Article

Measurement and identification of positive plant interactions: Overview and new perspective

WenJun Zhang
School of Life Sciences, Sun Yat-sen University, Guangzhou 510275, China; International Academy of Ecology and Environmental Sciences, Hong Kong
E-mail: zhwj@mail.sysu.edu.cn, wjzhang@iaees.org

Received 19 November 2016; *Accepted 10 December 2016*; *Published online 1 June 2017*

Abstract
Positive interactions play a key role in plant communities. The present study discusses measurement/identification methods of positive plant interactions. So far, some indices, e.g., RII, RCI, RNE and lnRR, and some models, e.g., site-based neighborhood models, individual-based models, etc., are usually used to measure and identify the type and strength of positive plant interactions. Most of these methods are based on interaction data of two species only. In a multi-species community or ecosystem, which occurs mostly in the nature, the interaction between two species is influenced by other species in the environment and may change as the time. Those indices and models may not exactly represent the true situations in the nature. Therefore, I argue that the inclusion of multi-species interactions in the network and utilization of theory and methods of network analysis and network evolution should be the focus in the future. The network evolution model, and correlation- and network-based methods in relation to species interactions were introduced and discussed. Finally, I think that network thinking and selforganizology are the basis for the future research of complex and dynamic species interactions.

Keywords positive plant interactions; measurement; identification; indices; models; sampling; network analysis; self-organization.

Network Biology
ISSN 2220-8879
URL: http://www.iaees.org/publications/journals/nb/online-version.asp
RSS: http://www.iaees.org/publications/journals/nb/rss.xml
E-mail: networkbiology@iaees.org
Editor-in-Chief: WenJun Zhang
Publisher: International Academy of Ecology and Environmental Sciences

1 Introduction

Both positive and negative interactions between organisms are the most important factor for both construction of communities and maintenance of biodiversity (Grime, 1979; Bertness and Callaway, 1994; Zhang, 2007; Damgaard, 2011; Zhang, 2011, 2012a-b, 2014a-c, 2015a-b, 2016a; Maihait and Zhang, 2014; Zhang and Li, 2015a-b; Zhang and Liu, 2015). They determine population dynamics, community structure and ecosystem functions. Negative interactions refer to decreased growth, survival or reproduction of organisms due to limited resources and space. Negative interactions include competition (-/-) and amensalism (-/0) (Zhang, 2011). Positive interactions are interactions beneficial to an organism and at least harmless to another organism, i.e., the existence of an organism increases the growth, survival or reproduction of orther organism. Callaway (2007) and Zhang (2011) defined positive interactions are interactions beneficial to at least one of two interactive organisms, i.e., the existence of an organism increases the growth, survival or reproduction of another organism. Therefore, positive interactions include such types, (1) mutualism (+/+): both organisms co-exist and depend on each other for a long time, and the two sides profit from each other; (2) commensalism (+/0): symbiosis is beneficial to an organism and not effective to another organism; (3) protocooperation (+/+): it is similar to mutualism, however, their collaboration is loose and any one of the two organisms can live independently; (4) nurse effect, and (5) predation/parasitism (+/-), which mostly occurs across different trophic levels. Furthermore, Zhang (2011) revealed the quantitative mechanism of positive interactions based on foundamental models for predation/parasitism and competition. Nevertheless, in plant ecology, positive interaction can occur within the same species, and can take place between different species, but are limited at the same trophic level, i.e., the interaction types (1)-(4) above (i.e., facilitation).

Similar to the importance of positive interactions in animal communities (Zhang, 2011), positive interactions play a key role in plant communities. As early as in 1914, Pearson conducted the first experiment of positive interactions. He proved that Douglas fir *Pseudotsuga menziesii* showed greater surviveship under the canopy of aspen *Populus tremuloides*. Atsatt and O'Dowd (1976) found that the possibility of a plant feeding by animals was related to released chemicals, morphological composition, distribution and abundance of the surrounding plants. In 1986, DeAngelis et al. discussed the effects of positive interactions on ecosystems. Since then Hunter and Aarssen (1988) demonstrated that positive interactions are an important and common process in plant communities. In 2003, Bruno et al. maintained to include facilitation into ecological theory. In his comprehensive book, Callaway (2007) discussed all aspects of positive interactions, including the development history and research status, and the future direction. Further, Brooker et al. (2008) organized a symposium with the theme of Positive Interactions in Plant Communities, in University of Aberdeen, UK. The symposium proposed to include positive interactions into mainstream ecology based on competition.

2 Mechanisms and Hypothesis of Positive Plant Interactions

2.1 Mechanisms

Some mechanisms of positive plant interactions have been suggested as follows

2.1.1 Direct mechanisms

(1) Hydraulic hydraulic lift. Water is uplifted along root system from the deep layer to the surface dry soil through potential gradient of water, which makes a considerable amount of soil water reallocated inside the plant through its root system (Callaway and Walker, 1997).

(2) Canopy interception. Precipitation is intercepted by plant canopy, which makes soil humidity higher around the plant canopy and thus creates the more humid environment for plants (Brooker et al., 2008).

(3) Shading. Shading help to protect plant tissue, make it prevent from lethal temperature, cut down breathing consumption, reduce ultraviolet irradiation, reduce transpiration and increase soil water content (Brooker et al., 2008).

(4) Nutrients' feedback. Plants absorb nutrients from the soil and return nutrient to the soil by the fallen leaves, thus improving the physical and chemical properties of soil and benefitting the surrounding plants (Callaway and Walker, 1997).

2.1.2 Indirect mechanisms

Indirect mechanisms include using morphological structure (e.g., thorn) or chemical defense to resist herbivores or seed feeders, which prevents the surrounding plants from being eaten. Other examples include helping the surrenounding plants attract pollinators/distributors, or helping maintain soil microorganisms, etc (Brooker et al., 2008).

2.2 Hypothesis

Biomass, survivership, height and other plant traits usually represent the net effect of offset action by positive and negative interactions. In the superior environment, the net effect is competition, and in the stress environment, the net effect is positive interactions.

Stress gradient hypothesis argues that the strength of positive interactions enhances with the intensification of environment stress. Symmetric facilitation (mutualism) significantly increases the survival rate of plants in the extreme stressed environment. Asymmetric facilitation (commensalism) increases the survival rate of plants in the moderate stressed environment.

3 Indices, Models and Methods

3.1 Indices

Some indices are used to measure the strength of plant interactions, RII (Relative Interaction Index), RCI (Relative Competition Index), RNE (Relative Neighbor effect), and lnRR (Log Response Ratio) (Armas et al., 2004).

(1) RII

RII is represented by

$$RII=(\alpha B_0-B_0)/(\alpha B_0+B_0)=(\alpha-1)/(\alpha+1)$$

where $B_0=B_w/\alpha$ is the mass of plants with neighbors, B_w is the mass of isolated individuals. $\alpha>1$, facilitation prevails; $\alpha=1$, neutral interaction; $0\leq\alpha<1$, competition prevails.

(2) RNE

RNE is represented by

$$\begin{aligned} RNE&=(B_0-B_w)/\max(B_0,\alpha B_0)=(B_0-\alpha B_0)/\max(B_0,\alpha B_0) \\ &=1-\alpha, \text{ if } 0\leq\alpha<1 \\ &=(1-\alpha)/\alpha, \text{ if } \alpha>1, \end{aligned}$$

(3) RCI

RCI is represented by

$$RCI=(B_0-B_w)/B_0=(B_0-\alpha B_0)/B_0=1-\alpha$$

(4) lnRR

lnRR is represented by

$$lnRR=\ln(B_0/B_w)=\ln(B_0/\alpha B_0)=-\ln\alpha$$

The criteria to determine the type of interactions using four indices are indicated in Table 1.

RII and lnRR are not so intuitionistic than RNE and RCI when competition prevails and than RNE when positive interactions prevail. RCI cannot be used to measure the strength of strong interaction similar to obligatory parasitism.

Table 1 Criteria to determine the type of interactions using four indices.

	RII	RNE	RCI	lnRR	Interactions
$B_w \to 0$	-1	1	1	∞	Competition
$B_w \to \infty$	1	-1	$-\infty$	$-\infty$	Facilitation
	0	0	0	0	Neutral

3.2 Models

Most models specifically containing positive interactions are derived from the competition models of plant individuals.

3.2.1 Site-based neighborhood models

The most popular site-based neighborhood model is the grid-based model, i.e., cellular automata (Chen et al., 2009; Xiao et al., 2009; Michalet et al., 2011; Ballestores Jr. and Qiu, 2012; Wang et al., 2012; Zhang et al., 2013; Zhang, 2012a, 2016a; Zhang et al., 2015).

3.2.2 Individual-based models

There are various individual-based models (Weiner et al., 2001; Xiao et al., 2009; Griebeler, 2011; Lin et al., 2012; Zhang et al., 2013), including tessellation model (McInnis et al., 2004) and distance model, and the latter futher includes fixed-radius-neighborhood model, zone-of-influence model (Chu et al., 2008; Weiner et al., 2001; Berger et al., 2008), and ecological field model (Wang, 1993).

Zone-of-influence model (ZOI) was proposed by Weiner et al. (2001). In ZOI, the plant obtains resources within the circular area around it (Weiner et al., 2001; Berger et al., 2008; Jia et al., 2011). The growth rate of the plant is

$$dB/dt=r(A-B^2/B_{max}^{4/3})=r(CB^{2/3}-B^2/B_{max}^{4/3})$$

where B is the size of a plant, B_{max} is the maximum mass of the plant, r is the initial (maximum) growth rate, A is the area of the zone of influence of the plant, which represents the potential resources it can obtain, and C is a constant (e.g., C=1).

A plant competes for resources with its target plant within their overlapped zone of influence.

3.2.3 State space model

Damgaard (2011) proposed a novel method for measuring plant-plant interactions in undisturbed semi-natural and natural plant communities where it is difficult to distinguish individual plants. He assumed that the ecological success of the different plant species in the plant community may be adequately measured by plant cover and vertical density, the latter is correlated to the 3-dimensional space occupancy and biomass. In the outlined competition model the vertical density at the end of the growing season is assumed to be a function of the cover of all species at the start of the growing season, and the cover at the start of the growing season is assumed to be a function of the vertical density of all species at the end of the previous growing season. The method allows direct measurements of the competitive effects of neighbouring plants on plant performance and the estimation of parameters that describe the ecological processes of plant interactions during the growing season as well as the process of survival and recruitment between growing seasons. The presented method is suited for testing different ecological hypothesis on competitive interactions along environmental gradients, investigating the importance of competition, as well as predicting the likelihood of different ecological scenarios. In his state space model , the studied competitive processes are assumed to act on latent variables that model plant cover and vertical density by two process equations (or structural equations), and the latent variables are coupled to the observed plant cover and vertical density by two measuring equations.

3.3 New research area: network methods of multiple-species interactions

Michalet et al. (2006) argued that in a moderate or highly stressed environment, a species may expand the niche of its competitive species. According to stress gradient hypothesis, the strength of positive interactions increases with the intensification of environmental stress. In a multi-species community or ecosystem, which occurs mostly in the nature, the interaction between two species is influenced by other species in the environment (Atsatt and O'Dowd, 1976; Michalet et al., 2006), and may change as the time (Zhang, 2015a). Experimental and quantitative methods based on two species only, as mentioned mostly in the sections 3.1 and 3.2 (in exception of state space model) may not exactly represent the true situations in the nature. Therefore, inclusion of multi-species interactions in the network and utilization of theory and methods of network analysis and network evolution should be the focus in the future.

3.3.1 Network evolution model

In the nature, a community or ecosystem acts as a network. A variety of network evolution models have been proposed (Zhang, 2015a, 2016b). Zhang (2015a) developed a generalized network evolution model on community assembly. Different from differential equations with fixed state variables (nodes in the network), his model is the one with changed nodes (species). The model is based on difference equations with different number of species in different stages of evolution. It consists of pioneer rule, invasion and growth rule, extinction rule, connection (flow) rule and termination rule, etc. The invasion, establishment, growth, and extinction of species follow a series of rules. Coefficients of variables in the equations represent the type and strength of interactions. The model provides the basis to build self-organization models with various interactions.

3.3.2 Sampling based network analysis and measurement of multiple-species interactions

Jointly use of partial correlations of various correlation measures, e.g., Pearson correlation, Spearman correlation, Jaccard coefficient, Point correlation, etc., based on sampling data, are effective to identify positive/negative/neutral interactions in a network/system with multiple species (e.g., plant community). Details of these correlation- and network- based methods can be found in Zhang (2011, 2012a-b, 2014a, 2015b-c, 2016a), and Zhang and Li (2015a-b).

4 Discussion

As the increase of findings on positive plant interactions, more and more scientists strongly suggest to include positive interactions in mainstream ecology (Hunter and Aarssen, 1988; Callaway, 2007; Brooker et al., 2008). Nevertheless, in my view, we must focus on various interactions globally in the network/system with multiple species rather than interactions between two species only. We should treat biological systems as self-organing systems. As maintained by Zhang (2015a, 2016a), biological systems, including communities and ecosystems, are mostly self-organizing systems, and the community assembly and succession is a self-organization process. And according to the self-organization theory (Zhang, 2016a), positive interactions play an important role in self-organizing systems. Thus, it is not strange to find a large amount of positive plant interactions in the nature. Network thinking and selforganizology are the basis for the research of complex and dynamic species interactions.

Acknowledgment
We are thankful to the support of Discovery and Crucial Node Analysis of Important Biological and Social Networks (2015.6-2020.6), from Yangling Institute of Modern Agricultural Standardization, and High-Quality Textbook *Network Biology* Project for Engineering of Teaching Quality and Teaching Reform of Undergraduate Universities of Guangdong Province (2015.6-2018.6), from Department of Education of Guangdong Province.

References

Armas C, Ordiales R, Pugnaire FI. 2004. Measuring plant interactions: a new comparative index. Ecology, 85(10): 2682-2686

Atsatt PR, O' Dowd DJ. 1976. Plant defense guilds. Science, 193(4247): 24-29

Ballestores Jr. F, Qiu ZY. 2012. An integrated parcel-based land use change model using cellular automata and decision tree. Proceedings of the International Academy of Ecology and Environmental Sciences, 2(2): 53-69

Berger U, Piou C, Schiffers K, Grimm V. 2008. Competition among plants: concepts, individual-based modeling approaches, and a proposal for a future research strategy. Perspectives in Plant Ecology Evolution and Systematics, 9: 121-135

Bertness MD, Callaway R (1994). Positive interactions in communities. Trends in Ecology & Evolution, 9: 191-193

Brooker RW, Maestre FT, Callaway RM, et al. 2008. Facilitation in plant communities: the past, the present, and the future. Journal of Ecology, 96: 18-34

Bruno JF, et al. 2003. Inclusion of facilitation into ecological theory. Trends in Ecology and Evolution, 18: 119-125

Callaway RM. 2007. Positive Interactions and Interdependence in Plant Communities. Springer, Netherlands

Callaway RM, Walker LR. 1997. Competition and facilitation: a synthetic approach to interactions in plant communities. Ecology, 78: 1958-1965

Chen SY, Xu J, Maestre FT, et al. 2009. Beyond dual-lattice models: incorporating plant strategies when modeling the interplay between facilitation and competition along environmental severity gradients. Journal of Theoretical Biology, 258: 266-273

Chu CJ, Maestre FT, Xiao S, et al. 2008. Balance between facilitation and resource competition determines biomass-density relationships in plant populations. Ecology Letters, 11: 1189-1197

Damgaard C. 2011. Measuring competition in plant communities where it is difficult to distinguish individual plants. Computational Ecology and Software, 1(3): 125-137

DeAngelis DL, Post WM, Travis CC. 1986. Positive Feedback in Natural Systems. Springer-Verlag, NY, USA

Griebeler EM. 2011. Are individual based models a suitable approach to estimate population vulnerability? - a case study. Computational Ecology and Software, 1(1): 14-24

Grime JP. 1979. Plant Strategies and Vegetation Processes. Wiley, Chichester, UK

Hunter AF, Aarssen LW. 1988. Plants helping plants: New evidence indicates that beneficence is important in vegetation. BioScience, 38(1): 34-40

Jia X. 2011. Plant Competition and Facilitation and Their Role in Driving Population Dynamics Across Environmental Gradients: A Study Based on Zone-of-Influence (ZOI) Models. PhD dissertation. Zhejiang University, Hangzhou, China

Lin Y, Berger U, Grimm V, Ji QR. 2012. Differences between symmetric and asymmetric facilitation matter:

exploring the interplay between modes of positive and negative plant interactions. Journal of Ecology, 100: 1482-1491

Maihait M, Zhang WJ. 2014. A mini review on theories and measures of interspecific associations. Selforganizology, 1(3-4): 206-210

McInnis LM, Oswald BP, Williams HM, et al. 2004. Growth response of *Pinus taeda* L. to herbicide, prescribed fire, and fertilizer. Forest Ecology and Management, 199: 231-242

Michalet R, Xiao S, Touzard B, et al. 2011. Phenotypic variation in nurse traits and community feedbacks define an alpine community. Ecology Letters, 14: 433-443

Michalet R, Brooker RW, Cavieres LA, et al. 2006. Do biotic interactions shape both sides of the humped-back model of species richness in plant communities? Ecology Letters, 9: 767-773

Pearson GA. 1914. The role of aspen in the reforestation of mountain burns in Arizona and New Mexico. Plant World, 17: 249-260

Wang GX. 1993. On Ecological Field. Henan Science and Technology Press, Zhengzhou, China

Wang Y, Ellwood MDF, Maestre FT, et al. 2012. Positive interactions can produce species-rich communities and increase species turnover through time. Journal of Plant Ecology, 5: 417-421

Weiner J, Stoll P, Muller-Landau H, Jasentuliyana A. 2001. The effects of density, spatial pattern, and competitive symmetry on size variation in simulated plant populations. The American Naturalist, 158: 438-450

Xiao S, Michalet R, Wang G, Chen SY. 2009. The interplay between species' positive and negative interactions shapes the community biomass-species richness relationship. Oikos, 118: 1343-1348

Zhang WJ. 2011. Constructing ecological interaction networks by correlation analysis: hints from community sampling. Network Biology, 1(2):81-98

Zhang WJ. 2012a. Computational Ecology: Graphs, Networks and Agent-based Modeling. World Scientific, Singapore

Zhang WJ. 2012b. How to construct the statistic network? An association network of herbaceous plants constructed from field sampling. Network Biology, 2(2): 57-68

Zhang WJ. 2014a. Interspecific associations and community structure: A local survey and analysis in a grass community. Selforganizology, 1(2): 89-129

Zhang WJ, et al. 2014b. Interspecific associations of weed species around rice fields in Pearl River Delta, China: A regional survey. Selforganizology, 1(3-4): 143-205

Zhang WJ. 2014c. Research advances in theories and methods of community assembly and succession. Environmental Skeptics and Critics, 3(3): 52-60

Zhang WJ. 2015a. A generalized network evolution model and self-organization theory on community assembly. Selforganizology, 2(3): 55-64

Zhang WJ. 2015b. A hierarchical method for finding interactions: Jointly using linear correlation and rank correlation analysis. Network Biology, 5(4): 137-145

Zhang WJ. 2015c. Calculation and statistic test of partial correlation of general correlation measures. Selforganizology, 2(4): 65-77

Zhang WJ. 2016a. Selforganizology: The Science of Self-Organization. World Scientific, Singapore

Zhang WJ. 2016b. A random network based, node attraction facilitated network evolution method. Selforganizology, 3(1): 1-9

Zhang WJ, Li X. 2015a. General correlation and partial correlation analysis in finding interactions: with Spearman rank correlation and proportion correlation as correlation measures. Network Biology, 5(4): 163-168

Zhang WJ, Li X. 2015b. Linear correlation analysis in finding interactions: Half of predicted interactions are undeterministic and one-third of candidate direct interactions are missed. Selforganizology, 2(3): 39-45

Zhang WJ, Liu GH. 2015. Coevolution: A synergy in biology and ecology. Selforganizology, 2(2): 35-38

Zhang WJ, Qi YH, Zhang ZG. 2015. A cellular automaton for population diffusion in the homogeneous rectangular area. Selforganizology, 2(1): 13-17

Zhang WP, Pan S, Jia X, et al. 2013. Effects of positive plant interactions on population dynamics and community structures: a review based on individual-based simulation models. Chinese Journal of Plant Ecology, 37(6): 571-582