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Current Opinion in Microbiology

Fungal diversity at fragmented landscapes: synthesis and future perspectives

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Fungi are organisms with important roles in ecosystem functioning and services, but knowledge about how habitat fragmentation affect fungal diversity is biased by experimental approaches and it is spread in different trophic groups. We analyzed the empirical evidences of fungal diversity in fragmented landscapes, and proposed future perspectives for the study of these organisms under land use changes. Fungal diversity might be negatively affected by habitat fragmentation; however, this trend may differ in magnitude depending on fungal groups and their nutritional habits. In addition, due to the fact that fungal diversity at fragmented landscapes has been studied mainly through few indicators (e.g. isolation, area and edge effect); we propose incorporating the landscape structure and accurate spatio-temporal scales to the study of fungal diversity responses to fragmented landscapes. Together, this methodological refinement may allow improving knowledge on fungi when designing proper strategies for landscape management.

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Current Opinion in Microbiology 2017, **37**:161–165

This review comes from a themed issue on **Environmental microbiology**

Edited by **Marcio C Silva-Filho** and **Jorge Vivanco**

http://dx.doi.org/10.1016/j.mib.2017.09.003

Introduction

Humans have triggered a wave of species extinction, threats, and local population declines across taxonomic groups that may be comparable in magnitude to previous mass extinctions of Earth's history [1]. In particular, land use changes are one of the main threats to biodiversity worldwide [2,3]. Losses and degradation of natural ecosystems, mainly promoted by agriculture and urbanism, strongly influences the structure and persistence of ecological communities [4–6,7••,8]. Among land use changes, the habitat fragmentation process is one of the most important anthropogenic impacts shaping the communities at current landscapes.

Habitat fragmentation affects a diverse array of living groups inhabiting the remaining fragments of natural habitat (e.g. birds, insects, mammals, vascular plants, fungi) having consequences on different attributes of biodiversity (compositional, structural and functional, sensu [9]). Among biological groups, fungi are one of the less studied groups at fragmented landscapes, despite of their importance in the ecosystem maintenance and functioning [10–12]. Fungal diversity encompasses an extremely diverse array of taxa, life forms, nutritional habits and functional types that can be clustered into ecological guilds according to trophic modes [13]. They have shown to be particularly sensitive to alterations promoted by land use changes, which draw the abiotic and biotic conditions of microhabitats [14,15]. However, the magnitude and direction of the response of fungal community attributes to these indicators have shown to be variable. Then, a synthetic analysis to evaluate fungi at fragmented landscapes would contribute to discuss if the responses of specific groups are biased by experimental approaches, and if they vary across different fungal nutritional habits.

Despite of the negative impacts of habitat fragmentation on biodiversity, the theoretical bases to assess the study of this landscape process are not clear-cut, yet they are in continuous development (e.g. [16]). Consequently, the theoretical framework of 'habitat fragmentation' goes from the most simply explanation, such as a disruption in the habitat continuity [17]; to the most complete overarching concept where the 'habitat fragmentation' concept implies more than fragmentation *per se*. The latter means that the remaining fragments of the original landscape are immersed in a new distinct matrix and may present different features (i.e. degrees of habitat quality, isolation, size, shape, age and connectivity). In addition, recently some new insights for the study of habitat fragmentation have been gained with the incorporation of the landscape structure and proper scales to evaluate different groups of organisms at modified landscapes [18]. Therefore, the habitat fragmentation process affecting fungi can be assessed through indicators at different spatial scales (e.g. landscape scale, patch scale) that may affect biodiversity differently.

Here, we analyze the responses of fungal diversity to common indicators used in the 'habitat fragmentation' framework, and propose future perspectives for the study of this landscape process on fungi. In particular, we identified which indicators were used in order to highlight possible bias on the use of them; and discuss new insights of the concept of habitat fragmentation that would introduce some avenues for promising studies of fungal diversity.

Response of fungal diversity to indicators of the habitat fragmentation process

In general, the available studies reveal that fungal diversity is negatively affected by habitat alterations promoted by habitat loss and fragmentation. These evidences are supported by three common indicators used when fungal responses to the habitat fragmentation process are evaluated: fragment area, edge effects, and spatio/temporal isolation [e.g. 19–21]. The trends associated to these indicators could be a consequence of severe alterations in soil abiotic conditions [19], reduction in microhabitat complexity for substrate-depending fungi, and increments in light availability due to a reduction in canopy cover [14], altered microclimatic conditions at fragment edges [11], or dispersal limitations due to patch isolation [22,23].

Regarding the attributes of fungal diversity (i.e. compositional, structural and functional), most studies are focused on variations of fungal composition and show negative effects of habitat fragmentation particularly on fungal richness and fungal interactions. A general decline of fungal diversity facing land use changes has been observed for some regions [24••,15]. On the other hand, fungi structural diversity (i.e. abundance) show response patterns in different directions, probably because fragmentation might increase the abundance of species tolerant to disturbances but decrease that of sensitive species [25,15]. Functional diversity was less studied in the context of habitat fragmentation, probably because natural history of many taxa are unknown and because reproductive and dispersal processes of many groups are difficult to measure and quantify [26,27].

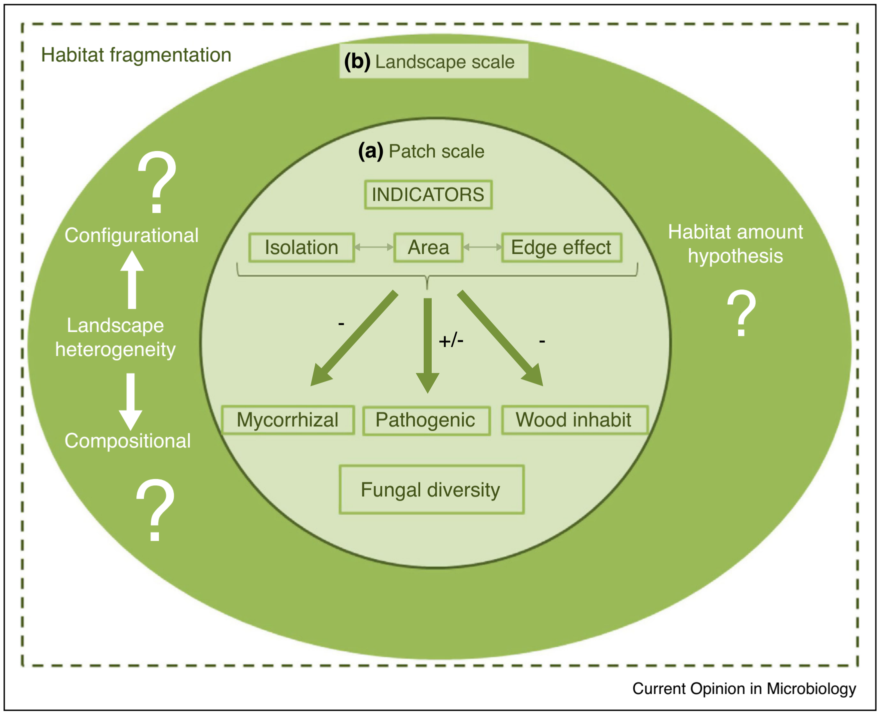
Finally, when considering the nutritional habits, mycorrhizal and xylophagous fungi seem to be more negatively affected by habitat fragmentation than pathogenic fungi. Some studies have shown how the relationship between mycorrhizal symbionts changed with the size and isolation of Chaco forest fragments at dry seasonal forests [19,28,29,30••]. Mycorrhizal fungi are affected by land use changes involving soil disturbance [6], diminution of fragment size [19,28,31], and habitat connectivity [32]. Other studies assessed the richness and abundance of xylophagous fungi at boreal forest fragments [14,20,33–35]. Xylophagous fungi strongly depend on resource availability and composition (i.e. number of logs, variety of woody debris, diameter of wood, decay stage, and so on) and the environmental variables that dramatically change with the reduction of forest fragment size, increasing edge proportion, and isolation [e.g. 14,20,33,34,36]. Conversely, patterns for pathogenic fungi with indicators of habitat fragmentation are not clear, possibly due to their ability to disperse over long distances [21] that attenuate the adverse effects of isolation and to their capacity of persisting in unfavorable conditions (i.e. fragment size reduction, increase of edge proportion) since they might present dormancy or latency [37,38].

Assessing fungal diversity at fragmented landscapes: future perspectives

We identified that fungal diversity in the habitat fragmentation context has been studied mostly through one or a few indicators. Particularly, these are patch size, isolation and edge effects, all of them indicators of habitat fragmentation at a patch scale. This finding highlights that fungal diversity responses to habitat fragmentation at broader scales are less known. For example, if we consider the complex responses of pathogenic fungi to habitat fragmentation, we might think that the long dispersal ability of these fungi was underestimated and cannot achieve the size effect of the habitat fragmentation indicator on the pathogenic fungi response, due to the small 'scale of effect' evaluated. Therefore, researchers do not always evaluate the adequate 'scale of effect' for every fungal group failing thus to identify the strongest fungal species-landscape relationship is occurring. The 'scale of effect' at which landscape configuration influences ecological processes vary among fungi and influences logistically the experimental design that must be carefully judged. Therefore, it would be promising for future studies to gain knowledge about the natural history of the studied fungi in order to properly select the scale of the study. In consequence, the assessment of the optimal scale of fragmentation effects for different fungi would reveal the appropriate outcomes of species interactions with landscape variables [39]. In this sense, several hypotheses were postulated to predict what determines the scale at which an environmental variable could influence biodiversity [40]. However, for many fungi groups empirical evidence is not enough to predict *a priori* the 'scale of effect' of the landscape changes that can be affecting fungal diversity. Meanwhile, the most feasible way to evaluate a biological response to landscape modifications is a multi-scale study where the most relevant 'scale of effect' is analyzed for specific organisms [39].

Fungi encompass a diverse array of living forms and different functional needs that must be supplied along the landscape. Human-modified landscapes may present high levels of heterogeneity in their cover types and might vary in a compositional (i.e. different cover types

Figure 1



The conceptual map shows **(a)** a synthesis of the empirical evidences on the literature of the effects of habitat fragmentation on fungal diversity at the patch scale, and **(b)** a landscape perspective for future analysis suggested for the study of fungal diversity at fragmented landscapes.

across the landscape) or/and in a configurational manner (i.e. spatial arrangement of cover types across the landscape; [41]). In consequence, if our goal is to evaluate the response of fungal diversity to landscape heterogeneity it is important characterizing the different cover types in the landscape according to the function provided for the fungal species studied. For example, whether different vegetation cover types represent a gradient of suitable substrate for the diversity of xylophagous fungi (e.g. substrate availability, diameter of wood, and so on). In this sense, some of these cover types might have not apparent differences to satellite or human eye perspectives, but could be biologically significant for the group of fungi studied. Therefore, the assessment of the particular fungal species needs and the suitable cover types to satisfy those needs might allow finding the proper approach to studying fungal diversity at increasing configurational and compositional heterogeneity of the landscapes.

Altogether, studying fungal diversity in the habitat fragmentation context is a conceptual and methodological challenge, considering the interdependence between the different effects of habitat fragmentation indicators [16]. There are different approaches to deal with this matter that can be mentioned. Smith *et al.* [42] suggest performing statistical analyses to evaluate this interdependence of highly correlated effects of the indicators of the habitat fragmentation, so the relative importance of each one of the indicators considered can be estimated separately. Another approach to carry out is to maintain constant some habitat fragmentation indicators (e.g. at patch scale: patch size or shape) in order to assess others that vary (e.g. at landscape scale: habitat amount or habitat heterogeneity), and vice versa [43]. This strategy would allow separating experimentally the effects of particular habitat fragmentation indicators on fungal diversity (Figure 1).

Knowledge gaps and conclusions

Although the number of studies investigating the fungal diversity at fragmented landscapes is still limited, the synthesis provided here suggests that fungal diversity is affected by habitat fragmentation. However, explicit test through a meta-analysis might provide clearer patterns on the magnitude and direction of these effects on fungal diversity. Then, studies involving different functional groups of fungi seem to be a fruitful way forward to assess for further generalization of these promising patterns. In addition, more studies oriented to elucidate the mechanisms behind these fungal diversity–landscape relationships together with those focused on the effects observed in fungal composition on plant communities, ecosystem functioning and services are evidently needed. Also, the evaluation of species–landscape relationships at optimal scales might allow a correct estimation of the biological responses for different fungi groups. Altogether, this knowledge supported by the incorporation of landscape structure and proper scale of effects for fungal responses will be a milestone when carrying out accurate strategies for sustainable land uses and landscape management in face of worldwide habitat fragmentation.

Acknowledgements

We thank MC Silva-Filho & J Vivanco for the invitation to write this review. This work was funded by FONCYT, the National University of Cordoba (SECyT — UNC) and CONICET. HPY, PM and VEG are fellows from CONICET. GG, LS, CU and LG are researchers from CONICET.

References and recommended reading

Papers of particular interest, published within the period of review, have been highlighted as:

•• of outstanding interest

1. Dirzo R, Young HS, Galetti M, Ceballos G, Isaac NJ, Collen B: **Defaunation in the Anthropocene**. *Science* 2014, **345**:401-406.

2. Sala OE, Chapin FS, Armesto JJ, Berlow E, Bloomfield J, Dirzo R, Huber-Sanwald E, Huenneke LF, Jackson RB, Kinzig A *et al.*: **Global biodiversity scenarios for the year 2100**. *Science* 2000, **287**:1770-1774.

3. Rands MR, Adams WM, Bennun L, Butchart SH, Clements A, Coomes D, Entwistle A, Hodge I, Kapos V, Scharlemann PW *et al.*: **Biodiversity conservation: challenges beyond 2010**. *Science* 2010, **329**:1298-1303.

4. Grez A, Galetto L: **Fragmentación del paisaje en América Latina: ¿en qué estamos**. *Conservación biológica: perspectivas desde América Latina*; *Editorial Universitaria, Santiago: 2011:63-78*.

5. Tscharntke T, Tylianakis JM, Rand TA, Didham RK, Fahrig L, Batary P, Bengtsson J, Clough Y, Crist TO, Dormann CF *et al.*: **Landscape moderation of biodiversity patterns and processes-eight hypotheses**. *Biol Rev* 2012, **87**:661-685.

6. Moora M, Davison J, Öpik M, Metsis M, Saks Ü, Jairus T, Vasar M, Zobel M: **Anthropogenic land use shapes the composition and phylogenetic structure of soil arbuscular mycorrhizal fungal communities**. *FEMS Microbiol Ecol* 2014, **90**:609-621.

7. •• Davison J, Moora M, Öpik M, Adholeya A, Ainsaar L, Bâ A, Burla S, Diedhiou GA, Hiiesalu I, Jairus T *et al.*: **Global assessment of arbuscular mycorrhizal fungus diversity reveals very low endemism**. *Science* 2015, **349**:970-973.
The authors discovered that some taxa are globally distributed and suggested that the biogeography of AM fungi is driven by unexpectedly efficient dispersal, probably via both abiotic and biotic vectors, including humans.

8. Keinath DA, Doak DF, Hodges KE, Prugh LR, Fagan W, Sekercioglu CH, Buchart SHM, Kauffman M: **A global analysis of traits predicting species sensitivity to habitat fragmentation**. *Global Ecol Biogeogr* 2017, **26**:115-127.

9. Noss RF: **Indicators for monitoring biodiversity: a hierarchical approach**. *Conserv Biol* 1990, **4**:355-364.

10. Mueller GM, Foster MS, Bills GF (Eds): *Biodiversity of Fungi: Inventory and Monitoring Methods*. Academic Press; 2011.

11. Crockatt ME: **Are there edge effects on forest fungi and if so do they matter?** *Fungal Biol Rev* 2012, **26**:94-101.

12. Fardila D, Kelly LT, Moore JL, McCarthy MA: **A systematic review reveals changes in where and how we have studied habitat loss and fragmentation over 20years**. *Biol Conserv* 2017, **212**:130-138.

13. Nguyen NH, Song Z, Bates ST, Branco S, Tedersoo L, Menke J, Shilling JS, Kennedy PG: **FUNGuild: an open annotation tool for parsing fungal community datasets by ecological guild**. *Fungal Ecol* 2016, **20**:241-248.

14. Abrego N, Salcedo I: **Response of wood-inhabiting fungal community to fragmentation in a beech forest landscape**. *Fungal Ecol* 2014, **8**:18-27.

15. Longo S, Cofré N, Soteras F, Grilli G, Lugo M, Urcelay C: **Taxonomic and functional response of arbuscular mycorrhizal fungi to land use change in central Argentina**. *Recent Advances on Mycorrhizal Fungi*. Springer International Publishing; 2016:81-90.

16. Didham RK, Kapos V, Ewers RM: **Rethinking the conceptual foundations of habitat fragmentation research**. *Oikos* 2012, **121**:161-170.

17. Lord JM, Norton DA: **Scale and the spatial concept of fragmentation**. *Conserv Biol* 1990, **4**:197-202.

18. Fahrig L: **Ecological responses to habitat fragmentation *per se***. *Annu Rev Ecol Evol Syst* 2017:48.

19. Grilli G, Urcelay C, Galetto L: **Forest fragment size and nutrient availability: complex responses of mycorrhizal fungi in native–exotic hosts**. *Plant Ecol* 2012, **213**:155-165.

20. Siitonen P, Lehtinen A, Siitonen M: **Effects of forest edges on the distribution, abundance, and regional persistence of wood-rotting fungi**. *Conserv Biol* 2005, **19**:250-260.

21. Helander M, Ahlholm J, Sieber TN, Hinneri S, Saikkonen K: **Fragmented environment affects birch leaf endophytes**. *New Phytol* 2007, **175**:547-553.

22. Drinnan IN: **The search for fragmentation thresholds in a southern Sydney suburb**. *Biol Conserv* 2005, **124**:339-349.

23. Peay KG, Bruns TD, Kennedy PG, Bergemann SE, Garbelotto M: **A strong species–area relationship for eukaryotic soil microbes: island size matters for ectomycorrhizal fungi**. *Ecol Lett* 2007, **10**:470-480.

24. •• Haddad NM, Brudvig LA, Clobert J, Davies KF, Gonzalez A, Holt RD, Lovejoy TE, Sexton JO, Austin MP, Collins CD *et al.*: **Habitat fragmentation and its lasting impact on Earth's ecosystems**. *Sci Adv* 2015, **1**:e1500052.
The authors showed how habitat fragmentation reduces biodiversity by 13–75% and impairs key ecosystem functions by decreasing biomass and altering nutrient cycles. Effects are greatest in the smallest and most isolated fragments, and they magnify with the passage of time.

25. Nordén J, Penttilä R, Siitonen J, Tomppo E, Ovaskainen O: **Specialist species of wood-inhabiting fungi struggle while generalists thrive in fragmented boreal forests**. *J Ecol* 2013, **101**:701-712.

26. McGuire KL, Bent E, Borneman J, Majumder A, Allison SD, Treseder KK: **Functional diversity in resource use by fungi**. *Ecology* 2010, **91**:2324-2332.

27. Mensah JA, Koch AM, Antunes PM, Kiers ET, Hart M, Bücking H: **High functional diversity within species of arbuscular mycorrhizal fungi is associated with differences in phosphate and nitrogen uptake and fungal phosphate metabolism**. *Mycorrhiza* 2015, **25**:533-546.

28. Grilli G, Urcelay C, Galetto L: **Linking mycorrhizal fungi and soil nutrients to vegetative and reproductive ruderal plant development in a fragmented forest at central Argentina**. *For Ecol Manage* 2013, **310**:442-449.

29. Grilli G, Urcelay C, Longo MS, Galetto L: **Mycorrhizal fungi affect plant growth: experimental evidence comparing native and invasive hosts in the context of forest fragmentation**. *Plant Ecol* 2014, **215**:1513-1525.

30. •• Grilli G, Urcelay C, Galetto L, Davison J, Vasar M, Saks Ü, Jarius T, Öpik M: **The composition of arbuscular mycorrhizal fungal communities in the roots of a ruderal forb is not related to the forest fragmentation process**. *Environ Microbiol* 2015, **17**:2709-2720.

Authors tested phylogenetic dispersion in AM fungal communities using a randomization based null-model approach and recorded either phylogenetic clustering and it is the only study that attempted to compare samples (from a single study area) against different species pools.

31. Kranabetter JM, De Montigny L, Ross G: **Effectiveness of green-tree retention in the conservation of ectomycorrhizal fungi**. *Fungal Ecol* 2013, **6**:430-438.

32. Vannette RL, Leopold DR, Fukami T: **Forest area and connectivity influence root-associated fungal communities in a fragmented landscape**. *Ecology* 2016, **97**:2374-2383.

33. Hottola J, Ovaskainen O, Hanski I: **A unified measure of the number, volume and diversity of dead trees and the response of fungal communities**. *J Ecol* 2009, **97**:1320-1328.

34. Abrego N, Salcedo I: **Taxonomic gap in wood-inhabiting fungi: identifying understudied groups by a systematic survey**. *Fungal Ecol* 2015, **15**:82-85.

35. Ylisirniö AL, Mönkkönen M, Hallikainen V, Ranta-Maunus T, Kouki J: **Woodland key habitats in preserving polypore diversity in boreal forests: effects of patch size, stand structure and microclimate**. *Forest Ecol Manage* 2016, **373**:138-148.

36. Olsson J, Jonsson BG, Hjältén J, Ericson L: **Addition of coarse woody debris — the early fungal succession on Picea abies logs in managed forests and reserves**. *Biol Conserv* 2011, **144**:1100-1110.

37. Saikkonen K, Wäli P, Helander M, Faeth SH: **Evolution of endophyte–plant symbioses**. *Trends Plant Sci* 2004, **9**: 275-280.

38. Avelino J, Romero-Gurdián A, Cruz-Cuellar HF, Declerck FAJ: **Landscape context and scale differentially impact coffee leaf rust, coffee berry borer, and coffee root-knot nematodes**. *Ecol Appl* 2012, **22**:584-596.

39. Jackson HB, Fahrig L: **Are ecologists conducting research at the optimal scale?** *Glob Ecol Biogeogr* 2015, **24**:52-63.

40. Miguet P, Jackson HB, Jackson ND, Martin AE, Fahrig L: **What determines the spatial extent of landscape effects on species?** *Landsc Ecol* 2016, **31**:1177-1194.

41. Fahrig L, Baudry J, Brotons L, Burel FG, Crist TO, Fuller RJ, Sirami C, Siriwardena GM, Martin JL: **Functional landscape heterogeneity and animal biodiversity in agricultural landscapes**. *Ecol Lett* 2011, **14**:101-112.

42. Smith AC, Koper N, Francis CM, Fahrig L: **Confronting collinearity: comparing methods for disentangling the effects of habitat loss and fragmentation**. *Landsc Ecol* 2009, **24**:1271.

43. Fahrig L: **Rethinking patch size and isolation effects: the habitat amount hypothesis**. *J Biogeogr* 2013, **40**: 1649-1663.