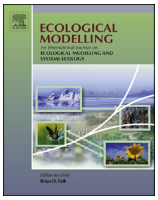
Ecological Modelling 314 (2015) 73–79

Contents lists available at ScienceDirect

Ecological Modelling

journal homepage: www.elsevier.com/locate/ecolmodel



Structure-dynamic relationship of plant–insect networks along a primary succession gradient on a glacier foreland

Gianalberto Losapio[a,b,*], Ferenc Jordán[c,d], Marco Caccianiga[a], Mauro Gobbi[e]

[a] *Department of Biosciences, University of Milan, Via Celoria 26, I-20133 Milan, Italy*
[b] *Institute of Evolutionary Biology and Environmental Studies, University of Zurich, Winterthurerstrasse 190, CH-8057 Zurich, Switzerland*
[c] *The Microsoft Research, University of Trento Centre for Computational and Systems Biology (COSBI), Piazza Manifattura 1, I-38068 Rovereto (Trento), Italy*
[d] *Danube Research Institute, Centre for Ecological Research, Hungarian Academy of Sciences, Karolina 29, H-1113 Budapest, Hungary*
[e] *Department of Invertebrate Zoology and Hydrobiology, MUSE–Museo delle Scienze, Corso del Lavoro e della Scienza 3, I-38123 Trento, Italy*

ARTICLE INFO

Article history:
Received 29 January 2015
Received in revised form 19 May 2015
Accepted 4 July 2015

Keywords:
Bipartite network
Chronosequence
Community assembly
Ecological network
Ecosystem stability

ABSTRACT

There is a growing interest in understanding the structure–dynamic relationship of ecological networks. Ecological network changes along primary successions are poorly known: to address such topic, gradient of primary succession on glacier forelands is an ideal model, as sites of different age since deglaciation stand for different ecosystem developmental stages. We aimed to investigate the assembly processes of plant–insect networks and to elucidate its functional implications for ecosystem stability along this time sequence succession. We collected data on the functional role of anthophilous insect groups and performed network analysis to evaluate their relative importance in the structure of plant–insect interaction networks with increasing time since deglaciation along the primary succession of a debris-covered glacier foreland. We sampled anthophilous insects visiting the flowers of two models plant species, *Leucanthemopsis alpina* and *Saxifraga bryoides*. Insects were identified and trophic roles were attributed to each *taxon* (detritivores, parasitoids, phytophagous, pollinators, predators, and opportunists) at five sites representing the primary succession gradient. Plant–insect interactions were visually represented by a bipartite network for each successional stage. For each plant species and insect group, centrality indices were computed quantifying their community importance. For the whole network, centralization and link density were calculated. Pollinators dominated pioneer communities on the debris-covered glacier and in recently deglaciated areas, while parasitoids, predators and opportunists characterised late-succession stages. Plant species centrality varied along the succession. Pollinators showed initially higher but then decreasing centrality, while the centrality of predators and parasitoids increased with time since deglaciation. Along the same gradient link density showed an increasing trend while network centralization tended to decrease. The present study provides new insight into the initial steps of plant–insect network assembly and sheds light on the relationship between structure and dynamic in ecological networks. In particular, during the succession process, more links are formed and plant–anthophilous insect interactions change from a network dominated by pollinators to a functionally more diversified food web. We conclude that applying network theory to the study of primary succession provides a useful framework to investigate the relationship between community structure and ecosystem stability.

1. Introduction

The study of ecological interaction networks is becoming a key approach for understanding ecological and evolutionary processes (Vázquez et al., 2009) as it provides useful depictions of biodiversity, species interactions, ecosystem structure and functioning (Dunne et al., 2002b). Despite the growing recognition of the importance in analysing the whole-community organization following an ecological network approach (Sridhar et al., 2013), there is still a lack of information on how ecological networks are assembled (Bascompte and Stouffer, 2009) and the relationship between ecosystem dynamics and network structure is still poorly understood (Jordán, 2009).

Recent researches on network ecology provided new insight into structural invariant patterns underlying species interactions. The organization in connected modules (Olesen et al., 2007) with

---

[*] Corresponding author at: University of Zurich, Institute of Evolutionary Biology and Environmental Studies, Winterthurerstrasse 190, CH-8057 Zurich, Switzerland. Tel.: +41 6356152.
E-mail address: gianalberto.losapio@ieu.uzh.ch (G. Losapio).

http://dx.doi.org/10.1016/j.ecolmodel.2015.07.014
0304-3800/

a heterogeneous distribution of the number of interactions per species (Dunne et al., 2002a) and asymmetric interaction strength among species (Bascompte, 2009) has been related to ecological network robustness (Pocock et al., 2012) and stability (Thébault and Fontaine, 2010). Little attention, however, is given to the spatial aspects and to the temporal dimension of ecological networks, despite their relevance for mechanisms of network formation (Bascompte and Stouffer, 2009) and for network robustness to species extinction (Pascual and Dunne, 2006).

Ecological succession (i.e. the change of species composition over time) provides temporal and spatial dimensions to analyse the change in the characteristics of populations, communities and ecosystems (Walker and del Moral, 2003), and may therefore be suitable to look at the temporal dynamics of ecological networks. Glacier forelands represent such a gradient of primary succession, as sites of different age since deglaciation stand for different ecosystem developmental stages (Matthews, 1992).

The use of the chronosequence as a space-for-time substitution (Foster and Tilman, 2000) along glacier foreland has provided significant insights into the patterns and mechanisms of plant (Walker et al., 2010) and arthropod (Kaufmann, 2001) community assembly. Vegetation cover, plant and arthropod diversity increase throughout the succession (Hodkinson et al., 2001; Gobbi et al., 2010). Plant community structure changes due to different efficient resource-use among pioneer and late-successional species (Caccianiga et al., 2006). In parallel, the turnover of arthropods is influenced by the stabilization of environmental conditions and vegetation structure (Gobbi et al., 2006). However, previous studies have focused on a single trophic level and very little is known about ecological network assembly during primary succession (Albrecht et al., 2010). The only plant-pollinator network examined along such a gradient showed an increase in interaction diversity and indicated an increase in pollinator diet breadth (Albrecht et al., 2010).

While the majority of ecological network studies examine one static network at a time, we aimed to analyse a network gradient, one of the important perspectives in ecological network analysis. Thus, we applied the network analysis by bipartite network and local to global importance indices analysis to describe the structure of plant-anthophilous insect network and we compared it among different successional stage of a glacier foreland, focusing on insect trophic roles. In particular we addressed the following questions: (i) Does the structural importance of plants and insects vary along the successional gradient? (ii) How does the network architecture change along the spatio-temporal gradient? Finally, by integrating structure with dynamic of ecological networks we provide new insight into network assembly and arise empirical models for species coexistence and ecosystem stability.

2. Material and methods

2.1. Data sampling

The study was performed along the glacier foreland of Vedretta d'Amola glacier (Central Italian Alps, 46°13′16″N, 10°40′41″E), which is a debris-covered glacier of about 82.1 ha, with two thirds covered by stony debris with variable depth, from few centimetres to approximately one meter. The glacier foreland is 1.23 km long, covers an altitudinal range from 2425 m to 2560 m a.s.l., and is characterized by a big moraine system dating back to the Little Ice Age (1500–1850 A.D.). Field observations and various sources including maps, reports, aerial photographs, iconography, and records of length change made over the last 100 years allowed the reconstruction of the glacier tongue position during the largest extent reached: at the end of the Little Ice Age (c. 1850 A.D.), in 1925 A.D., and in 1994 A.D (Fig. 1). Following this deglaciation gradient five sampling sites were located to represent the main successional stages: glacier surface (stage 0), 1–20 years (stage I), 21–90 years (stage II), 91–160 years (stage III), and more than 160 years (stage IV).

We selected the flowering plants *Leucanthemopsis alpina* (L.) Heyw. (Asteraceae) and *Saxifraga bryoides* L. (Saxifragaceae) as model species because they were the only two entomophilous plant species that occurred throughout the whole primary succession gradient. At each successional stage, two $25\,\text{m}^2$ plots were established and three *L. alpina* tufts and three *S. bryoides* cushions were selected for each species and marked for further use over the course of the study. The number of flowers of each tuft or cushion was recorded in July 2012. Plant–anthophilous insect interactions were observed during the flowering seasons (between the end of July and the end of August) of the summers of 2012 and 2013. All anthophilous insects visiting the flowers were sampled with an entomological aspirator by observing the three plant species units together during three periods of 40 min a day at 11am, 1pm and 3pm (90 samples in total per year). Anthophilous insects were identified at species level if possible, otherwise at genus or family level. Insects were classified into six ecological roles based on trophic habits (Fath and Killian, 2007; Gobbi and Latella, 2011) by literature survey (e.g. Mellini, 1997; Gregor et al., 2002; Oosterbroek, 2006; Jedlička et al., 2009): detritivores, parasitoids, phytophagous, pollinators, predators, and opportunists.

2.2. Data analysis

We quantified structural changes (Dunne et al., 2002a) of the plant–insect network at both local (node positions) and global (network architecture) levels along the primary succession gradient. The patterns and frequency of plant–insect interactions were represented and visualized by bipartite networks (Jordano, 1987; Memmott, 1999; Dormann et al., 2009). A bipartite network consists of two sets of nodes (i.e. plant species and insect functional groups) linked by a set of edges in such a way that each edge links two species belonging to different node sets. In the adjacency matrix plants were represented in the rows (=lower level in the network) and insect functional groups were represented in the columns (=upper level in the network). Link weights showed the number of insect individuals that visited the corresponding plant species. In the resulted bipartite network, the size of rectangles representing plants and insects was proportional to the relative number of visits received and made within each successional stage, respectively (Dormann et al., 2009).

In order to quantify the change in network structure along the successional gradient, we computed local indices describing nodes and global indicators of network architecture. Information about the changes in topological properties along the succession provides useful information to understand the relative importance of various functional groups and may shine a light on the dynamical consequence of network assembly.

2.3. Local (node level) indices

2.3.1. Weighted degree (wDi)

In a directed and weighted network, it is the sum of weights of the links connected directly to a node. This is the most local measure and often provides a fast and simple evaluation (Jordán, 2009).

2.3.2. Weighted topological importance index (WI_i^n)

We assume a network with undirected links where trophic effects can spread in many directions without bias. Indirect effects can spread in both bottom-up and top-down directions and, as a result, horizontally, too (i.e. from plant to plant and from insect to insect). We use WI_i^n as the topological importance of species *i* for