour densities measured at a previous sampling event. If a competitor grew rapidly between infrequent sampling events due to favourable environmental or biotic conditions, a discrete-time model would overestimate its competitive effect on neighbours (Billick & Case 1994). To accurately estimate the strength of biotic interactions, it is therefore necessary for phenomenological models to include non-additive terms (i.e., competitor  $\times$  environment) to account for changes in competitor densities [e.g., Coomes & Allen (2007); Bimler *et al.* (2018); Kunstler *et al.* (2011); Box 1].

In addition to indirect environmental effects, biotic interactions can themselves contain indirect effects or non-additivities (Levine *et al.* 2017; Mayfield & Stouffer 2017). Like the emergent pathways of abiotic non-additivity, non-additive or so-called higher-order biotic interactions (HOIs) can arise from both nonlinear density dependence and interaction modifiers (Billick & Case 1994; Kleinhesselink *et al.* 2019). Nonlinear density dependence arises from nonlinear functional responses of an organism to resource availability; e.g., the saturating light response curve of a plant. If the resource is depleted by increasing densities of a competing neighbour, then the nonlinear functional response to a resource concentration translates into nonlinear *density* dependence (Billick & Case 1994; Pacala *et al.* 1996; Letten & Stouffer 2019). Because the resource is depleted at the plateau of the focal plant's functional response curve, an increase in neighbour density from zero has little effect on the focal plant's growth. In contrast, when the resource is depleted around the steeper region of the focal plant's response curve, the same increase in neighbour density will have a greater competitive impact. At the same time, the competitor also experiences the changing environment and its density will change between discrete sampling events. Non-additive biotic interactions are therefore expected to be prevalent in ecological systems where organisms have nonlinear functional responses to resources (Kleinhesselink *et al.* 2019; Letten & Stouffer 2019). Alternatively, in multispecies assemblages, pairwise interactions can be modified by a third, intermediary species [Levine *et al.* (2017); Box 1]. In a forest, for instance, an intermediary-neighbour tree that shades a directly competing tree can cause the direct neighbour's phototropic crown to grow closer to the focal tree, thereby further depleting light for the focal tree. The key difference between non-additivity due to nonlinear density dependence and interaction modifiers is that the former process does not require the presence of a third species (for detailed explanation see Kleinhesselink *et al.* 2019). Regardless of their mechanisms, accounting for non-additive biotic interactions has been shown to improve the prediction of tree growth in natural forest ecosystems (Lai *et al.* 2021; Li *et al.* 2021).

That non-additivities can be associated with both abiotic and biotic factors makes it even more important to disentangle their effects on species performance and realised niches. An inability to do so will prevent us from correctly identifying the drivers of community patterns and the relative importance of abiotic and biotic drivers under different circumstances (Freckleton *et al.* 2009; Mayfield & Levine 2010; Cadotte & Tucker 2017). There have been empirical efforts to detect indirect abiotic effects (Coomes & Allen 2007; Kunstler *et al.* 2011; Soliveres *et al.* 2015; Bimler *et al.* 2018) or indirect biotic effects (Uriarte *et al.* 2004; Mayfield & Stouffer 2017; Xiao *et al.* 2020; Lai *et al.* 2021; Li *et al.* 2021) in plant–plant interactions, but rarely both. A key challenge when simultaneously disentangling non-additive abiotic and biotic effects lies in the large number of parameters that need to be fitted to what is often sparse observational data. In this study, we show how Bayesian shrinkage priors may alleviate the data–parameter constraint (see also Weiss-Lehman *et al.* 2021). We extend earlier attempts that sought to understand how the environment changes the competitive

responses to or effects of fewer tree species (Leathwick & Austin 2001; Leathwick 2002; Coomes & Allen 2007) by structuring the question following a recently developed statistical framework for detecting indirect biotic interactions (Mayfield & Stouffer 2017). Our study system is New Zealand’s temperate rain forest that covers about a quarter of the country’s land area. The dataset spans about 12° of latitude and provides an ideal opportunity to examine whether the strength of both direct and indirect biotic interactions change across broad environmental gradients. We show that multiple direct and indirect biotic interactions changed in magnitude and even reversed direction across large ambient temperature and moisture gradients, and discuss the implications of environmental dependence on the prevalence of non-additive biotic interactions and prediction accuracy under global change.

## Material and Methods

### Study area and data

Our forest inventory data originated from the Land Use and Carbon Analysis System (LUCAS) that monitors carbon stocks in New Zealand’s indigenous forests. Established between 2002 and 2007, LUCAS consists of 1,040 20 × 20 m<sup>2</sup> permanent plots that are spaced at intersections of an 8 × 8 km<sup>2</sup> grid representing the extent of the country’s pre-1990 natural forests and shrublands (for detailed field methodology see Allen *et al.* 2003; Bellingham *et al.* 2020) (Fig. S1). Within each plot, all live stems ≥ 2.5 cm in diameter-at-breast-height (DBH) were tagged, measured, and identified to species. During 2009–2014, the trees within a subset of 874 randomly-selected plots were re-measured once; of these, we selected all 739 plots that were classified as forest (Wiser *et al.* 2011). We next identified plots that contained any of six focal tree species: *Dacrydium cupressinum* Sol. ex G.Forst. (rimu), *Podocarpus laetus* Hooibr. ex Endl. (mountain tōtara), *Lophozonia menziesii* (Hook.f.) Heenan & Smissen (silver beech), *Fuscospora cliffortioides* (Hook.f.) Heenan & Smissen (mountain beech), *Weinmannia racemosa* L.f. [kāmahi, recently revised as *Pterophylla racemosa* (L.f.) Pillon & H.C. Hopkins], and *Quintinia serrata* A.Cunn. (tāwheowheo). These six represent the three major species groups that co-occur across broad environmental gradients in New Zealand’s indigenous forests: conifers, mainly in the family Podocarpaceae (*D. cupressinum* and *P. laetus*); small-leaved southern beech in the family Nothofagaceae (*L. menziesii* and *F. cliffortioides*); and broadleaf hardwood species [*W. racemosa* (Cunoniaceae) and *Q. serrata* (Paracryphiaceae)]. The resulting dataset consisted of 533 plots. Each species was represented by 189–2,986 individuals, totalling 7,471 trees across the dataset.

### Environmental data

We extracted two environmental variables from the New Zealand Environmental Data Stack (McCarthy *et al.* 2021): mean annual temperature (MAT, °C) and March vapour pressure deficit (VPD, kPa). These abiotic factors are strong drivers of plant species distribution across New Zealand (Leathwick 1995; Leathwick & Whitehead 2001). While MAT represents an energetic gradient of growing conditions, VPD complements MAT as an indicator of atmospheric moisture and hence evapotranspirational cost (Leathwick & Whitehead 2001). We chose VPD in March because it indicates whether water availability continues to be high when the summer-growth season transitions into autumn. Our final dataset spans 5.3–15.5°C in MAT and 0–0.49 kPa in VPD.

### Statistical model

$$G'_{mipq} = \begin{cases} G_{mipq}^{\nu}, & G_{mipq} \geq 0 \\ -[(-G_{mipq})^{\nu}], & G_{mipq} < 0. \end{cases}$$

To examine the effects of both abiotic and biotic factors on tree diameter growth, we calculated the annual diameter growth rate,  $G_{mipq} = \frac{\Delta D_{mipq}}{\Delta t}$  (cm yr<sup>-1</sup>), of tree  $m$  of species  $i$  in plot  $p$  and subplot  $q$  (see below for an explanation of subplot) as the change in DBH,  $\Delta D_{mipq}$  (cm), over census interval,  $\Delta t$  (yr). Following Condit *et al.* (2017) and Lai *et al.* (2021), we assume the generative process of  $G_{mipq}$  to follow a normal distribution (Equation (??)). This accommodates the zero and negative growth rates that comprised about a quarter of our data; ignoring them could introduce a systematic bias in the estimation of abiotic and biotic effects on growth. To fulfil the assumption of normality, we transformed  $G_{mipq}$  to rein in the right-skewed positive and left-skewed negative growth values (Condit *et al.* 2017):

We used the power  $\nu = 0.64$  because it gave transformed growth,  $G'_{mipq}$ , with the lowest skewness. The generative model is thus:

$$\sigma_{mipq} = s_0 + s_1 D_{mipq}.$$

where mean growth,  $\mu_{mipq}$ , is positivevalued and a function of both intrinsic and extrinsic factors. Meanwhile, sufficiently large variance,  $\sigma_{mipq}^2$ , allows for non-positive growth values. As measurement error varies between smaller and larger stems (Rger *et al.* 2011), we allow the standard deviation in growth to scale with diameter as  $s_1$ , with  $s_0$  as the intercept (see also Appendix S3):

We assumed that measurement error of diameter growth is equally variable across species following Holdaway *et al.* (2014).

The intrinsic factors include size dependencies following Zeide (1993):

$$(1) \quad f(D_{mipq}) = a_i + b_i \log(D_{mipq}) - c_i D_{mipq},$$

where the species-specific growth parameters  $a_i$  is the logarithmic diameter growth rate at very small diameters,  $b_i$  is the tendency of growth to compound with diameter, and  $c_i$  is the decline of growth with diameter due to physiological costs. The parameters  $b_i$  and  $c_i$  are constrained to be positive to produce a hump-shaped growth–diameter relationship.

To account for extrinsic influences on diameter growth, we included both the main and statistical interaction effects of abiotic and biotic factors (denoted  $E$  and  $N$ , respectively) in the surroundings of each focal individual following Box 1:

We included two abiotic factors at each plot  $p$ , MAT ( $E_{1p}$ ) and VPD ( $E_{2p}$ ), and the parameters  $\theta_{in}$  quantify the main effects of MAT and VPD on the diameter growth of species  $i$ . For biotic factors, we quantified neighbour density as  $N_{jpq}$ : the total basal area (m<sup>2</sup> ha<sup>-1</sup>) of neighbour species  $j$  in subplot  $q$  within plot

$p$  of each focal tree  $m$ . Each plot consisted of sixteen  $5 \times 5$  m<sup>2</sup> subplots. For each individual tree  $m$ , we defined its neighbourhood as the subplot where it was located plus its eight adjacent subplots (hereafter as ‘subplot’; Fig. S2) (Allen *et al.* 2020). To minimise edge effects, trees in the 12 edge subplots were not considered as focal individuals (but were considered as neighbours). Neighbour species  $j$  included the six focal species, as well as all remaining non-focal species aggregated as a seventh neighbour group (Martyn *et al.* 2021). Conspecific neighbour basal areas,  $N_{ipq}$ , were calculated without the basal area of conspecific focal individual  $m$ . The pairwise interaction coefficients,  $\alpha_{ij}$ , quantify the per-basal-area main effects of species  $j$  on the growth of focal individual  $m$  (of species  $i$ ). As density dependence among tree species has been shown to be non-additive (Lai *et al.* 2021; Li *et al.* 2021) (Box 1), we also included non-additive biotic interaction terms,  $\sum_j, k \geq j \beta_{ijk} N_{jpq} N_{kpq}$ , where each parameter  $\beta_{ijk}$  quantifies the moderating effect of the density of the  $k$ th intermediary neighbour species,  $N_{kpq}$ , on the main effect of direct neighbour species  $j$  in the same subplot. By modifying the pairwise interaction  $\alpha_{ij}$  between focal species  $i$  and direct neighbour  $j$ , the parameters  $\beta_{ijk}$  are referred to as the higher-order interaction effects of neighbour species  $k$  on focal species  $i$  (Mayfield & Stouffer 2017; Kleinhesselink *et al.* 2019; Letten & Stouffer 2019) (Box 1). As with convention of competitive models, positive and negative  $\alpha_{ij}$  and  $\beta_{ijk}$  values indicate competitive and facilitative effects, respectively. Furthermore, we included the statistical interactions between abiotic and biotic factors, where  $\kappa_{ijn}$  and  $\lambda_{ijkn}$  capture the environmental dependence of main and higher-order biotic effects, respectively (Box 1). Lastly, we included a plot-specific error term,  $\epsilon_p$ , to account for spatial non-independence.

Our full model (Equation (??)) contains a large number of abiotic and biotic effects (and their interactions). In practice, many of these parameters will be indistinguishable from zero either because some species are truly insensitive to changes in the environment and neighbour densities, or that they are strong effects but weakly identifiable by our data (e.g., because triplets of species rarely co-occur across all environmental conditions). There are two ways to determine which parameters to include for parsimony: model selection and Bayesian shrinkage. Model selection involves constructing candidate models that contain a subset of parameters in the full model, and then using information criteria to select one or multiple models that balance predictive accuracy with parsimony. In our case, we built six competing models that differ in the complexity of extrinsic factors:

$$g(E_{np}, N_{jpq}) = \begin{cases} 0, & \text{Model 1 (null)} \\ \sum_n \theta_{in} E_{np}, & \text{Model 2 (environment-only)} \\ - \sum_j \alpha_{ij} N_{jpq}, & \text{Model 3 (main-biotic-only)} \\ - \sum_j \alpha_{ij} N_{jpq} - \sum_{j, k \geq j} \beta_{ijk} N_{jpq} N_{kpq}, & \text{Model 4 (HOI-inclusive)} \\ \sum_n \theta_{in} E_{np} - \sum_j \alpha_{ij} N_{jpq} + \sum_{j, n} \kappa_{ijn} E_{np} N_{jpq}, & \text{Model 5 (env. } \times \text{ main-biotic-only)} \\ \text{as per Equation 3,} & \text{Model 6 (env. } \times \text{ HOI-inclusive).} \end{cases} \quad (2)$$

We opted to include or exclude entire sets of variables that share biological meaning, rather than constructing numerous candidate models with all possible variable combinations to avoid data dredging. However, this forces us to treat the importance of abiotic and biotic factors, as well as their interactions, as an ‘all or none’ question and assume that their effects are either equally important or equally unimportant (Lai *et al.* 2021; Martyn *et al.* 2021). Because there is no obvious biological basis for that assumption, we used Bayesian shrinkage simultaneously to achieve parsimony. In Bayesian inference, shrinkage priors—such as the regularised horseshoe prior distribution with most of its probability mass near zero but with thick tails—reflect the belief that most parameters will be near-zero while some are relatively large effects (Piironen & Vehtari 2017; Weiss-Lehman *et al.* 2021). Compared to more conventional priors, the regularised horseshoe

prior does not limit all effects to be either similarly small or similarly large, but instead allows the coexistence of many very small and few very large effects. The regularised horseshoe prior also relaxes the ‘all or none’ assumption, which is essentially a strong prior that ‘hard fixes’ all parameters deemed irrelevant to zero. We therefore imposed regularised horseshoe priors on parameters  $\theta_{in}$ ,  $\alpha_{ij}$ ,  $\beta_{ijk}$ ,  $\kappa_{ijn}$  and  $\lambda_{ijkn}$  to concentrate inference on relevant biotic interactions that vary strongly across environments. See Appendix S4 for details on priors.

Each candidate model was fitted via Bayesian inference using the **greta** package v0.3.1.9012 (Golding 2019) in **R** v4.1.1 (R Core Team 2021), with 3,000 Hamiltonian Monte Carlo (HMC) warmups and 1,000 post-warmup samplings across four chains, resulting in 4,000 HMC samples in total. To promote model convergence, we scaled and centred the environmental variables,  $E$ , to zero mean and unit standard deviation, used the **poly** function in **R** to calculate orthogonal polynomials of degree two for neighbour densities ( $N_j$  and  $N_k$ ), and tuned the number of HMC leapfrog steps to 25–30. Model convergence was assessed visually using trace plots. We compare the six candidate models using the Leave-One-Out Information Criteria (*LOOIC*) in the **loo** package v2.4.1 (Vehtari *et al.* 2017). As with other information criteria, smaller values of *LOOIC* are indicative of greater support for a model.

## Results

The best model as judged by *LOOIC* was the full model (Model 6; Equation (??); Bayes  $R^2 = 0.25$ ), despite having approximately 86 additional effective parameters than the null model. The effective number of additional parameters was much lower than the potential number of extra parameters because of Bayesian shrinkage (Fig. S4).

Under an average abiotic and biotic condition, the six focal tree species varied in intrinsic size-dependent growth (Fig. S5). The size-expansion and size-decline parameters ( $b_i$  and  $c_i$  in Equation 2, respectively) were positively correlated ( $\sim 0.63$ ), indicating a trade-off between growing fast early in life (e.g., *Lophozonia menziesii*) versus sustaining growth into late life (e.g., *Weinmannia racemosa*). Under average biotic conditions, the main abiotic effects of March vapour pressure deficit (VPD) on diameter growth were stronger than that of mean annual temperature (MAT; Figs 2 and S6). Both *W. racemosa* and *Dacrydium cupressinum* had weak negative growth responses to VPD, while others responded more positively to VPD (Figs 2 and S6). Under average abiotic conditions, the main biotic effects on diameter growth across focal species were variable but remained weak (Figs 3 and S7, middle-left panel), while the higher-order biotic effects were even weaker and sparser (Figs 3 and S7, middle-right panel).

When environmental dependence on VPD, but not MAT, was taken into account, however, a few key biotic effects increased in magnitude or even reversed in direction (Fig. 3 top and bottom panels; see also Fig. S4). In particular, multiple VPD-dependent higher-order biotic interactions had contrasting impacts on each of the realised main biotic effects of *F. cliffortioides*, *L. menziesii*, and *P. laetus* on the diameter growth of *W. racemosa* (Fig. 4).

From moist to dry environments, the realised main biotic effect of *F. cliffortioides* on growth of *W. racemosa* changed from competitive to facilitative (Line 2 versus Line 1 in Fig. 4a). Because of the on-average weak negative (facilitative) higher-order biotic effect from *L. menziesii* ( $\beta_{WFL}$  in Fig. 3), the main competitive effect of *F. cliffortioides* on *W. racemosa*’s growth was slightly reduced in the presence of *L. menziesii* (Line 3 in Fig. 4a). However, the strength of this *F. cliffortioides*–*L. menziesii* higher-order biotic effect depended strongly on VPD (Fig. 3), such that (i) the main competitive effect of *F. cliffortioides* on *W. racemosa*’s growth was alleviated by *L. menziesii* to a greater degree in moister environments but (ii) exacerbated by *L. menziesii* beyond  $\sim 0.25$  kPa VPD (compare Line 2 to Line 4 in Fig. 4a). Vice versa, the main biotic effect of *L. menziesii* on *W. racemosa*’s growth was facilitative in the presence of *F. cliffortioides* in moist environments but competitive as environments became drier (compare Line 2 to Line 4 in Fig. 4b). However, these biotic interactions only translated to a small variation in the proportional effect on *W. racemosa*’s diameter growth

along the VPD gradient (Line 4 in Fig. 4c). In a relatively moist environment (10th percentile of VPD: 0.12 kPa), the average *F. cliffortioides* and *L. menziesii* densities ( $\sim 9.2$  and  $\sim 14.3$  m<sup>2</sup> ha<sup>-1</sup>, respectively) reduced *W. racemosa* 's diameter growth to 89% of its average. This was slightly alleviated to 92% in a relatively dry environment (90th percentile: 0.34 kPa) (Figs 4c,d). At the peak growth of *W. racemosa*, these proportional growth reductions translate to  $-0.015$  and  $-0.008$  cm yr<sup>-1</sup> in moist and dry environments, respectively.

In contrast, the VPD-dependent higher-order biotic effects of *F. cliffortioides* and *P. laetus* translated to a greater difference in *W. racemosa* 's diameter growth under contrasting environments (Fig. 4 right panels). The realised main biotic effects of both *F. cliffortioides* and *P. laetus* on *W. racemosa* changed from competitive to facilitative with increasing VPD (Lines 2 in Figs 4e,f). Under average VPD, the higher-order biotic effect of *F. cliffortioides* and *P. laetus* ( $\beta_{WFP}$  in Fig. 3) on each of their main biotic effects was very weak (little difference between Lines 2 and 3 in Figs 4e-g). However, the *F. cliffortioides* - *P. laetus* higher-order biotic effect was highly VPD-dependent and changed from alleviating to exacerbating the main biotic effects along the VPD gradient (Fig. 3). This led to a two-fold variation in the proportional effect on *W. racemosa* 's diameter growth along the VPD gradient (Line 4 in Fig. 4g). In a relatively moist environment (0.12 kPa), the average *F. cliffortioides* and *P. laetus* densities ( $\sim 9.2$  and  $\sim 1.2$  m<sup>2</sup> ha<sup>-1</sup>, respectively) greatly reduced *W. racemosa* 's diameter growth to 74% of its average ( $-0.034$  cm yr<sup>-1</sup> at peak growth), but increased growth to 104% ( $+0.003$  cm yr<sup>-1</sup>) in a relatively dry environment (0.34 kPa) (Figs 4g,h).

## Discussion

Using a nationwide forest inventory that spans the long temperature and atmospheric moisture gradients of New Zealand, we showed that the main effects of climate and biotic interactions on the diameter growth of six focal tree species (two southern beech, two conifer, and two broadleaf hardwood species) were highly variable but relatively weak. However, the strengths and directions of some main biotic interactions depended on the density of a third species, giving rise to relevant higher-order biotic interactions. More importantly, these higher-order biotic interactions were very weak under average environmental conditions, but some became stronger towards both ends of the March vapour pressure deficit (VPD) gradient. In particular, these non-additivities were evident in the joint biotic effects of a conifer and two beech species on the diameter growth of a widespread broadleaf tree, *Weinmannia racemosa*. As judged by information criteria, the full model that included Bayesian shrinkage priors to detect these complex relationships had the best predictive accuracy and outranked simpler models that omitted them.

From moister to drier environments, the main biotic effect of either beech species (*Fuscospora cliffortioides* or *Lophozonia menziesii*) on the diameter growth of *W. racemosa* changed from competitive to facilitative. When both beech species are present, however, the joint beech-beech effect on *W. racemosa* remained competitive across the atmospheric moisture gradient. Beech species are typically thought to reach peak abundance in seasonally drier areas, but are less dominant in moister areas occupied by other broadleaf species such as *W. racemosa* (Leathwick 1995, 1998; Ogden *et al.* 1996). As such, we expected the biotic effects of beeches on *W. racemosa* to be competitive in the drier environments that are suboptimal for it. This expectation is supported by our results, but only when the higher-order interaction between *both* beech species is taken into account. Previous studies that used the combined densities of more than one beech species (historically as *Nothofagus* spp.) to estimate their competitive effects on other species (e.g., Leathwick & Austin 2001) could therefore be quantifying the non-additive *whole*, rather than a simple sum, of competition from multiple beech species. This also begs the question of how many non-additivities hid within other studies that grouped multiple neighbour species as, for example, heterospecifics or functional guilds.

In contrast, the joint beech-conifer (*F. cliffortioides* - *Podocarpus laetus*) effect on the diameter growth of *W. racemosa* was facilitative in drier areas. The difference between the realised beech-beech and beech-conifer biotic effects could be related to variations in the neighbour species' growth responses to water stress. Lower hydraulic stress in moister environments might have allowed both tall-statured beech and conifer

neighbours to attain greater heights per basal area (King 1990; Hulshof *et al.* 2015) when competing for light against one another, thereby imposing a greater light competition on *W. racemosa* individuals that are often subcanopy (Wardle 1966). As water becomes the limiting resource for photosynthetic growth in drier environments, a beech–conifer neighbourhood was more facilitative for *W. racemosa* compared to a beech–beech neighbourhood, possibly because of a different height–diameter allometry between beeches and conifers across moisture conditions. Alternatively, resource competition may shift belowground in drier areas (Coomes & Grubb 2000) and increase the role of the rhizosphere in moderating tree–tree interactions. Although the root morphology of New Zealand tree species remains understudied, seedling experiments showed that beech and conifer species occupy different ends of a fine-root trait spectrum, with *W. racemosa* positioned in between (Kramer-Walter *et al.* 2016). In drier areas, it is possible that the presence of two beech species with similar root physiomorphology generated a soil hydrology that was net detrimental to *W. racemosa*’s diameter growth; in contrast, the presence of a beech and a conifer species with distinct rhizospheres may have generated a soil hydrology that was net beneficial, though evidence of plant–water feedback is still weak (Ehrenfeld *et al.* 2005; Brantley *et al.* 2017). With these speculations, what remains clear is that more work is required to pinpoint the exact mechanisms behind the phenomenological non-additivities detected in our observational data.

Using Bayesian shrinkage priors (Piironen & Vehtari 2017; Weiss-Lehman *et al.* 2021), we overcame a long standing problem of computational tractability that an earlier endeavour also faced (Leathwick 2002) and detected the abiotic conditions and/or biotic milieus under which plant–plant interactions become more or less intense. The answers to these questions would have been very different if the environmental dependence of biotic interactions had been omitted in this study. Averaged across environments, and hence assumed as constant or implicit averages, our results show that biotic-interaction coefficients would be inferred as mostly weak and sparse effects (i.e., a tendency toward zeroes; Fig. 3 middle row). Furthermore, we risk downplaying the importance of both direct and higher-order biotic interactions if they are only detectable near climate extremes, which are expected to become more prevalent with climate change (Grossiord *et al.* 2020). Many of the disparities in the strength and direction of biotic interactions between similar sets of species could be due to environmental variations among studies that has not been taken into account (Kunstler *et al.* 2011; Copenhagen-Parry & Cannon 2016; Wainwright *et al.* 2019). Additional caution should therefore be taken when interpreting the lack of biotic interactions among other focal species (e.g., *D. cupressinum* and *Q. serrata*) in our study because there could be other context dependencies that we have not considered. Other putative determinants of the distributions of not only these focal species but also their competitors in New Zealand—such as storm disturbance, modern fires, and understorey herbivory—may reveal further shifts in competitive dominance (Leathwick 1995; Ogden *et al.* 1996; Hall & Hollinger 2000; Allen *et al.* 2013).

By demonstrating the context dependence of multiple biotic interactions, our study addresses not only the question ‘is competition important?’ but more crucially ‘when is competition important?’ (Brooker & Kikvidze 2008; Freckleton *et al.* 2009). For instance, the joint beech–conifer biotic effect on the diameter growth of *W. racemosa* became more competitive and more facilitative in moister and drier conditions, respectively. However, the intensity of biotic interactions does not guarantee their importance compared to other growth factors—such as abiotic resource availability or stress—that operate simultaneously (Kunstler *et al.* 2011; Copenhagen-Parry & Cannon 2016). Our results show that, not only did the joint beech–conifer biotic effects intensify towards VPD extremes, their effect size on the diameter growth of *W. racemosa* was greater than and in the opposite direction from the main abiotic effect of atmospheric moisture. Consequently, *W. racemosa* is expected to have *lower* diameter growth even under favourable, moist climates as a result of intensified competition. On the other hand, net facilitation of *W. racemosa* growth by *F. cliffortioides* and *P. laetus* counteracted and outweighed the detrimental effect of drier climates.

Contextualising the importance of biotic interaction alongside abiotic effects also highlights the alternative view of the same model: the biotic dependence of abiotic effects (Appendix S9). As much as our discussion has focussed on how the environment realises species’ Eltonian niches (i.e., how species impact and respond to one another), the realised Grinnellian niche (i.e., how species respond to the environment) is equally important in our understanding of a species’ abiotic resource requirements when it is not growing alone. In our



phenomenological model, a strong environmental dependence of biotic effects implies an equally strong biotic or density dependence of environmental responses (i.e., Fig. 4h can be viewed from either perspective; see also Appendix S9). In other contexts such as range shifts and biological invasions, competition or facilitation from invading species can alter resident species' environmental responses or tolerances thus influencing coexistence outcomes (Adler *et al.* 2012; Godsoe *et al.* 2015; Ford *et al.* 2017). Understanding the interplay between biotic and abiotic processes will become even more crucial as rising vapour pressure deficit under climate change severely impacts plant functions (Grossiord *et al.* 2020; Lpez *et al.* 2021).

## Conclusions

In our study, including sparse but strong environmentally dependent biotic interaction terms in a phenomenological model significantly improved the prediction of tree growth. Over-simplistic density dependence will fail to predict future biomass changes accurately because biotic interactions could vary in magnitude or even reverse in direction with climate and other abiotic factors. Similarly, putative growth–climate relationships (i.e., Grinnellian niches) can also be realised differently by environmentally dependent biotic interactions. Yet, an important question remains: are environmentally dependent biotic interactions generalisable or sufficiently important across taxa to warrant such a complex model (Levins 1993; Evans *et al.* 2013)? Although generalisation is difficult from this study that included only six focal species, environmentally dependent biotic interactions could be widespread phenomena in our study region because *W. racemosa* is the most abundant tree species in New Zealand (Wardle 1966). The beech and conifer species that interacted strongly are also widespread and form key vegetation associations with *W. racemosa* across long environmental gradients (Wardle 1964, 1966; Wiser *et al.* 2011). If the goal is to accurately predict major trends in biomass and carbon under changing climates and/or community compositions, then we cannot ignore sparse but complex interactions among the few *species* with disproportionately many *individuals* (Coomes *et al.* 2014). To move from prediction to understanding, however, it is imperative for future studies to reveal the specific mechanisms that gave rise to these non-additive phenomena. Ultimately, prediction and understanding work hand in hand to help us decide which non-additivities can be ignored, and which are especially prevalent.

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## Table

Tabelle 1:

Comparison of the six candidate models using the Leave-One-Out Information Criteria ( $LOOIC$ ), with better performing models exhibiting lower values of  $LOOIC$ . Models are arranged in increasing difference in  $LOOIC$  from the best model ( $\Delta LOOIC$ ). The column  $pLOOIC$  is the effective number of parameters in each model, while  $\Delta pLOOIC$  is the difference in  $pLOOIC$  from the null model.

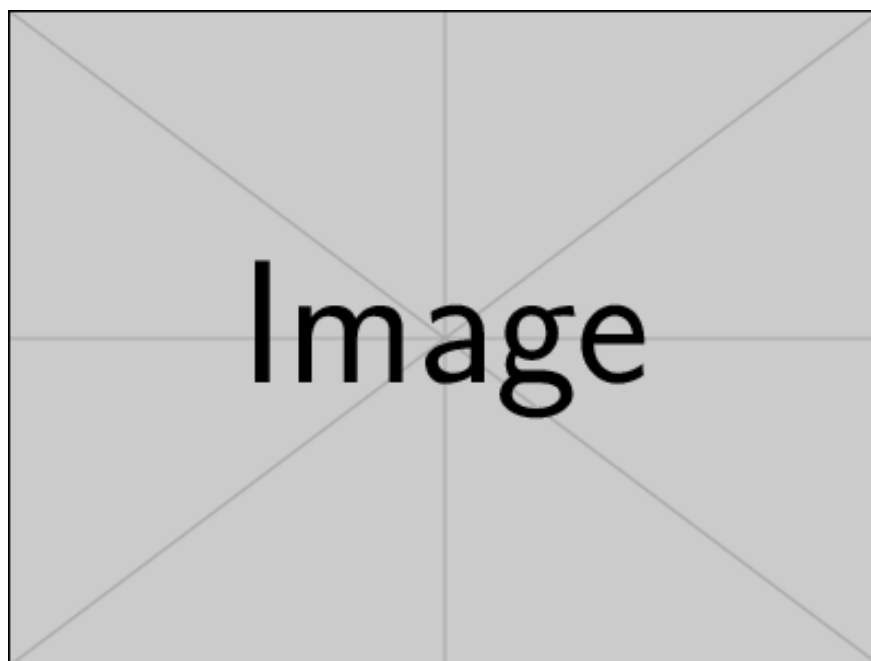
Model	$LOOIC$	$\Delta LOOIC$	$pLOOIC$	$\Delta pLOOIC$
6	-6731.7	0.0	493.3	85.8
5	-6719.2	12.5	455.7	48.2
4	-6653.9	77.8	467.3	59.8
3	-6650.5	81.3	428.2	20.7
2	-6638.5	93.2	414.4	6.9
1	-6614.1	117.7	407.5	0.0

## Figures

**Figure 2.** Main environmental effects of mean annual temperature (MAT),  $\theta_{i1}$ , and March vapour pressure deficit (VPD),  $\theta_{i2}$ , on the diameter growth of the six focal species. Open circles are medians while thick black and thin grey horizontal bars are 50%-tile and 90%-tile intervals of the posterior distributions, respectively. Key to species abbreviations: DACCUP = *Dacrydium cupressinum*, PODLAE = *Podocarpus laetus*, LOPMEN = *Lophozonia menziesii*, FUSCLI = *Fuscospora cliffortioides*, WEIRAC = *Weinmannia racemosa*, QUISER = *Quintinia serrata*.

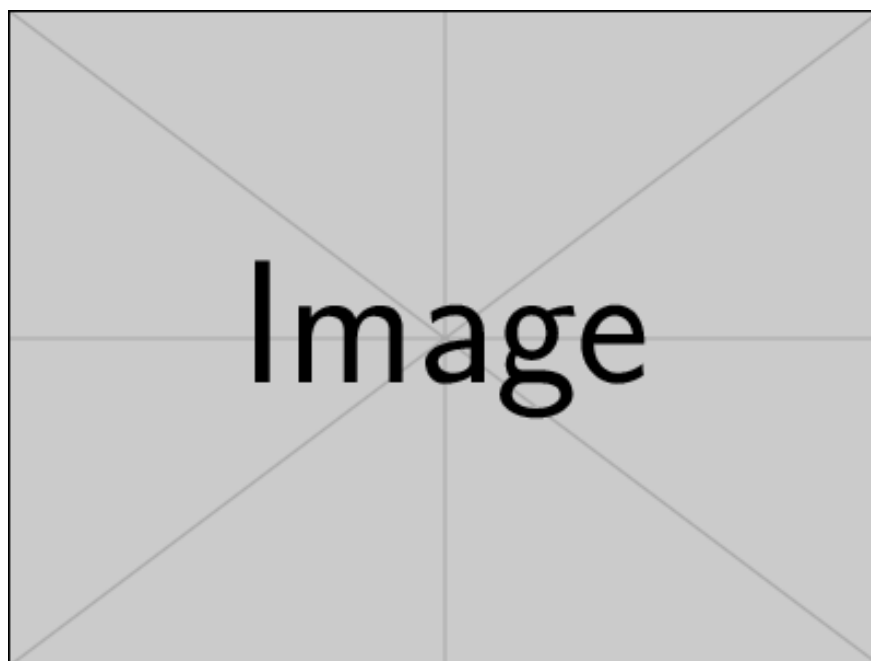
**Figure 3.** Median biotic-interaction coefficients in a moist, average, and dry environments (top, middle, and bottom panels, respectively). Dry and moist environments are the 10th and 90th percentiles, respectively, of March vapour pressure deficit (VPD). In each panel, each row is a focal species while each column is a biotic factor consisting of a direct-neighbour ( $\alpha_{ij}$ ; left panels) or indirect-neighbour predictor ( $\beta_{ijk}$ ; right panels). Row and column names are the first letter of species name, whereas “O” denotes all other species as a group. Positive (orange) and negative (purple) values correspond to competitive and facilitative biotic-interaction coefficients, respectively. In this sparse coefficient matrix, the cells with black outlines are higher-order biotic interactions that changed strongly across the VPD gradient (as judged by 90% credible intervals of  $\lambda_{ijkn}$  that do not overlap with zero; Fig. S4), while text labels denote the corresponding panels in Fig. 4.

**Figure 4.** Biotic effects of neighbouring species on the diameter growth of focal species *Weinmannia racemosa* (WEIRAC) and how they change across the March vapour pressure deficit (VPD) gradient. In the left column, the neighbours are *Fuscospora cliffortioides* (FUSCLI) and *Lophozonia menziesii* (LOPMEN); in the right column, the neighbours are *F. cliffortioides* (FUSCLI) and *Podocarpus laetus* (PODLAE). **Top row:** The average realised main biotic effect of FUSCLI on WEIRAC,  $\tilde{\alpha}_{WF}$ , following the four scenarios in Fig. 1c. In (a) and (e), the intermediary species that participated in the higher-order interaction was LOPMEN ( $\beta_{WFL}$ ) and PODLAE ( $\beta_{WFP}$ ), respectively, as indicated by the simplified directed acyclic graph (DAG). **Second row:** The average realised main biotic effect of LOPMEN and PODLAE, respectively, on WEIRAC ( $\tilde{\alpha}_{WL}$  or  $\tilde{\alpha}_{WP}$ ), under the same four scenarios. In both (b) and (f), the intermediary species that participated in the higher-order interaction was FUSCLI ( $\beta_{WFL}$  and  $\beta_{WFP}$ ), as indicated by the DAG. **Third row:** Combining the top and second rows into the average cumulative proportional effects of both neighbour species on the focal species’ diameter growth, when both neighbour species were set at their average densities. A proportion less than one leads to a reduction in the focal species’ growth (e.g., 0.8 means that growth became 80% of that without neighbours) whereas proportions greater than one lead to increased growth in the presence of neighbours. **Bottom row:** Translating the cumulative proportional effects of Line 4 (with environmental dependence of higher-order interaction) in the third row into the outcome scale—*W. racemosa*’s expected diameter growth—under a dry versus moist environment (light or dark lines) where both neighbour species are absent or present at average density (dashed or solid lines).

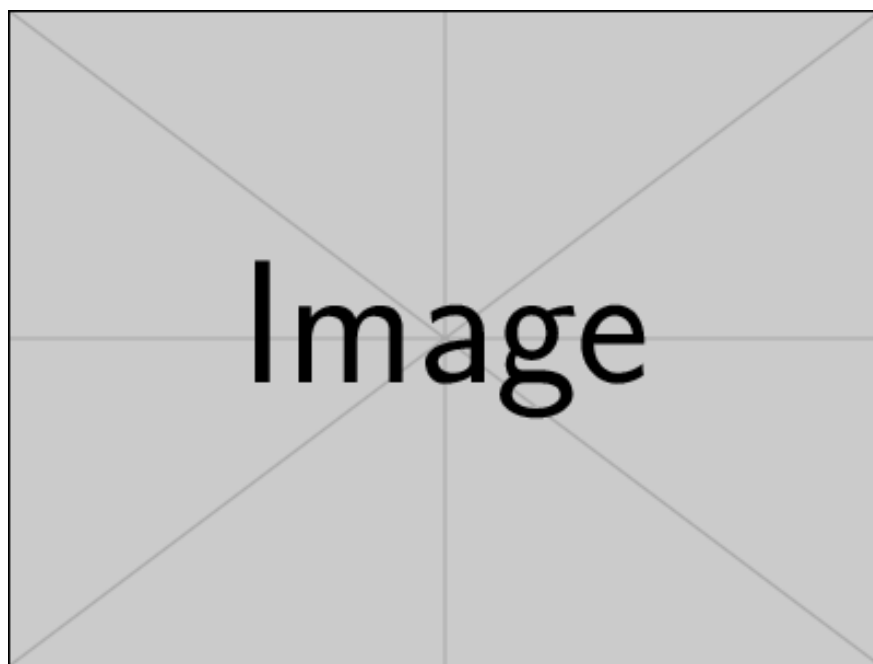


**Figure 2.**





**Figure 3.**



**Figure 4.**

## Text Box

### Box 1: Detecting biological non-additivities in statistical models

Non-additive biotic interactions arise when the strength of a direct interaction between a species pair (species  $i$  and  $j$  in Fig. 1a) is affected by the environment and/or by a third species (black and blue pathways in Figs 1a–b, respectively). Biologically, there are two broad groups of emergent pathways of non-additivities: indirect effects and interaction modifiers (Wootton 1993; Billick & Case 1994; Levine *et al.* 2017; Kleinhesselink *et al.* 2019; Letten & Stouffer 2019). Indirect effects on focal species  $i$ 's performance occur when an abiotic or biotic factor *directly* modifies neighbour  $j$ 's density, thereby *indirectly* changing the neighbour's subsequent competitive impact on focal species. Interaction modifiers are abiotic and/or biotic factors that *directly* modify the nature of biotic interactions by changing morphology or behaviour in the focal species, the neighbour species, or both.

Regardless of whether abiotic or biotic factors indirectly or directly modify how focal  $i$  and neighbour  $j$  interact, these non-additivities can be detected and tested as statistical interaction terms in regressions (Mayfield & Stouffer 2017; Martyn *et al.* 2021). Many phenomenological models estimate the impact of biotic interactions as an interaction coefficient  $\alpha_{ij}$  multiplied by the density  $N_j$  of neighbour species  $j$  (i.e.,  $\alpha_{ij}N_j$ ). The implicit assumption here is that the effect of neighbour  $j$  on focal species  $i$  is additive, i.e., every unit increase in  $N_j$  adds the same biotic effect on focal species  $i$  given by  $\alpha_{ij}$ . When indirect effects or interaction modifiers arise in the field, however, the same neighbour density no longer imposes consistent biotic effects under different environments or varied biotic milieus (Fig. 1a). Accordingly, the outcome of biotic interactions will differ from the predictions of the experimentally parameterised  $\alpha_{ij}N_j$ . Likewise, the field-parameterised, realised coefficient  $\tilde{\alpha}_{ij}$  will be inaccurate and different from the true  $\alpha_{ij}$  (Fig. 1c).

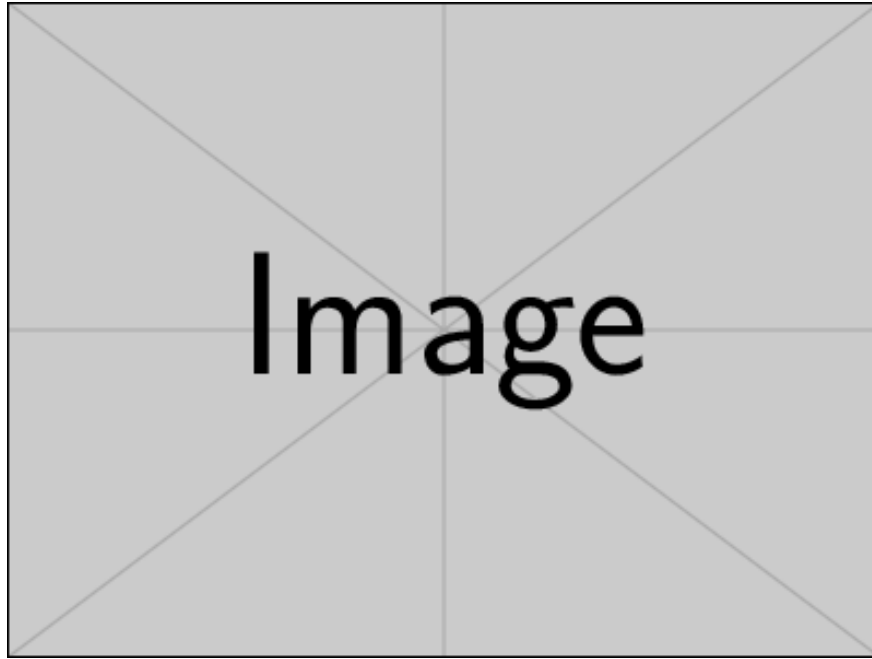
For more accurate predictions or parameter estimations, we can account for these potential non-additive effects statistically. To start, consider only the impact of abiotic non-additivity:

where the realised biotic effect in a particular environment,  $\tilde{\alpha}_{ij}$ , is partitioned into the main biotic effect,  $\alpha_{ij}$ , and its dependence on abiotic condition  $E$ ,  $\kappa_{ij}$  (Equation (??); Fig. 1). The expansion of Equation (??) into (??) demonstrates why non-additive biotic interactions can be detected as non-zero statistical interaction coefficients between  $E$  and  $N_j$  in regression models. Both Equations (??) and (??) are useful expressions because the former emphasises interaction modifiers that directly change the nature of  $\alpha_{ij}$ , while the latter emphasises the indirect effect of environment on focal  $i$  through neighbour  $j$ .

Non-additivity due to biotic factors can also be captured in a similar manner:

where  $\beta_{ijk}$  is the strength of 'higher-order biotic interaction' (HOI) that quantifies the density dependence of the density-dependent effect,  $\alpha_{ij}$ , on neighbour  $k$ 's density,  $N_k$  [blue pathway in Figs 1a–b; Mayfield & Stouffer (2017); Letten & Stouffer (2019); Kleinhesselink *et al.* (2019)]. If the HOI among three species also depends on the environment (red pathway in Figs 1a–b), then it is necessary to account for the environmental dependence of the HOI,  $\lambda_{ijk}$ , in the model:

In practice, when environmental dependence and HOIs are not accounted for, most inferences are actually capturing  $\tilde{\alpha}_{ij}$ , which is likely less comparable than  $\alpha_{ij}$  across datasets with different biogeography. From a generalised perspective (Levins 1993),  $\tilde{\alpha}_{ij} \equiv \alpha_{ij}$  is a special case when the interaction of a species pair happens to be independent of the environment and other intermediary species. Though most studies chose to assume constant biotic interactions because the number of parameters would otherwise be too large (but see *Material and Methods* on possible solutions using Bayesian shrinkage), by judiciously including non-additivities we could move from simply asking if biotic interactions are strong *on average* to asking when they are strong versus when they are not (Brooker & Kikvidze 2008; Freckleton *et al.* 2009).



**Figure 1.** (a) A graphical example of how the main biotic interaction,  $\alpha_{ij}$  (grey arrow segment), between a focal species  $i$  and neighbour species  $j$  may vary in strength across environments (arrow widths) in the presence of a third species. (b) A directed acyclic graph that links panel a to the full model in this study (Equation (??)). (c) How the realised main biotic effect,  $\tilde{\alpha}_{ij}$ , may change continuously along the environment, as depicted in panel a. Line numbers 1–4 respectively denote that: (1) The realised biotic interaction between species  $i$  and  $j$  is constant across environments and biotic milieus ( $\tilde{\alpha}_{ij} = \alpha_{ij}$ ). (2) The realised biotic interaction changes along an environment gradient ( $\tilde{\alpha}_{ij} = \alpha_{ij} + \kappa_{ij}E$ ; Equation (??)); in this example, it changes from more competitive to more facilitative due to a negative  $\kappa$ . (3) The environment-dependent biotic interaction is also influenced by a higher-order interaction effect from intermediary species  $k$  ( $\tilde{\alpha}_{ij} = \alpha_{ij} + \kappa_{ij}E + \beta_{ijk}N_k$ ; Equation (??)); here, a positive  $\beta$  makes the realised biotic interaction between species  $i$  and  $j$  more competitive. And (4) both the main and higher-order interactions are dependent on environment ( $\tilde{\alpha}_{ij} = \alpha_{ij} + \kappa_{ij}E + (\beta_{ijk} + \lambda_{ijk}E)N_k$ ; Equation (??)). In a and c, towards the left end of the environmental gradient, the abiotic condition strengthens the main biotic interaction between focal species and neighbour

species via  $\kappa_{ij}$  (black arrow segment in **b**). A third, intermediary neighbour species  $k$  exerts a higher-order biotic interaction (HOI) effect,  $\beta_{ijk}$  (blue arrow segment in **b**), on the main biotic interaction between focal  $i$  and neighbour  $j$ . Because the abiotic condition also strengthens the HOI effect via  $\lambda_{ijk}$  (red arrow segment in **b**), the realised biotic effect of neighbour  $j$  on focal  $i$ ,  $\tilde{\alpha}_{ij}$ , becomes much stronger and more competitive (left end of **c**). In contrast, towards the right end of the environmental gradient, the abiotic condition weakens both the main biotic interaction and HOI (thinner black and red inhibitory arrows, respectively), resulting in a less competitive (or more facilitative) relationship between neighbour  $j$  on focal  $i$  (right end of **c**). Note that the main biotic interactions (and their environmental dependence) also exist between species pairs  $ik$  and  $jk$ , and that species  $k$  can also be swapped with species  $i$  or  $j$ ; these effects were not shown for visual clarity. Furthermore, there is no particular order with which  $\kappa_{ij}$  or  $\lambda_{ijk}$  influence the main biotic effect—these effects were estimated simultaneously in the statistical model, which is likely how they operate in real communities.