Embracing plant-plant interactions - rethinking predictions of species range shifts

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Conflict of interest

The authors declare that there is no conflict of interest.

Author contribution

All authors contributed to the concept and design of the article; Pieter Sanczuk prepared the manuscript together with Pieter De Frenne and Miska Luoto for the introduction, and Pieter De Frenne, Dries Landuyt, Emiel De Lombaerde and Florian Zellweger for the concept development. Jonathan Lenoir and Koenraad Van Meerbeek performed the SDM review. Pieter Sanczuk performed all analyses of the worked example and prepared the figures. All authors provided input on each section and reviewed the final version of the manuscript.

Data Availability Statement

All data and code used in the worked example is available on FigShare (Sanczuk et al., 2024)

Abstract

1. Interactions among plants are changing across the globe resulting from a multitude of changes in the environment. Obtaining accurate predictions of plant species' range dynamics require us to account for plant-plant interactions, but this remains challenging using the existing species distribution modelling (SDM) techniques.
2. Advanced SDM techniques facilitate the integration of plant species interactions based on species-to-species associations. However, for uncharted environmental conditions in which the formerly derived species' correlations potentially no longer hold, a more process-based alternative is expected to become increasingly relevant.
3. We first review the most common SDM techniques that integrate plant-plant interactions, and then present the concept for a novel map product: a spatial Plant-plant Interaction Index (PII) depicting the link between a focal species' performance and the trait signature of the interacting vegetation. The latest developments in remote sensing and the increasing availability of vegetation plot data facilitate PII mapping based on vegetation trait-environment relationships.
4. ***Synthesis*** PII mapping holds the potential to advance next-generation biogeographical analyses as it can serve as a pivotal missing covariate layer necessary for the integration of plant-plant interactions into SDM applications. This data product adds flexibility to the ecologists' toolbox to analyze species range shifts and the formation of novel communities as a response to multiple environmental changes.

Keywords: plant-plant interactions, biogeography, competition, environmental change, experimental macroecology, spatial model, species distribution model, vegetation survey

1. Introduction

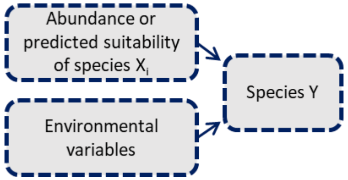
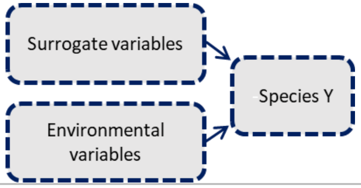
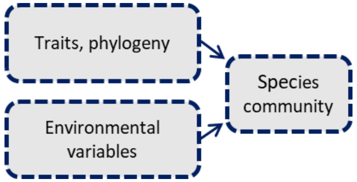
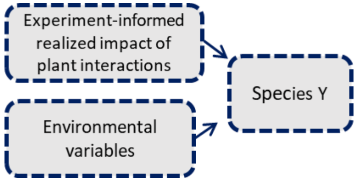
Species are rearranging distributions across the globe brought about by changes in the environment (Zellweger et al., 2020). Changing environmental conditions alter colonization and local extinction dynamics of species, resulting in biogeographical shifts at the larger geographic extent (Lenoir et al., 2020) and the emergence of new assemblages of interacting species that do not yet coexist at present (De Frenne, 2023). Such ‘novel communities’ will become increasingly apparent in response to uncharted sets of environmental conditions, often with unexpected functional implications to people and nature (Alexander et al., 2015a, 2016; Kerr et al., 2023; Williams & Jackson, 2007). Interactions among plant species, for example, can significantly reduce (e.g., due to competition) or enhance (e.g., due to facilitation) range shifts under climate change (Alexander et al., 2015b; HilleRisLambers et al., 2013; Lyu & Alexander, 2022), but are often neglected when projecting future distributions. If we are to adequately anticipate climate-change impacts on biodiversity and ecosystem functioning, we cannot longer ignore the mediating effects of plant-plant interactions on range shifts.

Accounting for plant-plant interactions into projections of species ranges is complex. It requires us to quantify how changes in biotic interactions, through acting on local population dynamics, impact species’ distributions at the continental extent. Species distribution models (SDMs) provide a quantitative analytical framework that allows the prediction of species range shifts due to climate and other environmental changes (Guisan & Thuiller, 2005; Merow et al., 2013), but considering species interactions into SDMs remains difficult (Dormann et al., 2018; Norberg et al., 2019). Advanced modeling techniques, such as direct interaction covariates (Pellissier et al., 2010) and joint SDMs (Ovaskainen & Soininen, 2011), facilitate the integration of biotic interaction effects into projections of species ranges based on species-to-species associations. Unfortunately, these methods often require an *a priori* selection of data on the set of assumed interacting species, while the residual covariance among species is easily confounded (Zurell et al., 2018), and, even more important, there is virtually no method to parameterize these models in the absence of present-day analog communities (i.e., when species do not yet co-occur; but see (Rohr et al., 2010)). Alternatively, biotic interaction effects have been approximated in SDMs using surrogate variables (i.e., variables assumed to correlate with the strength of plant-plant interactions, such as productivity or species richness (Wisz et al., 2013)). Surrogate variables, however, do not necessarily remain constant under a changing environment, making projections beyond the environmental range that was sampled more ambiguous. Furthermore, it is unlikely that surrogate variables will accurately describe interaction strengths within more hidden strata of plant communities such as for forest understorey plants below dense tree canopies and for communities in ravines, on cliffs and on steep mountain slopes (Morueta-Holme et al., 2023).

To expand the toolbox of ecologists, we need a complementary alternative that adds flexibility and facilitates a more general integration of plant-plant interactions in the prediction of species range dynamics. Ecological data are increasingly available at the continental and global extent, including species distribution, abundance and trait data, paving the way to step beyond the mere correlative nature of the existing methods. An experimentally informed approach to account for species interactions within SDMs holds the potential to overcome several of the known limitations. Leveraging the strengths of both experimental research and correlative SDMs will likely advance our understanding of plant-plant interaction effects on species' range dynamics.

Here we review the most prominent existing methods that allow the approximation of plant-plant interactions in SDM analyses. Second, we present the concept, development and potential application of a novel gridded map product: a Plant-plant Interaction Index (PII) map depicting the realized estimated impact of plant-plant interactions experienced by a focal plant species. The PII metric is quantified based on experimental research and links a focal species' performance to the trait signature of co-occurring species, and is mapped based on trait-environment relationships. PII maps hold the potential to advance next-generation biogeographical predictions, serving as a pivotal missing covariate layer necessary for the integration of plant-plant interactions effects into modern SDM applications.

Table 1 | Schematic representation of the basic principles and the main characteristics of three common species distribution modelling (SDM) techniques, and the proposed plant-plant interaction map as calculated based on field data from interaction-exclusion experiments, that allow integrating plant-plant interaction effects into predictions of the habitat suitability of a focal species (species Y in the diagrams)

	Direct interaction covariates	**Surrogate variables for interactions**	**Joint SDMs**	**Plant-plant Interaction Index**
				
Target species	Single species	Single species	Multiple species	Single or multiple species
How are species interactions modelled?	Abundance or predicted suitability of interacting species as predictor	Surrogate variables as predictor	Interactions are not incorporated in the model, but can be inferred from the model	Experimentally-informed surrogate (index) variable as predictor
Data needed	Abundance/occurrence data of target species or community data	Abundance/occurrence data of target species (or community data)	matrix of species presence/absence or abundance data	Performance data of target species in presence/absence of competitor(s)
Can trait data be incorporated in the model?	Yes, community-weighted mean traits if community data are available	Yes, community-weighted mean traits if community data are available	Yes, species-specific trait data help to estimate species niches	Yes, one or multiple traits of target species and interacting species
Can phylogenetic data be incorporated in the model?	Possible if community data are available, but not standard	Possible if community data is available, but not standard	Yes	No
A priori knowledge about species interactions necessary?	Yes, knowledge about interacting species is necessary	Yes, knowledge about interactions is necessary to select surrogate variables	No	preferentially informed by experiments
Applicable to rare species?	Difficult to estimate species niche for rare species	Difficult to estimate species niche for rare species	Rare species borrow information from abundant species	Difficult to estimate species niche for rare species
Type of interactions	Asymmetric interactions only	Asymmetric interactions only	Symmetric interaction only	asymmetric interaction only
Applicable to large communities?	Yes, but many interaction covariates could lead to multiple testing and overfitting	Yes, interactions are summarized in surrogate variables	Yes, latent variables substitute high-dimensional covariance matrix	Yes, interactions are summarized in surrogate index
Applicable to big data?	Yes, but computationally intensive	Yes, but computationally intensive	Joint modelling of species reduces run time	Yes
Spatial consistency of interactions assumed?	Yes (not if species-environment associations are included as predictors)	No	No	No

Temporal consistency of species interactions assumed?	Yes	Yes	No	No, the plant interaction index can be projected under environmental change scenarios
Prediction of unobserved interactions	Not possible	Possible	Possible	Possible, based on trait-environment associations

2. Accounting for plant-plant interactions into projections of species’ ranges: a review of existing methods

Species distribution models (SDMs) are conventionally employed to analyze the relationship between the distribution of a species - usually represented by presence-only, presence-absence or abundance data - and environmental factors. However, these models do not distinguish between the influence of biotic and abiotic environments (Araújo & Guisan, 2006). Several methods to overcome this issue and approximate species interactions in SDMs exist, ranging from methods directly accounting for the distribution of a selection of co-occurring species as covariates in the model to methods using covariates acting as surrogates for biotic interactions (**Table 1**). Furthermore, technological progress in numerical ecology has enhanced our ability to adapt statistical models to large community datasets (in so-called joint SDMs), thereby facilitating the consideration of both the environmental preferences of several species and their interdependence simultaneously.

2.1. Direct interaction covariates

Utilizing the abundance of one or several **co-occurring species as predictor variables** in SDMs stands as a primary method to account for biotic interaction effects on range predictions of a focal species. Various interaction types have been explored through this approach, such as the consideration of interspecific competition among plant species by adding plot-level predictors representing frequency or count data (Leathwick & Austin, 2001; Pellissier et al., 2010), basal area (Rouget et al., 2001), or proportion data (Meier et al., 2010) of co-occurring species. However, this method is sensitive to false absences of the co-occurring species used as a predictor in the model which introduces bias to the model predictions. An alternative method involves the use of model **outputs from the SDM of the interacting species as a covariate layer** into SDM predictions of the focal species, effectively leveraging predicted suitability (Leathwick & Austin, 2001). This method has advantages over the former approaches as it minimizes bias attributed to false absences in the co-occurring species. Yet, inaccurate predictions may in turn introduce other errors to the model.

While the use of empirical data (e.g., plot-level abundances) or predicted data (e.g., modelled habitat suitability) of co-occurring species as predictors presents a straightforward technique, it also bears certain limitations inherent to its simplicity. First, these methods model the unidirectional effect of the co-occurring species on the focal species, and thus fail to capture the bidirectional nature of most biotic interactions. For instance, the fitness benefits arising from mutualistic interactions can extend the ranges of both involved species (Afkhami et al. 2014). Species' co-occurrence may be attributed to indirect interactions, wherein both species respond to an external species, such as a common predator or herbivore (Dormann et al. 2018). A shared response to an unmeasured environmental variable could also result in a positive correlation between co-occurring species, even if species do not directly interact

(Poggiato et al. 2021). Issues may further arise when the predictor species and the focal species share a similar environmental niche, causing multicollinearity among predictor species and environmental covariables, ultimately blurring the determination of potential occurrences for the focal species (Zurell et al., 2018). Additionally, the suitable environmental range for the focal species might extend beyond that of the predictor species, causing SDMs to misinterpret empty cells as unsuitable environmental conditions rather than missing predictor species (Kissling et al., 2012). Finally, in communities with numerous species, the issue of multiple testing and overfitting arises, which can be mitigated by considering only the most abundant species as predictors (le Roux et al., 2014).

Another approach involves aggregating pairwise species interactions into **co-occurrence-based indices at the community level**, serving as proxies for interactions in SDMs (Boulangeat et al., 2012). When accounting for biotic interactions by including direct interaction covariates, knowledge of ecological links between species pairs, such as for obligate parasite plant species (common in e.g., *Orobanchaceae*), is crucial and should be supported by evidence. If the interacting species are unknown, inference from data - ideally considering geographic and environmental variation - can be achieved through (Bayesian) network analyses (Harris, 2016; Morueta-Holme et al., 2016; Pellissier et al., 2013; Staniczenko et al., 2017). Insights derived from network analyses or prior ecological knowledge can also help simplify the parameterization of biotic interactions within SDMs (Kissling et al., 2012).

Biotic modifiers (also referred to as ecosystem engineers, niche constructors, keystone species or foundation species) **significantly affect the growing conditions of the focal species**, and consequently, influence the presence of other interacting species reliant on the same resources and conditions (Linder et al., 2012). Remarkable examples of biotic modifiers are earthworms enhancing litter decomposition and soil turnover, trees possessing flammable biomass that can alter fire regimes (Bonanomi et al., 2008), nitrogen-fixing species that enhance nutrient conditions (Esther et al., 2008), and tree species that have the capacity to modulate forest-floor microclimates (De Frenne et al., 2021; Haesen, Lenoir, et al., 2023). Modeling the indirect interactions or mediating effects of these biotic modifiers on the distribution of the focal species finds natural application in structural equation modeling (SEM) or path analysis (Da Re et al., 2023). Nonetheless, within SDMs, environmental modulation can also be captured through the inclusion of the abundances or predicted suitability of the biotic modifiers (Linder et al., 2012) without necessarily involving a SEM framework. However, SEM or path analysis appear more powerful in this regard because they enable testing of both the direct and indirect effects of environmental factors on a focal species' occurrence. It does so by examining one or multiple species acting as biotic modifiers, which may provide a more accurate reflection of the natural complexity of the growing conditions (such as microclimatic conditions) experienced by the focal species.

2.2. Surrogate variables for plant interactions

In ecological systems, comprehensively deciphering the intricate web of interactions between multiple species is a great challenge. To overcome this complexity, **surrogate variables** have been included in SDMs that **approximate gradients of biotic interactions** within the landscape (Wisz et al., 2013). These methods necessitate a foundation of *a priori* ecological knowledge concerning the nature of relevant biotic interactions, such as competition for resources like light in the context of plant-plant interactions. Researchers have utilized species richness derived from macroecological models (Rahbek et al., 2007) or empirical models (Sabatini et al., 2022) as a surrogate indicator for the maximum potential co-occurrence of species within landscape pixels. Moreover, proxies like productivity, tree cover or vegetation height, often estimated through remote sensing, have been employed to gauge competition intensity of the more visible layers of the plant community (Maestre et al., 2010; Nieto-Lugilde et al., 2015; Weber et al., 2016). Such surrogates, however, are not often available to describe plant-plant interactions within the more hidden layers, such as for understorey vegetation in forest ecosystems.

Community-weighted means of trait values also serve as valuable surrogate variables to infer various ecological interactions within ecosystems (Morales-Castilla et al., 2015). Species traits could, for instance, be used to suggest competitive exclusion among ecologically similar species (Davies et al., 2007). Biotic interactions are thus able to shape the functional composition of complete communities (Gross et al., 2009). In instances where direct trait data might be unavailable, phylogenetic information emerges as a useful proxy (Morales-Castilla et al., 2015), given that closely related species tend to exhibit niche conservatism, thereby competing for analogous resources. Community phylogenetics could thus be employed to gauge plant-plant interactions with more competition associated with increasing phylogenetic relatedness (Valiente-Banuet & Verdú, 2008).

2.3. Joint species distribution models (jSDMs)

Multi-species or joint species distribution models (jSDMs) employ a hierarchical framework to **simultaneously fit multiple species-specific models**, wherein the regression coefficients originate from a common distribution (Ovaskainen & Soininen, 2011). This hierarchical structure enables the accommodation of species with limited data by ‘borrowing statistical information’ from more abundant species to estimate coefficients for rarer species (Hui et al., 2013; Ovaskainen & Soininen, 2011). Species co-occurrence data also facilitate the inference of biotic interactions. Species that co-occur more frequently than expected suggest facilitation, while occurrences less frequent than expected imply niche partitioning or negative interactions like competition. Evidence of species interactions could thus be found in the residuals of a jSDM after controlling for abiotic factors (Pollock et al., 2014). The inference of species associations from the residuals, rather than through predictor variables circumvents issues related to multicollinearity (Pollock et al., 2014), yet, overlooks the asymmetric nature of most interactions given the symmetrical parameterization of covariance matrices (Dormann et al., 2018). Importantly, the mere co-occurrence of species should not unilaterally indicate ecological interactions (Blanchet et al., 2020; Townsend Peterson et al., 2011). The residual species association patterns in jSDMs may arise from various sources, including missing environmental covariates or unaccounted biotic interactions (Dormann et al., 2018). As with direct interaction covariates, issues may arise with indirect interactions and shared responses to unmeasured environmental variables, as these can affect the residual correlation between species. Additionally, zero residual correlation between species should not be conclusively interpreted as evidence of an absence of interaction, as this might stem from insufficient data to estimate these interactions (Popovic et al., 2019). Furthermore, even if the residual correlation matrix would reflect species interactions, it likely encompasses the realized impact of direct negative (e.g., competition), direct positive (e.g., facilitation), and other more indirect (e.g., due to shared predators) associations between species (Poggiato et al. 2021). Some of these pitfalls also apply to other methods outlined above.

Joint SDMs delineate species distributions exclusively within the environmental space, while other factors including interaction effects are included within the residual covariance matrix and thus might not improve the assessment of the fundamental niche (Poggiato et al., 2021). The prevailing consensus now is that residual correlation is not necessarily indicative for species' interaction (Dormann et al., 2018). The interpretation of the residual covariance matrix should consider the context of unaccounted predictor variables, biotic interactions and model inaccuracies (Zurell et al., 2018). Joint SDMs may thus serve as a useful tool for hypothesis generation - rather than definitive detectors of interactions - where substantial residual correlation between species warrants further investigation (Dormann et al., 2018; Pollock et al., 2014). Nevertheless, jSDMs have the proven ability to increase the predictive accuracy of SDMs by incorporating the information inferred from species-to-species associations (Norberg et al., 2019).

Early jSDMs relied on the multivariate probit model, **inferring species-to-species associations through a full-rank covariance matrix** (Pollock et al., 2014). However, this approach faces limitations in handling species-rich datasets as the number of parameters to estimate increases quadratically with the number of species (Warton et al., 2015). To address this issue, most current methodologies substitute the **species covariance matrix with a reduced set of latent variables** (Warton et al., 2015). The reparameterization of large covariance matrices with latent variables enhances the computational efficiency of jSDMs. Species responding similarly or differently to these latent variables exhibit positive or negative associations (Warton et al., 2015). The factor loadings of the latent variables can thus be translated into a species-species covariance matrix. The gain in computational efficiency stems from the considerably fewer latent factors (and thus, number of parameters to estimate) in comparison to the number of species in the data set (Ovaskainen et al., 2016). Further methodological developments in jSDMs have facilitated the incorporation of species' traits and phylogenies in the estimation of species niches (Abrego et al., 2017; Pollock et al., 2012) and enabled species associations to covary with measured environmental covariates (Tikhonov et al., 2017).

Joint SDMs, unlike models employing direct interaction covariates, do not explicitly model species interactions and, as a result, do not necessitate *a priori* knowledge of these interactions. However, Ohlmann et al. (2023) presented a statistical model that allows to integrate the topological structure of a predefined metanetwork into the analysis of species distributions. In contrast to conventional jSDMs, this model explicitly incorporates known interactions, offering a practical implementation of embedding network ecology within jSDMs (Thuiller et al., 2023). This model condenses all local pairwise interactions into a unified metric, which can subsequently be mapped and correlated with spatial layers, enabling the exploration of the effects of spatial environmental variation on biotic interactions (Ohlmann et al., 2023).

2.4. Limitations of the existing SDM methods hindering the accurate integration of biotic interactions

Several existing SDM techniques require assumptions that hinder the accurate integration of biotic interaction effects. Most of these assumptions originate from insufficient understanding of the mechanisms at play, which nonetheless can be deduced from experimental macroecological approaches. For example, most SDM methods assume constant species-to-species associations in space. In natural communities, however, the strength and direction of plant-plant interactions is likely to vary under different environmental conditions (Morales-Castilla et al., 2015; Olsen et al., 2016). Similarly, several methods also assume stationarity in interaction strengths across time, which is probably unlikely. Interaction strengths within forest plant communities, for instance, have been shown to vary under changing climate and forest density scenarios (Sanczuk et al., 2023). This concern has motivated the modelling of temporal variation in species distribution via dynamic SDMs where environmental linkages or residual spatial variation is allowed to vary over time (DeVISSER et al., 2010; Merow et al., 2011), which is possible through an increased understanding of the operating processes (e.g., from demography-environment relations). An experimentally-informed spatial prediction of the strength and direction of plant-plant interactions is likely to advance our understanding on species-to-species associations by integrating new field evidence, hereby leveraging the strengths of both experimental research and correlative SDMs. Experimental macroecological approaches have already been successful in disentangling plant-plant interactions along large environmental gradients (Maestre et al., 2005; Sanczuk et al., 2022; Shepard et al., 2021), and can become particularly valuable when combined with manipulative treatments as they allow projections towards uncharted abiotic (De Frenne, 2023) and biotic conditions (Williams & Jackson, 2007).

3. Introduction of a novel concept: a plant-plant interaction index map

3.1. Rationale of the concept

Here we introduce the concept and potential application of a novel gridded map product: a plant-plant interaction map depicting the realized strength of plant interactions experienced by a focal species or functionally similar group of species. Fundamental to the plant-plant interaction map is the quantification of the Plant-plant Interaction Index (from here referred to as PII), a numerical index proportional to the impact of plant interactions on a focal species' performance, which can be assessed in terms of differences in fitness, demographic rates, cover or presence/absence in experimental vegetation plots with and without interactions with co-occurring plant species. The quantification of plant-plant interaction effects based on performance differences is not new (Armas et al., 2004). The PII of plant communities can be obtained preferably from manipulative experiments, but more opportunistic data-driven approximations may be considered too (**Fig. 1**). Since the magnitude and direction (e.g., positive under competition, negative under facilitation) of plant-plant interactions are driven by specific plant functional traits of the co-occurring species (Freckleton & Watkinson, 2001; Kunstler et al., 2012, 2016), we assume that the PII can be predicted for any given plant community based on community weighted mean (CWM) values of a selection of functional traits (e.g., plant height, specific leaf area, shoot and/or root biomass, rooting depth, etc.), trait syndromes (e.g., Grime C-scores (Hunt et al., 2004) or colonization capacities (Verheyen et al., 2003)), or more general community characteristics (e.g., total vegetation cover or leaf area index) (Salguero-Gómez et al., 2018). Following ecological theory, CWM trait values or communities characteristic are driven by environmental conditions at fine and coarse spatial grains (Govaert et al., 2023; Kemppinen et al., 2021; Moles et al., 2009, 2014; Sanczuk et al., 2021), such that community trait signatures, and the resulting PII for a focal species can be estimated based on the environmental covariates to arrive at a gridded data layer, i.e., a PII map.

The PII map provides a more process-based alternative to account for biotic interactions into SDM analyses compared to - for instance - surrogate approaches, and is expected to become increasingly relevant for the prediction of species' distributions under novel biotic and abiotic conditions (De Frenne, 2023; Williams & Jackson, 2007). In particular for novel environmental conditions that entail biotic communities that have no present-day analog, and in which the formerly derived correlations between plant interaction effects and the assumed environmental surrogates potentially no longer hold (Kerr et al., 2023).

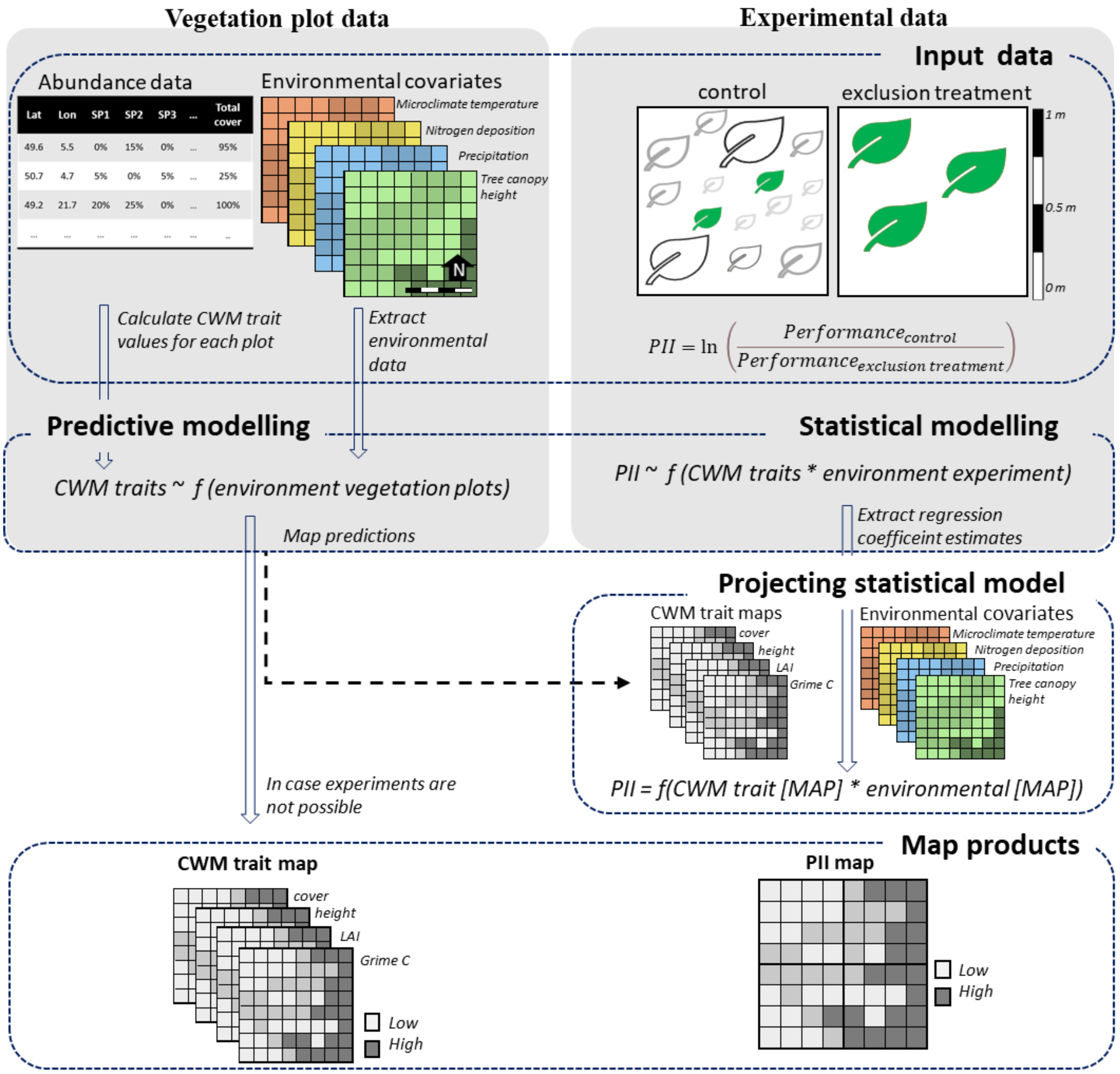


Figure 1 | Concept summary and flowchart of data to calculate a Plant-plant Interaction Index (PII) map. Input data: based on experimental data from interaction-exclusion experiments replicated in different environments (with the removal of all other species; or the removal/absence of only one interacting species if a focal pairwise interaction is considered), the PII is quantified as the natural log-transformed (ln) response ratio of performance differences (performance in control *versus* performance in exclusion treatment). The PII represents a numerical index proportional to the impact of plant-plant interactions on a focal species' performance. Vegetation plot data and gridded environmental covariates are required for trait mapping. Modeling: Statistical models relate the PII derived from interaction-exclusion experiments to the Community-Weighted Mean (CWM) trait values of the co-occurring species and the environment in the experimental plots. Note that more general community characteristics (e.g., total cover or leaf area index (LAI)) may be considered too. Predictive models such as random forest or boosted regression trees are used to develop CWM trait maps based on the trait-environment relations based on the vegetation plot data set. Note that the CWM trait model and PII model relies on independent environmental data. Projecting statistical model: The coefficient estimates extracted from the statistical model and the gridded CWM trait- and environmental data allow to project the PII across the study area. Map products: a spatially-explicit prediction of PII that estimates the realized strength of plant-plant interactions experienced by a focal species. In case interaction-exclusion experiments are impossible, the PII map may be approximated by one or multiple CWM trait maps of the vegetation for a selection of traits assumed to determine interactions strength within the focal stratum of the community.

3.2. Steps to develop the plant-plant interaction map

The development of the PII map based on environmental data and the trait signatures of plant communities requires a four-step process: (i) quantification of the PII from experimental data based on differences in plant performance following variation in plant-plant interactions, (ii) parametrization of a statistical plant interaction model by linking the PII the environmental data and CWM trait data for traits determining plant interaction strengths within the plant community in the experimental sites; (iii) parameterization of a predictive model using vegetation survey data to map CWM trait values across the study area based on environmental data, and (iv) projecting the plant-plant interaction model across the study area using gridded CWM trait and environmental data layers.

3.2.1. Quantifying the PII, a proxy for plant-plant interaction strength

The quantification of the PII based on differences in plant performance following variation in plant-plant interactions ideally requires manipulative experiments (**Box 1**) (Armas et al., 2004). Spatially replicated manipulative experiments (cf., experimental macroecology) are highly suited to unravel the relations between community trait characteristics and the focal species' performance in great detail, and allows us to disentangle biotic effects from effects brought about by other environmental conditions such as temperature, precipitation or soil characteristics (Dunne et al., 2004; Nemer et al., 2021; Shepard et al., 2021). In these experiments, the focal species is transplanted or sown into paired plots with and without co-occurring plant species (by e.g., clipping all above-ground plant biomass; e.g., Sanczuk et al., 2022). It is not the identity of the interacting species itself, but rather the trait information of these species that is used for predicting the PII. The PII may also depict plant-plant interactions between only one focal species pair, in which case the PII is predicted based on key characteristics of the focal interacting species while also accounting for interaction effects with other resident species (such as demonstrated in the worked example, **Box 2**). Comparing the plant performances in the paired experimental plots allows us to calculate the PII as the natural-log transformed response ratio between both treatments (Hedges et al., 1999) (see also **Box 1**), which can be statistically linked to the trait-signature of the interacting plant community (or one single interacting species) and the environmental covariates measured at the experimental sites. Using the response ratio (i.e., the PII) calculated from paired plots as a dependent variable allows us to isolate the effects brought about by the unique contribution of individual traits of the co-occurring species from other environmental conditions on the focal species' performance. Especially when spatially replicated into different environmental conditions along multi-scale gradients, interaction-exclusion transplant experiments become highly valuable to gain detailed understanding on the relative importance of biotic interactions *versus* other environmental conditions (e.g., macro- and microclimatic conditions, soil moisture or nutrient contents) (Olsen et al., 2016; Sanczuk et al., 2023; Töpper et al., 2018). Plant-herbivore interactions may also be modelled using this framework, for instance, by calculating the PII metric from paired herbivore-exclusion treatments applied on plant communities (cf., experimental designs like the ECOSHRUB research network; https://www.ntnu.edu/biology/research/ecoshrub/). Interaction-exclusion treatments are likely the most feasible for smaller or short-lived species. In case experiments are impossible, more opportunistic data-driven approaches may be considered (section 3.2.4).

The performance of the focal species can be assessed based on one or multiple performance attributes at a single point in time (such as fitness, plant height, cover or fitness (De Pauw et al., 2022; Pérez-Harguindeguy et al., 2016)) or based on population-level demographic rates (e.g., vital rates such as the survival and growth rate, or population growth rate) inferred from time series data (Fernández-Fernández et al., 2022; Merow et al., 2014) (**Box 1**). These approaches are technically challenging, but may greatly benefit from recent developments in near-surface remote sensing. For example, plant trait- and performance-measurements, such as species-specific abundances, plant height or volume estimates, can be obtained from photogrammetry, which is increasingly used in experimental ecology (Iglhaut et al., 2019; Luscier et al., 2006). Photogrammetry overcomes common limitations inherent to field observations (e.g., lack of consistency and objectivity) and can operate autonomously and continuously at remote locations, which facilitates studying plant interactions through time.

Manipulative transplant experiments are ubiquitous for herbaceous species due to their short generation times and prompt responses to environmental variation, but become often impractical to run for many species together and even impossible to conduct for certain taxa. For tree species that have long generation times, the *in-situ* quantification of PIIs is generally impossible based on experiments, and alternative surrogate approaches (section 2.2) may be preferred (cf., Morales-Castilla et al., 2015).

3.2.2. Parameterizing a statistical Plant-plant Interaction Index model

The PII values of a focal species inferred from spatially replicated interaction-exclusion experiments can be related to the trait-signature of the co-occurring species and experimental environmental covariate data using multivariate regression models (with CWM traits and environmental covariates as predictors; hereafter referred to as PII models). The PII can also be considered for multiple focal species simultaneously, in which case also the trait values of (or, trait dissimilarity between) these focal species can be included in the PII model. PII models provide the information to project (map) the PII across the study area based on gridded environmental and CWM trait data (described in *section 3.2.4*).

The plant characteristics of the co-occurring species can be described in terms of CWM functional traits, but also other summary statistics of the traits' distributions (e.g., maximum) or community characteristics such as community below- or aboveground biomass, total cover or the leaf area index (LAI) may be considered. Differences in trait values between the focal species and the interacting vegetation (rather than absolute trait values of the interacting vegetation) can also be relevant. The selection of relevant traits and/or community characteristics as predictor variables in the PII model will depend on the nature of the biotic interactions under investigation. If, for example, competition for light is considered the dominant type of interaction determining the performance of the focal species within the community, community characteristics that relate to shading (e.g., CWM plant height in combination with community LAI) should be focused upon for modelling. If belowground competition is dominant, other community characteristics including, for example, belowground plant biomass and CWM root traits (e.g., specific root length, rooting depth) will be more relevant. If no prior information on the types of plant-plant interaction is available, one can consider more general community characteristics that relate to plant competition in general, such as the CWM colonization capacity index (Verheyen et al., 2003) or CWM Grime-C (competition) score (Grime, 1977).

PII model development will depend on the data types considered: in experiments, trait data of the co-occurring species in the community will mostly be available from *in situ* measurements. Direct plant trait measurements are especially relevant when (i) traits are very plastic and adapt to the environment and (ii) in case the required trait data are not available in existing databases. In case the *in situ* trait measurements are not available, species-specific average trait values can be extracted from globally-available trait databases such as LEDA (Kleyer et al., 2008) or TRY (Kattge et al., 2020). Based on collected trait data and focal species' performance data, a PII model can be fitted using a variety of candidate models, going from simple linear regressions to more complex non-linear models such as additive models or polynomial regression models. Models that explicitly test for interaction effects between the CWM trait and environmental conditions, are more likely to describe the natural complexity of the system (Shepard et al., 2021; Töpper et al., 2018).

Box 1 | Optimal experimental design to quantify the Plant-plant interactions index in the field

A well-chosen design of spatial interaction-exclusion experiments is key to develop a PII-map with spatial detail (i.e., grain size) and extent relevant for biogeographical predictions. Interaction-exclusion experiments (**Fig. 2**) become particularly valuable when replicated at fine spatial grains (for example, 100 m or smaller if micro-gradients are deemed to be important) and across several locations covering a large spatial extent (for example, >1,000 km) in order to understand, and predict, the effects along multi-scale environmental gradients (see **Box 2** for an example).

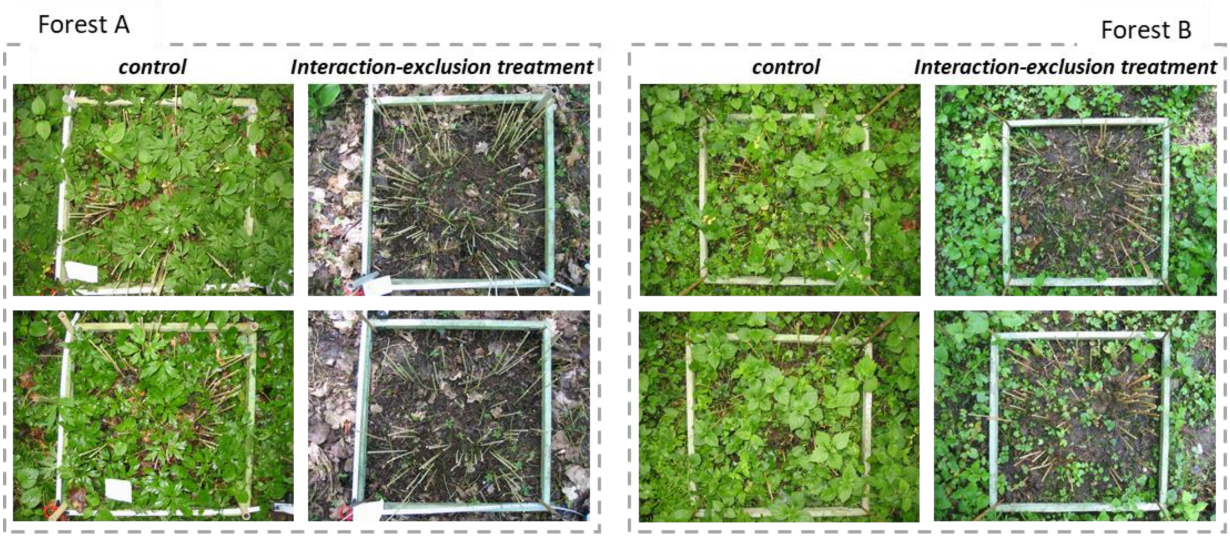
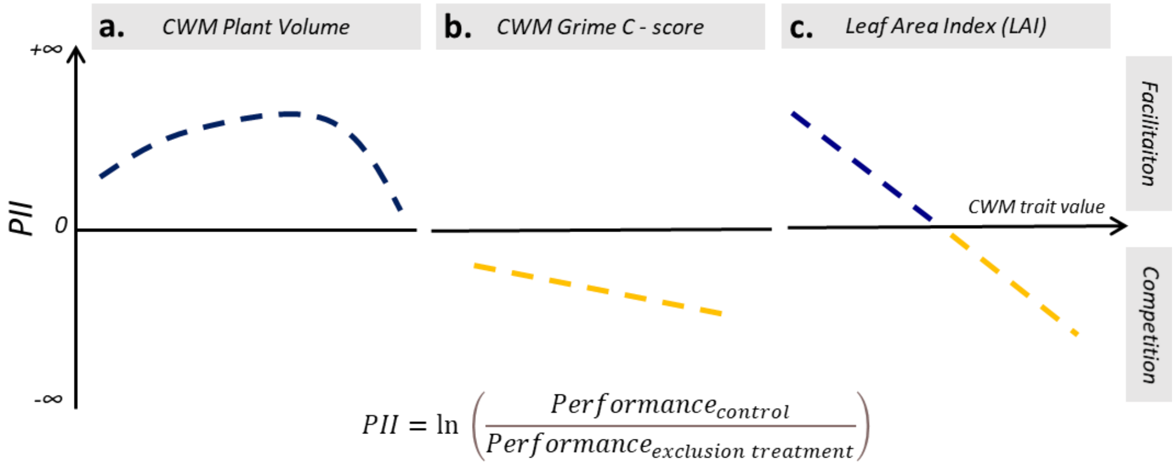


Figure 2 | Example of an interaction-exclusion experiment replicated in an understorey community of two different forest sites in Belgium. Control plots are plots where the focal species (*Ornithogalum pyrenaicum*) has been sown within the resident vegetation. Interaction-exclusion treatments were performed by clipping and removing all above-ground biomass. Wooden sticks indicated germinated seedlings. See (Sanczuk et al., 2022) for details.

Several performance attributes can be considered to quantify PIIs. Single sample estimates of performances (such as derived from plant height, volume estimates or an integrated metric across multiple traits (Verheyen & Hermy, 2004)) are evidently easier. However, such performance metrics are more prone to bias introduced by stochastic environmental processes and individual outliers. Population-level performance estimates inferred from annual transition data such as survival, fecundity or population growth rates appear more robust and better accommodate environmental stochasticity across the entire study period (Sanczuk et al., 2022).

A focal species likely experiences different types of interactions, including ones that can both negatively and positively impact its performance. For example, certain trait signatures of the co-occurring species might have facilitative effects brought about by e.g., the protection against drought or herbivory by high above-ground volume (**Fig. 3a**) (Rothstein & Zak, 2001), while simultaneously impacting the focal species negatively due to, for example root competition (**Fig. 3b**) or high leaf area index (**Fig. 3c**). Although the PII estimate is determined based on the overall realized impact of all different aspects of the co-occurring vegetation, statistical modeling allows us to disentangle individual PII – CWM trait relations such that the overall effect of each investigated CWM trait of the co-occurring species can be estimated.



$$PII = \ln\left(\frac{Performance_{control}}{Performance_{exclusion\ treatment}}\right)$$

Figure 3 | Schematic illustration of hypothetical plant interaction models and formula of the Plant-plant Interaction Index (PII). Illustration of a hypothetical relation between the PII and community weighted mean (CWM) trait values (e.g., CWM plant volume (a)), CWM plant syndromes (e.g., CWM Grime-C (competition) score (b)) or general community characteristic (e.g., Leaf Area Index (c)) under positive (e.g., due to facilitation) and negative (e.g., due to competition) plant-plant interactions. A PII of zero indicates that plant-plant interaction had no effects on the focal species performance.

3.2.3. Predicting and mapping CWM traits based on environmental covariates

After modelling the PII based on the trait signature of plant communities and the environment in the experimental sites, the PII can be calculated for virtually any georeferenced assemblage of plant species that have been described in terms of species composition, and for which environmental data and trait characteristics for all co-occurring species are measured or can be extracted from databases. In order to develop a PII map, gridded data layers of each predictor in the PII model (*section 3.2.2*) are required. While spatial environmental data layers are available with an increasing level of detail (both in terms of quality and grain size), CWM trait maps generally don’t exist. Most recent developments in predictive modelling, however, enable mapping of the CWM trait values as a function of environmental covariates with increasing accuracy. Machine learning models such as random forest models or boosted regression trees can be trained based on vegetation survey databases (e.g., following the protocol of (Haesen et al., 2021)) and relate CWM trait values to environmental covariates of each plot in the database (extracted from gridded environmental data layers (Haesen et al., 2021; Hansen et al., 2010; Karger et al., 2017), soilGrids.org or derived from more advanced high-resolution remote sensing techniques (Ewald et al., 2018)). Using this model, CWM trait values for the set of traits considered in the PII model can be mapped for each grid cell in the study area at the relevant grain size – resulting in maps of CWM trait values. CWM trait model prediction can be validated independently based on experimental site data (*section 3.2.1*).

Networks of vegetation survey plots are possibly the most important source of community-level plant data, as they have been performed for various layers within the communities and generally contain data on at least species identity and (relative) abundance. At the continental to global extent, numerous vegetation survey databases (e.g., sPlotOpen (Sabatini et al., 2021), forestREplot (https://forestreplot.ugent.be/), GLORIA (https://www.gloria.ac.at/home), EVA (Chytrý et al., 2016) or AVA (https://www.geobotany.uaf.edu/ava/)) are available that contain exactly this type of information, often for an enormous amount of vegetation plots spanning large environmental gradients at coarse (i.e., along macroclimate gradients of temperature or precipitation) and finer spatial grains (e.g., along gradients of microclimate or tree cover density).

Trait mapping is facilitated by the growing level of detail and availability of spatial environmental data to describe the growing conditions of plant species. Latest developments in remote sensing, in particular, increasingly enable the direct inference of trait values at the community level (CWM traits data), or indirectly through describing the biotic growing conditions of the focal plant community, because many remote sensing technologies are now able to capture different aspects of key plant community traits (Chen et al., 2022; Cho et al., 2012). Prominent examples of such traits include plant height, volume, leaf area, canopy cover and biomass, some of which have already been mapped in great detail at continental and global scales by linking satellite imagery to 3-D Light Detection and Ranging (LiDAR) data (Lang et al., 2023; Liu et al., 2023). LiDAR data is especially useful to map 3-D morphological traits that are indicative of interaction strengths, e.g., forest understorey density estimates or vertical profiles of leaf area and light availability (Kükenbrink et al., 2021). These attributes can be complemented with recently developed layers describing leaf physiological and functional trait information derived from hyperspectral imaging, such as photosynthetic pigments, nutrient content and defensive compounds (Asner et al., 2015; Ewald et al., 2018; Wang et al., 2020). Furthermore, remote sensing tools are also providing new insights into below-ground interactions, e.g., by using magnetic resonance imaging (MRI) or ground penetrating radar, however these close-range techniques are yet to be upscaled (Chen et al., 2022).

Biotic covariates can also be combined with abiotic covariates. For example, advances in microclimate modelling and mapping improve the estimation of species climatic niches and (re-)distributions and are thus expected to improve PII- and CWM trait-mapping (Haesen, Lenoir, et al., 2023; Maclean & Early, 2023). Microclimate maps are increasingly available at national, continental and even global scales (Haesen, Lembrechts, et al., 2023; Lembrechts et al., 2022; Zellweger et al., 2023) and can be complemented with coarser grained macroclimate data, as well as datasets describing soil properties (Hengl et al., 2017; Karger et al., 2017). Mapping the PII and CWM trait values is thus increasingly possible across a range of scales.

3.2.4. Calculating the PII-map

Combining the knowledge of the PII model (regression coefficients) and the spatial derivates of each predictor variable in the PII model allows us to calculate an experimentally informed PII map. The resulting spatial extent and grain size of the PII map inherently depends on the spatial design of the interaction-exclusion experiment (*section 3.2.1*). Note that, although fine-grained large-extent map predictions based on plant responses measured in experimental macroecological settings have already been performed with success (Merow et al., 2017; Sanczuk et al., 2023), the accuracy of the PII- and CWM trait-predictions far beyond the (biotic and abiotic) environmental range that is sampled can be less accurate due to extrapolation uncertainty. In particular for novel environmental conditions that entail biotic communities that have no present-day analog, the accuracy of PII model predictions remains to be validated since formerly derived PIIs – trait- and environmental-relations potentially no longer hold.

In the case experiments are impossible for the focal species, one may explore the use of CWM trait maps directly as a covariate layer into SDM (cf. section 2.2; surrogate variables of interactions). Although CWM trait maps don't capture direct information (from field evidence) on the link between the focal species' performances and the trait signature of the resident vegetation, integrating these maps for certain traits selected based on prior knowledge may still improve the accuracy of SDM predictions (Morales-Castilla et al., 2015).

Box 2 | Worked example: PII-mapping using plant community data from a transplant experiment

To illustrate a potential workflow, we here develop a PII-map for the common European forest herb *Geum urbanum* based on the realized impacts of the competitive generalist herb *Urtica dioica. Urtica* is a strongly competitive herb species that can produce large volumes of biomass on nutrient-rich soils and when light is not limited, such as in forest edges. We focus on the individual effects brought about by *Urtica* on the performance of *Geum* while also accounting for potential interaction effects with other resident herb species. To do so, we estimate the PII based on data from a fine-grained large-extent plant community transplant experiment (Sanczuk et al., 2023). We then link the PII estimates to the environment of the experiment and the proportional cover of the competitive generalist *Urtica* (here, as a single plant community trait).

Step 1 - Quantifying the PII, a proxy for plant-plant interaction strength: The PII is quantified as the log-ratio of *Geum*'s biomass volume (calculated as cover × average plant height in the plot) in paired plots (i.e., in the same environment next to each other) with and without *Urtica*, using data from a spatially replicated community transplant experiment (see Sanczuk et al., 2023 and **Fig. 4**)

Step 2 - Parameterizing a statistical Plant-plant Interaction Index model: The PII is linked to the percentage cover of *Urtica* and the environmental variation at coarse (growing-season temperature and precipitation) and fine spatial grains (tree cover density) within the experiment using a linear model. A model selection based on AICc (Akaike information criterion corrected for small sample size) is applied to identify the most parsimonious model structure and avoid overfitting.

Step 3 - Predicting and mapping CWM traits based on environmental covariates: We predict the percentage cover of *Urtica* across the study area based on an independent vegetation plot data set (sPlotOpen; Sabatini et al., 2021), and gridded environmental covariates. The percentage cover of *Urtica* across the vegetation plots is linked to three gridded environmental predictor variables (for illustration we used the same variables as in step 2, but these don't necessarily have to be the same), using the predictive Random Forest algorithm. The trained model was projected across the study area to obtain the 'community trait map'.

Step 4 - Calculating the PII-map: Finally, a PII measure is estimated for each grid cell in the study area using the optimal model structure and coefficient estimates of the linear model (data from step 2) and the gridded environmental (temperature, precipitation and tree cover density) and trait variable (predicted cover of *Urtica*, data from step 3).

The PII map product may be integrated in SDMs to account for biotic interaction effects brought about by *Urtica* on the habitat suitability of *Geum.* This PII map will be especially relevant to obtain high-resolution predictions of the habitat suitability in habitat types where Urtica is expected to be a determinant driver of the presence of *Geum* – such as in forest edges. Knowing the link between *Geum* performance and the percentage cover of *Urtica*, we can, for instance, assess the possible impacts of changes in tree cover density on the percentage cover of *Urtica* and how this affects the PII, to ultimately analyze to what extent these biotic changes propagate up to biogeographical range shifts of *Geum*. This way, PII mapping is a powerful and flexible tool that effectively leverages the strengths of both experimental research and correlative SDMs.

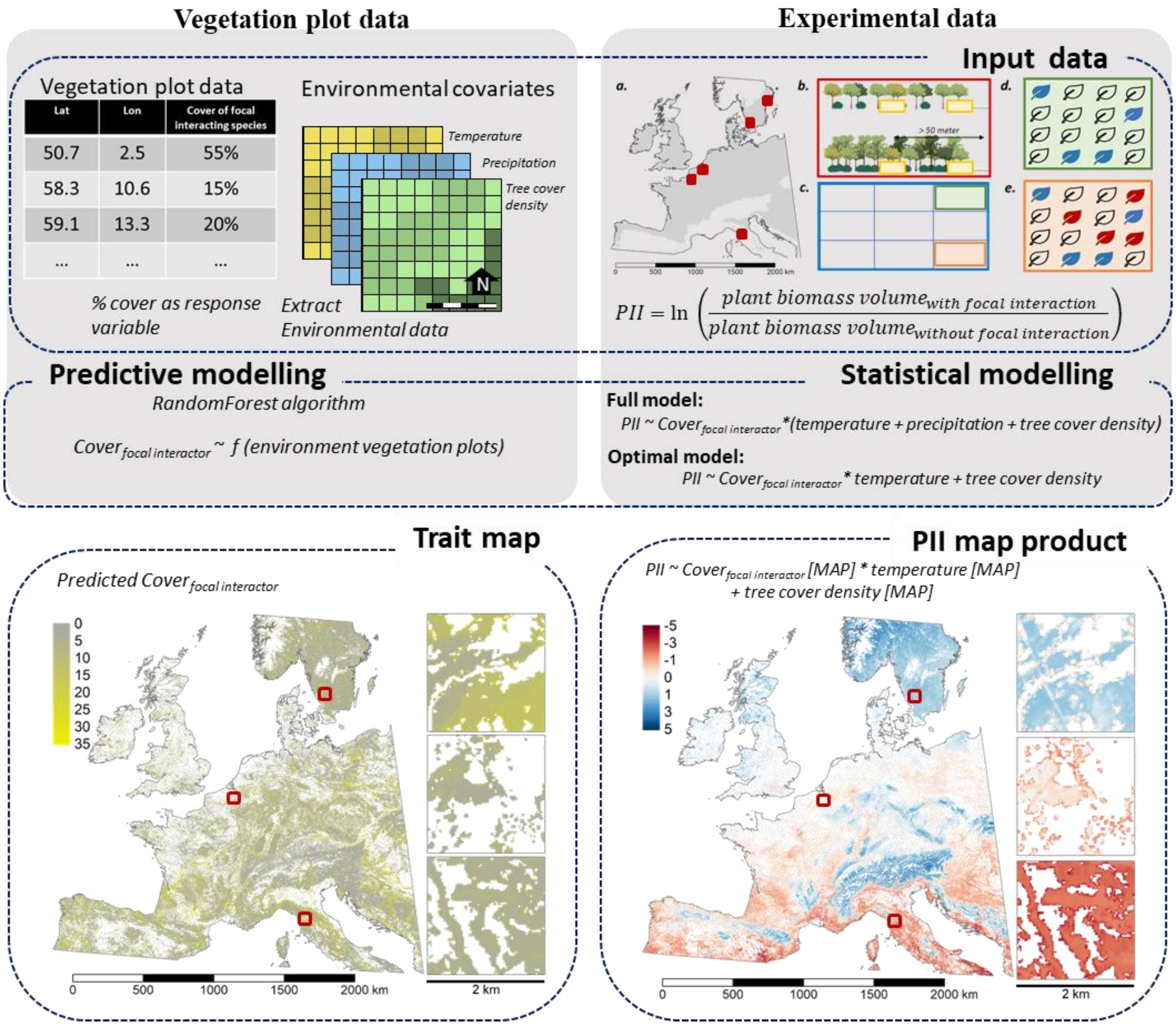


Figure 4 | Methods summary and data to calculate a Plant-plant Interaction Index (PII) map used in the worked example. We mapped the PII for the forest herb *Geum urbanum* based on the realized impact of the competitive generalist herb *Urtica dioica*. We thus focus on the individual effects brought about by *Urtica* on the performance of *Geum* while accounting for the effects of ambient plant interaction with other resident herb species. We estimate the PII based on data from a fine-grained large-extent plant community transplant experiment (right grey panel, a-c) (Sanczuk et al., 2023). The PII is quantified as the log-ratio of *Geum*'s biomass in plant communities with and without *Urtica* (right grey panel, d-e). The PII is linked to the percentage cover of Urtica and the environmental variation at coarse (temperature and precipitation) and fine spatial grains (tree cover density) within the experiment using a linear model. A model selection on the full model is applied based on AICc (Akaike information criterion corrected for small sample size). We map the proportional cover of the *Urtica* across the study area based on an independent vegetation plot data set (sPlotOpen), and gridded environmental covariates (left grey panel) using a predictive Random Forest algorithm, to obtain a 'trait map' (i.e., predicted cover (%) of *Urtica*). Trait map predictions are made at 25 m resolution for the extent of temperate Europe. Red squares indicate the raster prediction of landscape windows illustrated at the right. The PII map product is estimated for 1,000,000 random forested locations in the study area and of each forested grid cell within the three landscape windows by projecting the linear model across the (abiotic and biotic) environment. Note that, as expected, forest edges and regions with warmer macroclimate generally have a higher estimated PII.

3.5. Challenges for plant-plant interaction mapping

Plant-plant interaction mapping based on the link between species' performances and the trait-landscape of the co-occurring plant species poses several challenges. First, the accuracy of the map predictions inherently depends on the predictive performance of the PII model. It remains to be evaluated based on real-world data to what extent PII models allow us to accurately predict plant-plant interactions strengths, and which experimental designs, plant community and remote sensing data sources are most promising. Second, model predictions beyond the environmental range that was sampled might be less accurate as a result of extrapolation uncertainty. Third, unaccounted biotic interactions such as plant-animal dynamics may substantially impact plant communities and these effects do not necessarily remain constant along an environmental gradient (see e.g., variable effects of herbivory along a nitrogen gradient (Segar et al., 2022)). Last, a focal species likely experiences different modes of interactions, with likely divergent effects on the species' performances (e.g., both facilitative and competitive interactions; **Fig. 3**). The PII is not able to depict these different aspects of the biotic environment, and its final estimate will be determined based on the overall, realized impact of the resident vegetation.

4. Conclusions and outlook

Changing environmental conditions lead to novel assemblages of species that may start interacting within an uncharted portion of the environmental space. Accounting for plant-plant interactions using existing SDM techniques remains challenging. Advanced SDMs facilitate the integration of biotic interaction effects based on species-to-species associations. However, when novel environmental conditions arise in which the formerly derived species' correlations potentially no longer hold, a more process-based approach is warranted.

By linking species performances to the trait characteristics of interacting species, biotic interactions maps can be obtained for virtually any focal natural community, including maps for less visible vegetation layers as well as for plant-herbivore interactions or interactions within animal communities. Upscaling manipulative experiments at macroecological settings to generate broad-scale plant-plant interaction maps hold promise for an improved integration of biotic interaction effects by leveraging the strengths of experimental research and correlative SDMs. In terms of perspectives, PII mapping may also be deployed to aid the prediction of impacts of alterations in community trait values on the focal species' performance, even if certain combinations of species do not yet co-occur. For example, knowing the link between a focal species performance and the trait signature of the co-occurring species, one can assess the possible impacts of a successful invasive species (with known trait values) on the community PII, and analyzes to what extent these biotic alterations propagate up to biogeographical range shifts of the focal species. Hence, PII mapping adds an additional layer of flexibility to the ecologists' toolbox.

Data Availability Statement

All data and code of used in the worked example will be made available on FigShare (https://figshare.com/).

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