RESTORATION ECOLOGY
The Journal of the Society for Ecological Restoration
SER SOCIETY FOR ECOLOGICAL RESTORATION

RE-New (Opinion) Article

Using ectomycorrhizae to improve the restoration of Neotropical coastal zones

Emanuela W. A. Weidlich[1,2], Paulo T. Mioto[1], Ariadne N. M. Furtado[1], Lara M. Ferst[1], João P. Ernzen[1], Maria A. Neves[1]

As restoration ecology begins to engage more formally with the role of belowground interactions, we note that there is an even greater gap in knowledge of the role ectomycorrhizae (ECMs) have in ecological restoration in the Neotropical region. Even though there are a few records of ECMs in the Neotropics not much is known about their function. Here we highlight the underestimated importance of ECMs in Neotropical coastal zones, discuss how we could use the vegetation on the coast of the Atlantic Forest, called *restinga*, as a model to investigate tropical ECMs, and explore further possibilities that can be used in restoration projects.

Key words: coastal restoration, mycorrhizae, *restinga*, subtropical ecosystems, tropical diversity

Implications for Practice

- A better understanding of the underestimated distribution and functional roles of ectomycorrhizae should improve the outcomes of ecological restoration in the Neotropical region.
- There are advances in examining how ecological restoration can be improved by research on ectomycorrhizae in coastal zones in Brazil.

Introduction

Consistent with global trends, research in restoration ecology in tropical and subtropical ecosystems has been more plant than microbial focused. More focus on microbial communities (especially mycorrhizae; Sun et al. 2017; Neuenkamp et al. 2019) likely will enhance the success of restoration projects. Studies on mycorrhizae and restoration, especially in the tropics and subtropics, tend to focus on arbuscular mycorrhizal fungi (Ramos-Zapata et al. 2006; Leal et al. 2016; Bermúdez-Contreras et al. 2020; Ngugi et al. 2020). Even though there are records of ectomycorrhizae (ECMs) in the Neotropical region (Singer et al. 1983; Roy et al. 2016) not much is known about their function.

The lack of studies on ECMs in South America seems to have been driven by a lack of fungal taxonomists compounded by a premature generalization that ECMs were considered rare or absent in the Neotropical region. The latter generalization is incorrect as ECMs are widespread in the tropics (Corrales et al. 2018). For example, members of our research group recently reviewed the fungi in white-sand forests in Brazil (in Caatinga, Atlantic Forest, and the Amazon), which provided corroborating evidence for ECMs being much more common in the Neotropical region than previously thought (Roy et al. 2016, 2017). Since little is known about the diversity of ECMs in this region, these organisms have been overlooked in restoration projects, even though they may play an important role in plant interactions in coastal zones. Thus, our RE-New article focuses on the importance of considering ECMs to improve restoration projects, discusses how we are using a Brazilian coastal ecosystem as a model to investigate ECMs, and explores further gaps in research on ECMs that can be used in restoration.

Recognizing the Roles of Ectomycorrhizae and Overcoming Knowledge Gaps

It is likely that in Neotropical ecosystems, ECMs increase carbon sequestration and soil nutrient mobilization from organic matter and soil minerals within individual plants (Huang et al. 2019). Ectomycorrhizae can improve pathogen resistance of their host plant by direct competition, inducing the production of pathogenesis-related biomolecules, or developing antagonist microbiota (Barto et al. 2012). Ectomycorrhizae also can enhance plant tolerance to drought by improving the plant–soil contact surface, water conductivity in the host plant, and resistance to high soil salinity by restricting sodium uptake into plant tissues and activating stress response pathways (Pickles &

Author contributions: EWAW led the writing; all authors actively partook in writing and approved the manuscript.

[1]Department of Botany, University of Santa Catarina, Florianópolis, 88040-535, Brazil
[2]Address correspondence to E. W. A. Weidlich, email emanuela.ww@gmail.com

doi: 10.1111/rec.13284

Simard 2017). As in most ecosystems, Neotropical communities rely on adults (hub trees) to support seedling growth and maintain diversity (Simard 2018). Therefore, ecological restoration should strive to enhance the establishment of these interactions.

Introduced native seedlings (via restoration) may not succeed if the native microbial communities are not introduced concurrently, especially those associated with initial colonization. Restoration efforts often involve controlling invasive species (Weidlich et al. 2020), which may rely on mutualists (Vogelsang & Bever 2009; Moyano et al. 2020), but little is known about the consequences of having exotic soil microbiota in areas where exotic plants have been removed. For ECMs, interactions between native plants and exotic fungi do not necessarily cease after the removal of exotic plant species (Lofgren et al. 2018).

Specific ectomycorrhizal fungi enhance the survival rates and early growth performance of several plant species (Carey 2016). Inoculation of nurse seedling species with appropriate fungal partners is one of the most efficient environmental approaches, especially in disturbed ecosystems. The presence of endemic symbionts in an ecosystem is an indicator of a well-diversified community (Mueller & Halling 1995) either above or belowground. Studying ectomycorrhizal fungi in native vegetation in Brazil began in the 1960s with Singer's research in the Amazon (Singer & Morello 1960; Singer et al. 1983). Subsequently, many other studies continue to reveal the diversity of putatively ectomycorrhizal fungi in Brazilian forests (Sulzbacher 2013; Sulzbacher et al. 2013; Roy et al. 2016). Still, the relative dearth of knowledge about ECMs and many other belowground interactions means that there is ample room and need for further research in neotropical ecological restoration projects.

Using Brazilian Coastal Atlantic Forest as a Model for Investigating the Role of ECMs in Restoration

Our research group has been studying the diversity of ECMs in the Atlantic Forest in Brazil (Sulzbacher 2013; Furtado et al. 2016; Roy et al. 2016, 2017; Vanegas-León et al. 2019; Duque Barbosa et al. 2020). We are currently looking more closely at *restinga*, an important ecosystem in the coastal Atlantic Forest characterized by high irradiance, salinity, and sandy, nutrient-poor soils (Barcelos et al. 2012). We are testing the hypothesis that ECM formation could be one of the reasons plants manage to establish and survive in harsh environments like *restinga*, since the plants rely on belowground interactions, including mutualism, decomposition, and pathogenicity (Pickett et al. 2019). These interactions may be quite complex. For example, *Guapira opposita* is a facilitator in *restinga* by acting as a nurse plant (Dalotto et al. 2018); it is also associated with more than one species of ectomycorrhizal fungi (Vanegas-León et al. 2019). We continue to investigate the morpho-anatomical and molecular evidence of native ECMs and their symbiont plants in *restinga*. We are testing if *G. opposita* ECMs could be facilitating other plant species to become established by (1) ameliorating microclimatic conditions on site, (2) changing soil microbiota to favor other ECM-forming plants, or (3) acting as a hub tree, directly transferring resources through ectomycorrhizal connections. Thus, we postulate that ECMs should be considered a key component in restoration projects in *restinga*.

The generally well-established role of ECMs for plant nutrient uptake could be applied to *restinga*, but we are still lacking data. This lack of knowledge emphasizes the need to develop projects that identify the diversity and better explain the ecology of ECMs and their functions so these organisms can be properly used in *restinga* restoration. To use *restinga* as a model to investigate using ECMs in restoration, we need to do the following: (1) learn more about the diversity and ecophysiology of ECMs in coastal Atlantic Forest; (2) find out if other plants in *restinga* form ECM associations and how frequently these associations occur; and (3) investigate if ECMs in the Neotropical region function in the same way as temperate ECMs. A better understanding of ECMs in the coastal Atlantic Forest will allow us to infer how we can include them in restoration projects in the same way endomycorrhizae have been used. We are confident that by answering these questions we will be able to explore the role of ECMs in *restinga*. We hope that our pioneering work will encourage other groups to join us to explore the diversity, physiology, and application of ECMs in the neotropical region.

Acknowledgments

We thank S. Murphy and N. Smith for reviewing the manuscript and for providing thoughtful suggestions. E.W.A.W. and A.N.M.F. were financed by the Coordenação de Aperfeiçoamento Pessoal de Nível Superior–Brazil—Finance Code 001 (CAPES-DS and PDSE fellowship grants). L.M.F. and J.P.E. were supported by the Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq, PIBIC Fellowship).

LITERATURE CITED

Barcelos MEF, Riguete Julia R, Silva Lorena TP, Ferreira Paulo D Jr (2012) Uma visão panorâmica sobre os solos das restingas e seu papel na definição de comunidades vegetais nas planícies costeiras do sudeste do Brasil [An outlook on sandbank soils and their roles on the definition of plant communities in costal sand plains from southeastern Brazil]. Natureza Online 10:71–76

Barto EK, Weidenhamer Jeffrey D, Cipollini Don, Rillig Matthias C (2012) Fungal superhighways: do common mycorrhizal networks enhance below ground communication? Trends in Plant Science 17:633–637

Bermúdez-Contreras AI, Ede F, Waymouth V, Miller RE, Aponte C (2020) Revegetation technique changes root mycorrhizal colonisation and root fungal communities: the advantage of direct seeding over transplanting tube-stock in riparian ecosystems. Plant Ecology 221:813–828

Carey J (2016) Crucial role of belowground biodiversity. Proceedings of the National Academy of Sciences of the United States of America 113: 7682–7685

Corrales A, Henkel TW, Smith ME (2018) Ectomycorrhizal associations in the tropics—biogeography, diversity patterns and ecosystem roles. New Phytologist 220:1076–1091

Dalotto CES, Sühs RB, Dechoum MS, Pugnaire FI, Peroni N, Castellani TT (2018) Facilitation influences patterns of perennial species abundance and richness in a subtropical dune system. AoB PLANTS 10:ply017

Duque Barbosa JA, Delgat L, Elias SG, Verbeken A, Neves MA, de Carvalho AA Jr (2020) A new section, *Lactifluus* section *Neotropicus* (Russulaceae), and two new *Lactifluus* species from the Atlantic Forest, Brazil. Systematics and Biodiversity 18:347–361

Furtado ANM, Daniëls PP, Neves MA (2016) New species and new records of Clavariaceae (Agaricales) from Brazil. Phytotaxa 253:1–26

Huang AC, Jiang T, Liu Y-X, Bai YC, Reed J, Qu B, Goossens A, Nützmann H-W, Bai Y, Osbourn A (2019) A specialized metabolic network selectively modulates *Arabidopsis* root microbiota. Science 364:eaau6389

Leal PL, Varón-López M, de Oliveira Prado IG, dos Santos JV, Soares CRFS, Siqueira JO, de Souza Moreiraa FM (2016) Enrichment of arbuscular mycorrhizal fungi in a contaminated soil after rehabilitation. Brazilian Journal of Microbiology 47:853–862

Lofgren L, Nguyen NH, Kennedy PG (2018) Ectomycorrhizal host specificity in a changing world: can legacy effects explain anomalous current associations? New Phytologist 220:1273–1284

Moyano J, Rodriguez-Cabal MA, Andres Nuñez M (2020) Highly invasive tree species are more dependent on mutualisms. Ecology 101:e02997

Mueller GM, Halling RE (1995) Evidence for high biodiversity of Agaricales (fungi) in Neotropical montane Quercus forests. Pages 303–312. In: *Biodiversity and conservation of Neotropical montane forests. Proceedings of a symposium*, New York Botanical Garden, New York

Neuenkamp L, Prober SM, Price JN, Zobel M, Standish RJ (2019) Benefits of mycorrhizal inoculation to ecological restoration depend on plant functional type, restoration context and time. Fungal Ecology 40:140–149

Ngugi MR, Fechner N, Neldner VJ, Dennis PG (2020) Successional dynamics of soil fungal diversity along a restoration chronosequence post-coal mining. Restoration Ecology 28:543–552

Pickett B, Irvine IC, Bullock E, Arogyaswamy K, Aronson E (2019) Legacy effects of invasive grass impact soil microbes and native shrub growth. Invasive Plant Science and Management 12:22–35

Pickles BJ, Simard SW (2017) Mycorrhizal networks and forest resilience to drought. Chapter 18. In: Johnson NC, Gehring C, Jansa J (eds) *Mycorrhizal mediation of soil: fertility, structure, and carbon storage*. Elsevier, New York

Ramos-Zapata JA, Orellana R, Allen EB (2006) Establishment of *Desmoncus orthacanthos* Martius (Arecaceae): effect of inoculation with arbuscular mycorrhizae. Revista de Biologia Tropical 54:65–72

Roy M, Schimann H, Braga-Neto R, Da Silva RAE, Duque J, Frame D, Wartchow F, Neves MA (2016) Diversity and distribution of ectomycorrhizal fungi from Amazonian lowland white-sand forests in Brazil and French Guiana. Biotropica 48:90–100

Roy M, Vasco-Palacios A, Geml J, Buyck B, Delgat L, Giachini A, et al. (2017) The (re)discovery of ectomycorrhizal symbioses in Neotropical ecosystems sketched in Florianópolis. New Phytologist 214:920–923

Simard SW (2018) Mycorrhizal networks facilitate tree communication, learning, and memory. Pages 191–213. In: Baluska F, Gagliano M, Witzany G (eds) Memory and learning in plants. Signaling and communication in plants. Springer, Cham, Switzerland

Singer R, Morello JH (1960) Ectotrophic forest tree mycorrhizae and forest communities. Ecology 41:549–551

Singer R, Araujo I, Ivory MH (1983) The ectotrophically mycorrhizal fungi of the neotropical lowlands, especially central Amazonia. *Nova Hedwigia* 77: 1–352

Sulzbacher M (2013) A survey of an ectotrophic sand dune forest in the northeast Brazil. Mycosphere 4:1106–1116

Sulzbacher M, Grebenc T, Rjs J, Antoniolli Z (2013) Ectomycorrhizal fungi from southern Brazil—a literature-based review, their origin and potential hosts. Mycosphere 4:61–95

Sun S, Li S, Avera BN, Strahm BD, Badgley BD (2017) Soil bacterial and fungal communities show distinct recovery patterns during forest ecosystem restoration. Applied and Environmental Microbiology 83(14), e00966-17. https://doi.org/10.1128/AEM.00966-17.

Vanegas-León ML, Sulzbacher MA, Rinaldi AC, Roy M, Selosse M-A, Neves MA (2019) Are Trechisporales ectomycorrhizal or non-mycorrhizal root endophytes? Mycological Progress 18:1231–1240

Vogelsang KM, Bever JD (2009) Mycorrhizal densities decline in association with normative plants and contribute to plant invasion. Ecology 90:399–407

Weidlich EWA, Flórido FG, Sorrini TB, Brancalion PHS (2020) Controlling invasive plant species in ecological restoration: a global review. Journal of Applied Ecology 57:1806–1817

Coordinating Editor: Stephen Murphy

Received: 17 August, 2020; First decision: 18 August, 2020; Revised: 8 September, 2020; Accepted: 10 September, 2020