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

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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 model 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.

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

3

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17 ABSTRACT

18 There is a growing interest in understanding the structure–dynamic relationship of ecological
19 networks. Ecological network changes along primary successions are poorly known: to address
20 such topic, gradient of primary succession on glacier forelands is an ideal model, as sites of
21 different age since deglaciation stand for different ecosystem developmental stages. We aimed to
22 investigate the assembly processes of plant-insect networks and to elucidate its functional
23 implications for ecosystem stability along this time sequence succession. We collected data on the
24 functional role of anthophilous insect groups and performed network analysis to evaluate their
25 relative importance in the structure of plant-insect interaction networks with increasing time since

26 deglaciation along the primary succession of a debris-covered glacier foreland. We sampled
27 anthophilous insects visiting the flowers of two models plant species, *Leucanthemopsis alpina* and
28 *Saxifraga bryoides*. Insects were identified and trophic roles were attributed to each *taxon*
29 (detritivores, parasitoids, phytophagous, pollinators, predators, and opportunists) at five sites
30 representing the primary succession gradient. Plant-insect interactions were visually represented by
31 a bipartite network for each successional stage. For each plant species and insect group, centrality
32 indices were computed quantifying their community importance. For the whole network,
33 centralization and link density were calculated. Pollinators dominated pioneer communities in
34 recently deglaciated areas, while parasitoids, predators and opportunists characterised late-
35 succession stages. Plant species centrality varied along the succession. Pollinators showed initially
36 higher but then decreasing centrality, while the centrality of predators and parasitoids increased with
37 time since deglaciation. Along the same gradient link density showed an increasing trend while
38 network centralization tended to decrease. The present study provides new insight into the initial
39 steps of plant–insect network assembly and sheds light on the relationship between structure and
40 dynamic in ecological networks. In particular, during the succession process, more links are formed
41 and plant-anthophilous insect interactions change from a network dominated by pollinators to a
42 functionally more diversified food web. We conclude that applying network theory to the study of
43 primary succession provides a useful framework to investigate the relationship between community
44 structure and ecosystem stability.

45

46 Keywords: bipartite network, chronosequence, community assembly, ecological network,
47 ecosystem stability

48

49 **1. Introduction**

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

57 Recent researches on network ecology provided new insight into structural invariant patterns
58 underlying species interactions. The organization in connected modules (Olesen et al 2007) with a
59 heterogeneous distribution of the number of interactions per species (Dunne et al. 2002a) and
60 asymmetric interaction strength among species (Bascompte 2009) has been related to ecological
61 network robustness (Pocock et al. 2012) and stability (Thébault and Fontaine 2010). Little attention,
62 however, is given to the spatial aspects and to the temporal dimension of ecological networks,
63 despite their relevance for mechanisms of network formation (Bascompte and Stouffer 2009) and
64 for network robustness to species extinction (Pascual and Dunne 2006).

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

71 The use of the chronosequence as a space-for-time substitution (Foster and Tilman 2000) along
72 glacier foreland has provided significant insights into the patterns and mechanisms of plant (Walker
73 et al. 2010) and arthropod (Kaufmann 2001) community assembly. Vegetation cover, plant and

74 arthropod diversity increase throughout the succession (Hodkinson et al. 2001, Gobbi et al. 2010).
75 Plant community structure changes due to different efficient resource-use among pioneer and late-
76 successional species (Caccianiga et al. 2006). In parallel, the turnover of arthropods is influenced by
77 the stabilization of environmental conditions and vegetation structure (Gobbi et al. 2006). However,
78 previous studies have focused on a single trophic level and very little is known about ecological
79 network assembly during primary succession (Albrecht et al. 2010). The only plant-pollinator
80 network examined along such a gradient showed an increase in interaction diversity and indicated
81 an increase in pollinator diet breadth (Albrecht et al. 2010).

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

93

94 **2. Material and methods**

95

96 *Data sampling*

97 The study was performed along the glacier foreland of Vedretta d'Amola glacier (Central Italian
98 Alps, 46°13'16"N, 10°40'41"E), which is a debris-covered glacier of about 82.1 ha, with two thirds

99 covered by stony debris with variable depth, from few centimetres to approximately one meter. The
100 glacier foreland is 1.23km long, covers an altitudinal range from 2425m to 2560m a.s.l., and is
101 characterized by a big moraine system dating back to the Little Ice Age (1500-1850 A.D.). Field
102 observations and various sources including maps, reports, aerial photographs, iconography, and
103 records of length change made over the last 100 years allowed the reconstruction of the glacier
104 tongue position during the largest extent reached: at the end of the Little Ice Age (c. 1850 A.D.), in
105 1925 A.D., and in 1994 A.D (Fig.1). Following this deglaciation gradient five sampling sites were
106 located to represent the main successional stages: glacier surface (stage 0), 1-20 years (stage I), 21-
107 90 years (stage II), 91-160 years (stage III), and more than 160 years (stage IV).

108 We selected the flowering plants *Leucanthemopsis alpina* (L.) Heyw. (Asteraceae) and *Saxifraga*
109 *bryoides* L. (Saxifragaceae) as model species because they were the only two entomophilous plant
110 species that occurred throughout the whole primary succession gradient. At each successional stage,
111 two 25 m² plots were established and three *L. alpina* tufts and three *S. bryoides* cushions were
112 selected for each species and marked for further use over the course of the study. The number of
113 flowers of each tuft or cushion was recorded in July 2012. Plant-anthophilous insect interactions
114 were observed during the flowering seasons (between the end of July and the end of August) of the
115 summers of 2012 and 2013. All anthophilous insects visiting the flowers were sampled with an
116 entomological aspirator by observing the three plant species units together during three periods of
117 40 minutes a day at 11am, 1pm and 3pm (90 samples in total per year). Anthophilous insects were
118 identified at species level if possible, otherwise at genus or family level. Insects were classified into
119 six ecological roles based on trophic habits (Fath and Killian 2007; Gobbi and Latella 2011) by
120 literature survey (e.g. Mellini 1997; Gregor et al. 2002; Oosterbroek 2006; Jedlička et al. 2009):
121 detritivores, parasitoids, phytophagous, pollinators, predators, and opportunists.

122

123 *Data analysis*

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

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

140

141 *Local (node level) indices*

142

143 *Weighted degree (wD_i)*

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

146

147 *Weighted topological importance index (WI_i^n)*

148 We assume a network with undirected links where trophic effects can spread in many directions

149 without bias. Indirect effects can spread in both bottom-up and top-down directions and, as a result,
150 horizontally, too (i.e. from plant to plant and from insect to insect). We use WI_i^n as the topological
151 importance of species i for plant-insect network with weighted links when effects “up to” n steps
152 are considered as

153

$$154 \quad WI_i^n = \frac{\sum_{m=1}^n \sigma_{m,i}}{n} = \frac{\sum_{m=1}^n \sum_{j=1}^N a_{m,ji}}{n}$$

155

156 which is the sum of effects originated from species i up to n steps averaged over by the maximum
157 number of steps considered (n). By this index, it is possible to quantify the internal interactions
158 structure of the network (Jordán 2009).

159 Both wD and WI^n were calculated according to Valentini and Jordán (2010). These structural
160 importance indices assume that well-connected nodes are more important in the network in a
161 structural and possibly also in a dynamical sense (Jordán et al. 2007, Jordán et al. 2008). As
162 pollinators, predators and parasitoids were the consistently most abundant groups, the indices were
163 calculated only for these.

164

165 *Global (network level) indices*

166

167 *Density*

168 The density of a network is the number of links divided by the maximal number of potential links.
169 In the case of weighted networks, Wasserman and Faust (1994) suggests to use the sum of link
170 weights instead of the number of links. Also, in the case of bipartite networks, the denominator
171 should be NM , where N and M are the number of nodes in the first (plants) and in the second set
172 (insects) of nodes, respectively. Thus, we used the following formula for our weighted and bipartite

173 networks:

174

175
$$d = \frac{\sum_{i=1}^L W_i}{N \times M}$$

176

177 where L is the number of links, W_i is the weight on the i^{th} link, N is the number of plant species and
178 M is the number of insect functional groups.

179

180 *Centralization (NCI^D)*

181 We calculated the degree-based network centrality index (NCI^D), where degree (D) is the number of
182 neighbours of a graph node (Wasserman and Faust 1994). Note that network centrality, expressed in
183 percentages, is maximal (100%) if a central node is directly connected to all other nodes and there is
184 no other link in the network (i.e. a perfect star-shape), and it is minimal (0%) if the positions of all
185 nodes are topologically equal (i.e. a lattice).

186

187 **3. Results**

188

189 A total of 911 insects specimens belonging to 40 families and 6 functional groups were sampled.
190 The *L. alpina* anthophilous insect community was dominated by pollinators (84%), predators (9%)
191 and opportunists (5%); phytophagous and detritivores both accounted for 1%. The *S. bryoides*
192 insect community was composed of pollinators (59%), followed by parasitoids (15%), opportunists
193 (14%), predators (8%); phytophagous and detritivores made up 3% and 1%, respectively.

194

195 *Plant-anthophilous insect bipartite network*

196 Pollinators dominated the insect community of the debris-covered glacier (stage 0) as well as of

197 stages I and II (Fig. 2). In stage III, the insect community was more diverse and structured, as
198 opportunists, parasitoids and predators increased particularly on *S. bryoides* flowers. On the oldest
199 terrain in stage IV, the insect community on *L. alpina* was still mainly represented by pollinators,
200 while *S. bryoides* showed a more functionally diverse insect community (Fig. 2). In this late-
201 successional stage, *S. bryoides* interacted mainly with parasitoids, while opportunists and predators
202 increased their frequency and pollinators became relatively less abundant (Fig. 2).

203

204 *Network indices*

205 *L. alpina* had higher wD in stage 0, and among all other stages no evident trend coherent with the
206 successional gradient emerged (Fig. 3a). The WI^2 of *L. alpina* generally increased from stage 0 to
207 IV, with a major change between stage II and stage III (Fig. 3b). The wD of *S. bryoides* increased
208 from stage 0 to II, where it reached the maximum and later decreased to stage IV (Fig. 3c). The WI^2
209 of *S. bryoides* increased from stage 0 to III, then weakly decreased in stage IV (Fig. 3d).

210 The wD of pollinators tended to decrease along the primary succession gradient towards earlier
211 deglaciation (Fig. 4a), whereas WI^2 of pollinators increased with later successional stages (Fig. 4b).
212 The wD and WI^2 of predators increased from stage 0 to IV (Fig. 4c), with a major change between
213 stage III and IV (Fig. 4d). The wD and WI^2 of parasitoids remained low during the early and mid
214 successional stages, then increased mainly from stage III to IV (Fig. 4e-f). Pollinators had, on
215 average, higher wD and WI^2 compared to predators and parasitoids.

216 Regarding the network-level properties, link density (d) increased (Fig. 5a) while network
217 centralisation (NCI^D) decreased with increasing successional stage (Fig. 5b). This means that the
218 various species and functional groups in the community developed more and more interactions
219 among themselves and became more and more connected, while their relative importance became
220 less heterogeneous with more equally distributed importance among them.

221

222 **4. Discussion**

223

224 Our study represents one of the first applications of bipartite network centrality analysis to the study
225 of ecological succession. The key finding of our work is that, during succession, the importance of
226 different insect ecological groups and the global network structure changed. Plant-anthophilous
227 insect interactions changed from a network dominated by pollinators to a functionally more
228 diversified food web, where the density of interactions increased while the network became
229 decentralized and homogeneous. We hypothesize that such process may increase the robustness of
230 the network against the local extinction of species, providing new insight into the relationship
231 between structure and dynamic in ecological networks.

232

233 **Plant-anthophilous insect bipartite network**

234 *L. alpina* interacted mainly with pollinators, which were the dominant insect group along the entire
235 successional gradient studied here. In contrast, *S. bryoides* interacted with a wider ecological
236 spectrum where pollinators were not the dominant group along the whole successional gradient.
237 Difference in the ecological role of anthophilous insects between plant species may be due to the
238 presence of floral nectaries in *S. bryoides* but not in *L. alpina*, suggesting that more insect
239 ecological roles may benefit from this sugar resource. In the *S. bryoides* community pollinators
240 remained the dominant group during the early and mid successional stages, whereas in the late
241 successional stage parasitoids, predators and opportunists strongly increased and pollinators
242 decreased.

243 Albeit our study does not allow the inference of direct trophic relationship among insects, it may be
244 possible that the relative decrease of pollinators is linked to the increase in predators (Raso et al.
245 2014) and parasitoids with the succession proceeding. Indeed, a mature ecosystem, found at the late
246 successional stages showing high plant productivity and community diversity (Gobbi et al. 2010),

247 may boost more parasitoids and predators that will interact with pollinators. By meaning of bipartite
248 networks dynamically linked we showed for the first time how different insect ecological groups are
249 assembled and differentially interact with plants along an ecological succession gradient.

250

251 **Local (node) structural changes**

252 Weighted centrality indices of *L. alpina* showed contrasting trends. Although no clear variation
253 emerged in wD , the increase in WI^2 indicates that, even if the number of direct links may not vary,
254 indirect effects became more important with later successional stages. Highest values of the two
255 topological indices at the successional stages II and III for *S. bryoides* indicated a more important
256 structural position (rich interaction structure) at the intermediate successional stages. This
257 corresponds with the abundance distribution of this species along the successional gradient,
258 suggesting a relationship between the species environmental requirement (i.e. the species niche) and
259 its importance in structuring the network.

260 With succession proceeding, pollinator wD decreased and that of predators and parasitoids
261 increased: these opposite trends indicate a change in positional importance from a local to a
262 mesoscale view (Jordán 2009). Due to different roles of species in the network (Jordán 2009),
263 changes in their relative importance along the successional gradient causes structural changes in the
264 network architecture. This local change may influence the global dynamic of plant-anthophilous
265 insect interaction network, which is varying from a pollination-driven system to a more complex
266 ecological network. In other words, the plant-anthophilous insect interactions change along the
267 successional gradient from predominantly mutualistic interactions to a diverse set of interactions
268 including mutualism, parasitism and predation.

269 Indirect effects play an important role in governing ecosystem dynamics (Jordán et al. 2008). The
270 consistent increase in WI^2 indices for all insect ecological roles makes them more functionally
271 important along the primary succession gradient. The importance of nodes is therefore likely to be

272 determined by the interaction between insect functional role type and community features along the
273 primary succession gradient, the later mainly represented by the increase in plant species diversity
274 and ecosystem productivity (Gobbi et al. 2010).

275 Thus, the use of centrality indices highlights the link in the assembly process of plant and related
276 anthophilous insect communities and the functioning of this interaction system. Our study showed
277 that the local importance of insect ecological roles changed within as well as among the groups
278 along the succession gradient, suggesting a role in the dynamic of global network properties.

279

280 **Global (network) structural changes**

281 Our results show that with succession proceeding more and more links among plants and insects are
282 formed. This may be due to the effect of time: directly, by increasing the interaction probability
283 among the species pool, and indirectly, as a consequence of a more structured and diversified
284 network that lastly enhances trait matching and complementarity (Vázquez et al. 2009) between
285 plants and anthophilous insects. Furthermore, link density is affected by network dimension
286 (Dormann et al. 2009), the latter being a consequence, in our study system, of the increase in insect
287 abundance and plant community maturity. The increase in link density with proceeding succession
288 is in accordance with Albrecht et al. (2010) who found an increase in the unweighted number of
289 links per species along the Morteratsch glacier foreland (Switzerland). As link density is an
290 indicator of complexity (May 1973), the increase of network complexity along the primary
291 succession gradient confers stability and robustness against potential local species losses (Montoya
292 et al. 2006) because highly connected networks will tend to be more robust to stochastic removal of
293 nodes (Dunne et al. 2002b). Conversely, a very densely connected network is more vulnerable to
294 species invasion as a perturbation is more likely to spread rapidly (Scheffer et al. 2012).

295 Patchy pioneer communities in early successional stages are highly centralised, with few nodes
296 playing a key role while most nodes occupy peripheral positions. Throughout the primary

297 succession the network became de-centralised, as all nodes are connected with a similar number of
298 links. This highlights a gradient towards a more homogeneous structural organisation: the network
299 architecture shifts from a star-like network, where few central nodes have many connections, to a
300 lattice-like network with no central nodes but a balanced number of edges per node (Wassermann &
301 Faust 1994). The network de-centralisation may emerge from the decrease in direct structural
302 importance of pollinators and the parallel increase in importance of parasitoids and predators
303 towards later successional stages. As reported in others studies on pollination and mutualistic
304 networks (Olesen et al. 2007, Bascompte and Stouffer 2009, Pocock et al. 2012), low interaction
305 richness makes a network less cohesive, thus making the network more vulnerable to the removal of
306 nodes. Thus, we could hypothesise that the observed network de-centralisation may increase the
307 local extinction risk of species, especially in a global warming context causing glacier retreat.

308 In summary, considering simultaneously all the global network properties, the network shows
309 increasing link density and increasing de-centralisation during primary succession. These two
310 assembly processes appear to confer two contrasting properties: the former may lead to network
311 robustness against local species extinctions whereas the latter may confer the opposite feature.
312 Indeed, as some simulation studies suggested (Bascompte & Stouffer 2009, Pocock et al. 2012), a
313 cohesive organization make the network more robust and stable. In our study system, probably the
314 outcome is a balance between these two functions (i.e. increase in link density and decrease in
315 centralisation) and the importance of species getting extinct (i.e. the species ecological group and
316 their structural role within the network). More studies are require to understand the dynamic
317 consequence of network structural evolution along primary succession gradients; however, our
318 application of local and global centrality indices has proved to give important insights into these
319 processes and their consequences.

320

321 **Conclusion**

322 We shed light on dynamically linked ecological networks in a natural time-sequence succession.
323 Although in our study we analysed the anthophilous insect network of two ubiquitous plant species,
324 we believe that the emerged trends may also be extended to a wider community-level pattern. New
325 insight was provided into the initial steps of plant–insect network assembly and new light was shed
326 on the relationship between structure and dynamic in network ecology. In conclusion, our
327 framework highlighted the relevance of combining ecological trait and network theory to increase
328 the link between community structure, network assembly and ecosystem functioning. Indeed, by
329 applying network theory we will move away from pairwise comparisons and start searching for the
330 existence of network-wide patterns of species dependence (Ings et al. 2009). We emphasize that, in
331 the present context of climate and environmental changes, network analysis of primary succession
332 gradients by means of bipartite networks and centrality indices may provide a useful framework
333 also for the management of endangered habitat and species.

334

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344

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