Original research article

Complex network analysis reveals novel essential properties of competition among individuals in an even-aged plant population

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A R T I C L E   I N F O

A B S T R A C T

Little is known about the network structure of competition in large populations of plants, despite the importance of such knowledge for understanding population dynamics. In this study, we used complex network analysis to examine temporal changes in the network structure of competition in an even-aged multi-individual stand of the Sakhalin fir *Abies sachalinensis* in Hokkaido, Japan. Using census data, which were measured over 30 years (1948–1978; seedlings were planted in 1929), on the sizes and locations of these plants, we regarded a plant as a node and competition between plants as a link. We then introduced two indices, the binary and weighted out-degrees (*BO* and *WO*, respectively), to interpret complicated plant interactions. The *BO* of a plant represents the number of links from the target plant to its neighbors, and the *WO* is the total strength of competition from the target plant to its neighbors. The analysis showed that the distributions of *BO* and *WO* were heavy-tailed in all years and that large plants had large *BO* and *WO*. These results suggest that only a few (i.e., large) plants have a very large impact on the growth and survival of a much larger number of neighboring plants and thus on population dynamics, whereas most of the others (i.e., small and medium-sized plants) have only a small impact on a few neighbors. By introducing binary and weighted connectivities (*BC'* and *WC'*, respectively), we were able to identify the size classes of neighbors with which the target plant preferentially and strongly competed. The *BC'* and *WC'* results showed that large plants competed preferentially and more strongly with other large plants in 1948, but they competed more strongly with small plants after 1963. These results clarify targets of the very large impact of large plants, as shown by the results of *BO* and *WO*: the impact was exerted on the growth and survival of other large plants in 1948, whereas the impact was exerted on those of small plants after 1963. Our study demonstrates that the statistical properties of the competition network structure, which have been largely ignored in plant competition research, are important for understanding plant population dynamics.

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1. Introduction

Competition among individuals for resources (e.g., light or below-ground resources such as water and nutrients) is important in the spatiotemporal dynamics of plant populations (e.g., spatial configurations of plants, size structures, and population sizes). To explain and describe the dynamics, two perspectives on the essential properties of competition are required. First, the properties of competition between any two plants need to be determined. For example, competition between two plants is often size-asymmetric (Schwinning and Weiner, 1998; Thomas and Weiner, 1989; Weiner, 1990) and the effect is attenuated with distance, and plants have no detectable effect on each other beyond a certain distance (Stoll and Weiner, 2000). The second requirement is to understand the network structure (i.e., graph) of competitive relationships among a large number of plants. Although the first of these two perspectives has been well studied, the second has been largely ignored. In some kinds of mean-field model for plant populations (e.g., Yokozawa and Hara, 1995) and gap model (e.g., Botkin et al., 1972), there is an implicit assumption that a plant competes with all other plants in some large spatial region or relatively small patch (the model assumes the complete graph (i.e., every pair of vertices is connected by an edge) as the network structure of competition among plants in some large

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spatial region or relatively small patch) and the distances between plants in the region or patch are equal. In the two-dimensional lattice models for plant populations (models that implement the explicit network structure of competition among plants; e.g., Hendry et al., 1996; Yokozawa et al., 1998), there is also an implicit assumption that a plant competes with no more than 4–24 neighbors (4 in the case of the von Neumann neighborhood, e.g., Tommaso and Norman, 1987; 24 in the case of the second Moore neighborhood, Moore, 1962) and the distances between nearest neighbors are almost equal. Thus, competition among plants in these models (i.e., the mean-field model, gap model and lattice model) is relatively uniform (or less dispersed). We refer to these implicit assumptions of the models as the assumption of relative uniformity.

The analysis method used in the study of complex networks (e.g., Barabási, 2002) is useful to examine the network structure of relationships among a large number of components. Three unique characteristics of complex network analysis support the choice of this approach. First, complex network analysis examines relationships among large numbers of nodes in a network. Second, complex network analysis derives the graph-theoretical and statistical properties of these interactions. Although interactions among a large number of plants have been implemented in individual-based models of plant populations (e.g., Botkin et al., 1972; Pacala et al., 1996; Weiner et al., 2001), the interactions served only as a means to simulate population dynamics, individual size, spatial configuration, etc., without providing an understanding of the graph-theoretical and statistical properties of the interactions. Third, network analysis provides a cross-sectoral understanding of complex phenomena in fields ranging from computer science to biology, including insights into the scale-free (Barabási and Albert, 1999) or small-world (Watts and Strogatz, 1998) properties of networks and important practical knowledge, such as the robustness or vulnerability of the network (Barabási, 2002; Callaway et al., 2000; Cohen et al., 2001; Jeong et al., 2001; Sole and Montoya, 2001). In the science of complex networks, the meaning of "network" includes both flows, such as those in a communication network and energy- or matter-flow pathways in ecosystems (Jørgensen and Fath, 2006), and cause-and-effect relationships (including the presence of interactions), such as those in climate networks (Yamasaki et al., 2008) and competition networks among companies (Yang et al., 2007). Complex network analysis has been applied to study a broad range of ecological relationships (May, 2006; Proulx et al., 2005), such as food webs (Bascompte et al., 2005; Neutel et al., 2002), host–parasite relationships (Vázquez et al., 2005), mutualistic interactions (Jordano et al., 2003), plant–pollinator relationships (Dupont and Olsen, 2012; Ramos-Jiliberto et al., 2010), and energy- or matter-flow pathways in ecosystems (Jørgensen and Fath, 2006). Several ecological studies have used complex network analysis to investigate the characteristics of plant communities, such as the interaction patterns among species in forests (Aderhold et al., 2012; Fuller et al., 2008; Saiz and Alados, 2011) the antagonistic interactions between arboreal plants (e.g., epiphytes, mistletoe, and lianas) and their host plants (Blick and Burns, 2009; Burns, 2007; Burns and Zotz, 2010; Sfair et al., 2010) and two kinds of interaction (i.e., facilitation and competition) between plant species under grazing and nongrazing (Saiz and Alados, 2014; Saiz et al., 2014). These studies have revealed that the complex networks embedded in ecosystems are not randomly assembled and that they have important effects on essential ecological phenomena, such as the stability of ecosystems (Kondoh, 2008).

Moreover, in most ecological network studies, nodes and links are defined as species and their interactions respectively (e.g., Aderhold et al., 2012; Blick and Burns, 2009; Burns, 2007; Burns and Zotz, 2010; Fuller et al., 2008; Sfair et al., 2010). Such species-based network has been very useful in terms of developing simple theory and exploring macro-ecological pattern (Ings et al., 2009). On the other hand, ecological studies came into use complex network analysis for investigations at the individual level (i.e., individual-based network, Araújo et al., 2008; Dupont et al., 2011), but have focused on animals rather than plants. In plants, the size, growing stage and local environment (e.g., neighboring competitors) of individual plants are heterogeneous within a species. Therefore, within a species, the manner of interaction (i.e., network structure) between plants would vary with individuals (for example, the network structure may change with growing stages). These heterogeneities within a species would affect the dynamics of the plant population and community (e.g., Hara, 1995). The species-based network cannot describe such heterogeneity within a species because it regards the average traits of species as nodes (Ings et al., 2009) while the individual based-network can do it.

The objectives of this study were to (1) confirm the assumption of relative uniformity, (2) explain and describe a more realistic network structure of competition among plants, and (3) evaluate the causal relationship between the network structure of competition among plants and the spatiotemporal dynamics of plant populations. In particular, we examined the network structure of competition relationships among a large number of plants in an even-aged stand of the Sakhalin fir *Abies sachalinensis* using complex network analysis. To examine the network structure at the individual level, we constructed the "competition-among-individuals network" (CAIN) by defining nodes as individual plants and links as competition among them for resources (i.e., light or soil resources). Based on the properties of the network structure constructed, we discussed the effect of the network structure on the spatiotemporal dynamics of plant populations. If the real network structure is very different from the assumptions of relative uniformity (e.g., the actual network structure has scale-free properties), then the spatiotemporal population dynamics in the simulation based on the assumption will differ from those of the real world, and the real network structure should be included in most competition models. Finally, we discussed the mechanisms underlying the formation of the network structure of competition within the population examined in this study, which revealed the determinants of network structures of the CAIN and provided guides for future studies of the CAIN of different plant populations.

2. Materials and methods

2.1. Field data

Our data came from an experimental forest of even-aged fir plants (*Abies sachalinensis* [F. Schmidt] Mast.) in Kubo, Ikeda District, Hokkaido, Japan. Detailed data were provided by the Hokkaido Prefectural Forest Office (1982). The study area was 0.202 ha. Seedlings (4200/ha) were planted in 1929 using a square planting pattern and were never artificially thinned thereafter. The diameter at breast height (DBH) of every plant in the study plot was measured in 1948, 1951, 1953, 1958, 1963, 1968, 1973, 1975, and 1978. We used data from those census years, except 1953, as the data from that year were inaccurate (detailed data provided by Hokkaido Prefectural Forest Office, 1982). In 1948, 806 plants were alive. By the end of the study period, the number of plants had decreased to 449 because of self-thinning.

There are unvegetated buffers outside the northwest and southeast edges of the study plot. The forest, which has never been artificially thinned, continues outside the northeast and southwest edges of the study plot. Thus, to avoid these edge effects, we estimated the parameters of the models by using one dataset for plants at least 10 m inside the northeast and southwest edges and conducted complex network analysis using another dataset for