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2 **Modified source-sink dynamics govern resource exchange in**

3 **ectomycorrhizal symbiosis**

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21 **Contents**

22 Summary

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29 **Summary**

30

31 Ectomycorrhizal symbiosis between roots and fungi is founded on the movement of

32 carbon from plants to fungi, and of soil resources from fungi to plants. Framing this

33 movement as a trade can facilitate an understanding of how this mutualism has

34 developed over evolutionary time, but fails to explain experimental observations of

35 carbon and nutrient movement. Here, I propose that source-sink dynamics are an

36 essential basic model to explain the movement of plant and fungal resources, which

37 may be modified by plant immune response, variability in fungal molecular

38 repertoires, and competition in the soil. Source-sink dynamics provide testable

39 hypotheses to illuminate mechanisms of ectomycorrhizal resource movement and

40 its consequences for mutualism stability and forest function under climate change.

41

44

45 **I.   Introduction**

46

47 Ectomycorrhizal symbiosis is an essential mechanism by which many temperate

48 forest trees associate with fungi to acquire crucial nutrients, while fungi receive

49 carbon from the plants (Smith & Read, 2008). Discussions of these processes often

50 frame the movement of resources as a reciprocal trade of plant carbon for fungal

51 resources like nitrogen (Stuart & Plett, 2020; Bogar *et al.*, 2022; Horning *et al.*,

52 2023). This framework is appealing because, if reciprocity regulates resource

53 movement, mutual cooperation could be naturally reinforced: Fungi must bring

54 resources to the plant to receive carbon, and plants must support fungi with carbon

55 to receive resources. This process seems to operate in arbuscular mycorrhizal

56 associations (Kiers *et al.*, 2011; Ji & Bever, 2016).

57   However, the evidence for rewards in ectomycorrhizal symbiosis is mixed.

58 Occasionally, we find evidence for increased plant carbon investment in fungi

59 providing nitrogen (Bogar *et al.*, 2019, 2022; Horning *et al.*, 2023), but more often,

60 plant carbon investment is uncorrelated (Näsholm *et al.*, 2013; Hortal *et al.*, 2017;

61 Plett *et al.*, 2020) or negatively correlated (Hasselquist *et al.*, 2016) with fungal

62 nitrogen provisioning. Phosphorus flow seems to correspond better to plant carbon

63 allocation (Finlay, 1989; Horning *et al.*, 2023), but has not been adequately
64 explored in ectomycorrhizal systems. Even when plant carbon rewards for fungal
65 resources are detected, they are context- and scale-dependent. For example,
66 Mayerhofer *et al.* (2021) found that at cellular scale, plant-derived carbon and
67 fungal-derived nitrogen were tightly coupled in ectomycorrhizas of *Fagus sylvatica*,
68 but this pattern disintegrated at larger spatial scales. We must look beyond carbon-
69 for-nutrient rewards to fully understand controls on ectomycorrhizal resource
70 movement.
71   Here I suggest that source-sink dynamics remain the most useful basic
72 framework for understanding organismal and ecological-scale resource movement
73 in ectomycorrhizal symbiosis. However, these dynamics can be modified. External
74 resource availability, the chemical interplay between plant and fungal partners, and
75 competition in the soil could alter source-sink expectations to produce diverse
76 resource movement patterns in ectomycorrhizal associations. By comparing the
77 circumstances under which ectomycorrhizal mycelium and plant tissues act as a
78 continuous whole against circumstances where the divergent evolutionary
79 pressures and disparate physiologies of two partners lead to non-source-sink
80 interactions, we can uncover valuable mechanistic insight into how resource
81 movement is regulated in this symbiosis. Understanding what drives this resource
82 movement will provide insight at the community scale, as resource allocation may
83 shape the composition and function of ectomycorrhizal plant and fungal
84 communities, and at the ecosystem scale, clarifying how carbon and soil resources
85 move through forested landscapes.
86
87 **II.   Source-sink dynamics remain a useful model for resource movement**
88
89 At the scale of organs and organisms, source-sink dynamics are a useful model for
90 resource movement in ectomycorrhizal symbiosis. Here I use the phrase "source-
91 sink dynamics" to refer broadly to processes wherein a resource moves from an
92 area of relatively high density to an area of lower density, regardless of the
93 mechanism of travel. When, for example, plant carbon supplies in leaves exceed the
94 carbon in roots or fungal mycelium, carbon movement into the fungus might be
95 explained by the mycelium representing a physiological "sink" (Cairney, 2012).
96 Source-sink processes can happen more easily across steeper concentration

97   gradients (e.g. if a plant is grown in elevated light or CO_2) (Choi *et al.*, 2005; Trocha

98   *et al.*, 2016). Alternatively, increased conductance in the relevant pathways

99   between the source and the sink might speed source-sink dynamics, either through

100   increased surface area across which a resource can flow (e.g. Hartig net depth, or

101   hyphal proliferation in a resource patch) (Leake *et al.*, 2001; Stuart *et al.*, 2023), or

102   with increased transport capacity at the hypha-soil, root-soil, or hypha-root interface

103   (perhaps via increased density or kinetic efficiency of transporters) (Garcia *et al.*,

104   2016). By adjusting local concentration gradients and pathway conductance,

105   ectomycorrhizal symbiosis facilitates resource movement between sources and

106   sinks.

107   Carbon movement through plants into fungi is usefully explained in terms of

108   source-sink dynamics. Carbon in leaves (and in the plant as a whole) can generally

109   be seen as an excess resource (Corrêa *et al.*, 2012; Prescott, 2022) that flows

110   towards sinks without requiring much active regulation. A fungus may be expected

111   to receive carbon from the plant roughly proportional to the rate at which that

112   fungus is respiring, extending its hyphae, or producing biomass. Fungal sink

113   strength can vary depending on the nutritional environment, with hyphal

114   proliferation in rich patches increasing the sink strength of the fungus locally (Leake

115   *et al.*, 2001). This effect is likely driven by fungal biomass (rather than linear growth

116   rate), as hyphal density can predict host carbon contributions to ectomycorrhizal

117   fungi (Wu *et al.*, 2002; Stuart *et al.*, 2023). Complicating the situation, plant carbon

118   investment may increase the biomass of a fungus and thus increase the carbon

119   demand or sink strength of the mycelium – this kind of positive feedback is probably

120   common. Fungi could also exert different sink strengths depending on the rates at

121   which they convert plant carbon into storage compounds like trehalose (Stuart *et*

122   *al.*, 2023). Further, these dynamics may depend on which host plants and fungi are

123   involved. Once a mycorrhiza is mature, sink strength of the distal mycelium may be

124   controlled by the area across which symbiotic resource exchange may take place

125   (Stuart *et al.*, 2023), as well as immunological and resource transfer properties of

126   the symbiotic membranes themselves.

127   Ectomycorrhizal fungal contributions to plant nutrition can likewise be

128   explained by source-sink dynamics. Ectomycorrhizal fungal mycelium is typically a

129   source of soil resources such as phosphorus and nitrogen, expanding plant-usable

130   soil volume beyond what roots could access alone (Torres Aquino & Plassard, 2004),

131   and deploying enzymes to improve resource availability (Sun *et al.*, 2023).
132   Ectomycorrhizal fungi generally improve plant access to resources when
133   background concentrations are low, with mycorrhization benefit and plant carbon
134   investment into fungi falling off at higher levels (Torres Aquino & Plassard, 2004;
135   Högberg *et al.*, 2021). At the highest levels of available nitrogen, ectomycorrhizal
136   fungi can induce artificial scarcity by monopolizing nitrogen (Franklin *et al.*, 2014;
137   Hasselquist *et al.*, 2016) and rendering added nitrogen inaccessible (Albarracín *et*
138   *al.*, 2013; Karst *et al.*, 2021). The relationship between mycorrhization and nutrient
139   access may vary greatly depending on the availability of limiting resources in the
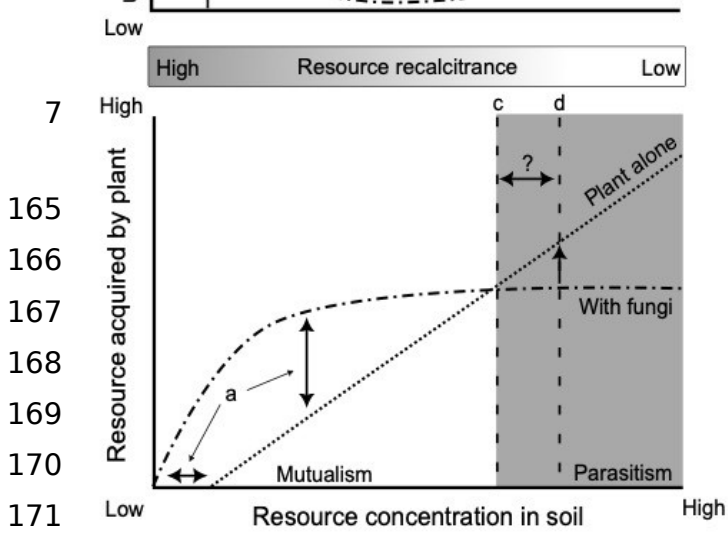140   soil.
141   Water, too, moves from sources to sinks in soils, mycelium, and plants. This is
142   driven largely by pressure differentials (water potential) produced through
143   evaporation and physical interactions between water, soil, and organismal transport
144   systems. The rate of water transport from roots to leaves is known to be governed
145   by water potential differences and the conductance of the flow path (hydraulic
146   conductivity) (Boyer, 1985). Ectomycorrhizal fungi are unlikely to alter the pressure
147   gradient driving water movement from soil into plant tissues, as that is largely
148   controlled by transpiration rate and soil matric potential, but the fungi themselves
149   may affect the hydraulic conductivity facilitating water movement. Although
150   ectomycorrhizal fungi can improve plant performance during droughts, the
151   mechanisms driving these effects remain somewhat unclear (Lehto & Zwiazek,
152   2011). Direct transfer of water via hyphae has not been demonstrated in
153   ectomycorrhizas, but can be significant for arbuscular mycorrhizal symbiosis
154   (Kakouridis *et al.*, 2022). Some ectomycorrhizal fungi have been shown to improve
155   plant hydraulic status (Wang *et al.*, 2021), possibly by increasing the production of
156   water transporters (aquaporins) in roots (Marjanović *et al.*, 2005) and hyphae (Xu &
157   Zwiazek, 2020) to improve hydraulic conductivity. Elucidating to what extent
158   ectomycorrhizal fungi alter plant root hydraulic conductance, and how variable this
159   is with fungal species and environmental stress, represents a promising area for
160   future research.
161   Although source-sink relationships can explain basic patterns of resource
162   movement in ectomycorrhizal symbiosis, they are often modified in complex ways.
163   The saturating response of ectomycorrhizal plants to resource availability gradients,
164   discussed above, is one prominent example (Fig. 1): the plant alone might take up

Fig. 1: Ectomycorrhizal symbiosis may change how resources move between sources and sinks: an illustrated hypothesis across a resource gradient. (a) With ectomycorrhizal fungi, a plant

resources that would be unavailable to roots alone, which can improve resource access at low soil concentrations. The plant alone illustrates a simple source-sink expectation, while fungi modify uptake dynamics. (b) As resources become increasingly accessible, the amount of plant carbon (C) required to take up resources via fungi may fall relative to uptake via roots alone. At higher concentrations, however, fungi may monopolize available resources (c). It remains unclear how intense or prolonged this resource immobilization might be before a plant begins to divest from or sanction fungal partners (d). control of carbon supply may modify the rates and scales on which these source-sink processes operate. To understand and predict ectomycorrhizal resource movement, we must account for how ecological, physiological, and molecular mechanisms modify resource movement to deviate from a simple source-sink framework.

III. Beyond source-sink: modifications to resource movement

Source-sink dynamics are a useful null hypothesis for resource movement in the ectomycorrhizal symbiosis; however, ectomycorrhizal plants and fungi are separate organisms with divergent needs and asymmetrical capabilities. Deviations from simple source-sink expectations may account for their most interesting and influential interactions. Plants often have more carbon than they need, and many mechanisms by which to acquire the soil resources provided by fungi. Each fungus is typically obliged to rely on plant-provided carbon, and has little recourse if the relationship fails. Thus, many ecological factors may modulate ectomycorrhizal resource movement to shift outcomes away from simple source-sink expectations. Here, I explore the influence of plant immune response to the fungi, variation in plant and fungal resource transport traits, and competition between roots, fungi, and other organisms in the soil.

Plant immune response to ectomycorrhizal colonization may be the principal means by which a plant can modulate resource (carbon) transfer to fungal partners, and may defy source-sink predictions of resource movement. It is well established that ectomycorrhizal fungal colonization of a root system rewires plant immunity both locally and systemically (Plett *et al.*, 2014; Dreischhoff *et al.*, 2020); these shifts in plant defense may also change resource transfer. Recent work by Stuart *et al.* (2023) found that plant carbon transfer to different strains of *Pisolithus*

199 *microcarpus* was best predicted by the expression of genes involved in plant
200 defense and stress response, not by the proportion of root tips colonized by the
201 fungus. The expression of these defense-oriented genes may be sensitive to the
202 context in which a symbiosis is occurring, and to the movement of other resources
203 within the root system. For instance, *Eucalyptus* seedlings with multiple strains of
204 fungi on their roots expressed more defense genes with an isolate that provided
205 less nitrogen than they did with the other, more cooperative partners (Hortal *et al.*,
206 2017), and *Larix* seedlings inhibited colonization by a non-preferred fungus only
207 when alternative fungi were present elsewhere on the root system (Bogar *et al.*,
208 2019). However, it remains unclear what controls the variation in plant defense
209 activation between individual colonized roots, different fungal strains and species,
210 and different environments, and how these changes affect carbon flow and fungal
211 community assembly. Future research should identify plant defense pathways that
212 correspond to changes in carbon provisioning, and determine the extent to which
213 these changes are tunable, changing carbon flow within a given symbiotic root tip,
214 or binary, cutting off resource flow entirely when a fungus is disfavored. Given the
215 diversity of ectomycorrhizal plants and fungi, it is likely that plant immune response
216 to fungi varies extensively, with many possible outcomes on resource flow to the
217 fungi.

218   Variation in plant immune response, however, is just one dimension of the
219 immense diversity in molecular traits of interacting ectomycorrhizal plants and fungi
220 (Garcia *et al.*, 2016; Nehls & Plassard, 2018; Plassard *et al.*, 2019) which may affect
221 source-sink movement of resources. Different ectomycorrhizal fungi are known to
222 demand different quantities of plant carbon, and to respond heterogeneously to the
223 addition of nutrients (Colpaert *et al.*, 1996; Bidartondo *et al.*, 2001; Treseder, 2004;
224 Lilleskov *et al.*, 2011). Different taxa also access different nitrogen sources
225 depending on their morphologies (exploration types) and evolutionary histories
226 (Hobbie & Agerer, 2010; Koide *et al.*, 2014; Pellitier & Zak, 2018), potentially
227 navigating a trade-off between carbon requirements and their ability to access
228 organic nitrogen (Pellitier *et al.*, 2021). This functional diversity among
229 ectomycorrhizal fungi may produce complementarity, potentially explaining why
230 diverse fungal partners can improve host plant performance under some
231 circumstances, such as when available resources are difficult for a plant to access
232 alone (Baxter & Dighton, 2005; Diagne *et al.*, 2013).

233   This diversity in both resource uptake and transport functions is likely driven

234 by diversity in the molecular tools that ectomycorrhizal fungi employ in symbiosis,

235 but significant gaps exist in our understanding of these mechanisms. Phosphorus

236 and nitrogen transport have been mechanistically described in a small number of

237 tractable fungi, but many fungi lack homologues for the identified transporters

238 (Garcia *et al.*, 2016; Plassard *et al.*, 2019). And, although ectomycorrhizal plants are

239 known to provide carbon resources (hexoses) to fungi, the molecular details have

240 been characterized only in *Populus* host plants with few fungal partners (Grunze *et*

241 *al.*, 2004; Garcia *et al.*, 2016). Across the diversity of ectomycorrhizal symbioses,

242 alternative carbon forms and transport mechanisms likely remain undescribed. The

243 molecular details of resource movement between fungi and plants may vary

244 considerably with evolutionary history, with important implications for regulation of

245 the symbiosis.

246   Competition among fungi, as well as competitive interactions between fungi

247 and roots, may also change the flow of resources between host plants and

248 ectomycorrhizal fungi. The

249 presence of a competitor, direct or

250 indirect, can reduce both the

251 number of root tips an

252 ectomycorrhizal fungus can

253 occupy (Kennedy & Bruns, 2005;

254 Hortal *et al.*, 2017; Bogar *et al.*,

255 2019) and diminish the growth

256 benefit of colonization to a plant

257 (Hortal *et al.*, 2016). Competing

258 with other mycelia for space can

259 reduce the carbon sink strength of

260 an ectomycorrhizal fungus by

261 reducing its hyphal extension rate

262 (Leake *et al.*, 2001), and

263 competing with another fungus on

264 a shared root system can change

265 the relative amount of plant

266 carbon that a fungus can access

Box 1: Key outstanding questions regarding resource movement in ectomycorrhizas

1) How does the strength of a resource gradient affect source-sink dynamics in ectomycorrhizas with respect to carbon, nitrogen, phosphorus, water, and other resources?

2) To what extent does ectomycorrhizal fungal diversity improve plant access to resources (particularly those beyond nitrogen), and how does this change depending on the resource and level of availability considered?

3) At what level of resource do fungi hinder plant uptake, instead of helping? How does this relate to the "critical load" of resources like nitrogen that can be detected in ecological studies, and does it vary by resource?

4) How sensitive are plants to this shift from helpful to unhelpful fungal partners? And how variable is this process across different plant-fungus combinations?

5) On what spatial scale can a plant

267 (Bogar *et al.*, 2022). On the other ha[...]   ,

268 competing) ectomycorrhizal fungi ma[...]

269 competitive context of a symbiotic in[...]

270 which the competition occurs, can shift ectomycorrhizal resource movement in

271 significant ways.

272

273 **IV.   Conclusions**

274

275 Despite the complex molecular regulation that underlies resource movement in

276 ectomycorrhizal symbiosis, source-sink dynamics remain a useful first

277 approximation to predict how resources may move between fungi and plants. These

278 processes can be modulated significantly by plant immune response to the fungi,

279 fungal diversity in resource transport traits, and competition in the soil. Within this

280 framework, plant rewards for fungal cooperation are possible – source-sink

281 dynamics would reward a fungus proliferating in a resource patch – but far from

282 guaranteed, which may explain the heterogeneous results of experiments

283 examining this question thus far. Understanding the mechanisms of resource

284 movement, and their diversity, will illuminate the forces that have stabilized

285 ectomycorrhizal mutualisms across dozens of independent origins; I suggest several

286 promising research directions in box 1. As ectomycorrhizal forests face new

287 environmental challenges, a better mechanistic understanding of plant and fungal

288 resource movement will be essential, both to improve forest management and

289 carbon sequestration, and to be able to predict how these ecosystems will respond

290 to climate change.

291

292 **Acknowledgements**

293

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