Implications of microbial community assembly for ecosystem restoration: patterns, process, and potential

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Abstract.

While it is now widely accepted that microorganisms provide essential functions in restoration ecology, the nature of relationships between microbial community assembly and ecosystem recovery remain unclear. There has been a longstanding challenge to decipher whether microorganisms facilitate or simply follow ecosystem recovery, and evidence for each is mixed at best. We propose that understanding microbial community assembly processes during ecosystem restoration is critical to optimizing management strategies. We examine how the connection between environment, community structure, and function is fundamentally underpinned by the processes governing community assembly of these microbial communities. We review important factors to consider in evaluating microbial community structure in the context of ecosystem recovery as revealed in studies of microbial succession: 1) variation in community assembly processes, 2) measurable microbial community attributes, and 3) linkages to ecosystem function. We seek to empower restoration ecology with microbial assembly and successional understandings that can generate actionable insights and vital contexts for ecosystem restoration efforts.

Keywords: microbiome, disturbance ecology, succession, restoration ecology, microbial community assembly, community ecology

Introduction.

Restoration of degraded ecosystems is essential to maintaining global biodiversity and ecosystem services [1-4]. Yet despite large economic investments [5], restored ecosystems are often strikingly different in species composition and edaphic factors than their more pristine counterparts [6-10]. While restoration efforts have long focused on aboveground communities [11-13], there is increasing interest in the role of belowground systems, including their interactions with aboveground processes, as restoration tools. A central challenge in this new line of inquiry, as succinctly stated by Harris [14], is whether microorganisms follow or facilitate restoration. That is, do microorganisms simply reflect broader ecosystem succession or can they drive the restoration of degraded ecosystems?

Much evidence has been gathered to support both sides of this argument [6, 15-24]. For instance, restored habitats may promote microbial pollutant degradation [25, 26] and increased diversity and function of soil microbiota [20, 27, 28]; conversely mycorrhizal fungi are widely considered as facilitators of plant establishment [6, 23, 24]. In reality, each side of the equation likely plays a role in ecosystem restoration, with the relative balance dependent on ecosystem and species characteristics. Indeed, Van der Bij et al. [24] suggest the simultaneous application of belowground and aboveground biomass as an optimal restoration strategy. Understanding the coupled changes of below- and aboveground ecosystems during ecosystem restoration may be key to improving its efficacy. Whether microorganisms follow or facilitate restoration, application of concepts in microbial community assembly and succession can better attainment of desired restoration outcomes.

The study of ecological succession has long provided testable theory to understand factors that control changes in community structure and ecosystem function over time. More recently, the application and examination of such theory to microbial communities has built insights into when and how microbial community structure changes through ecosystem recovery. Increasingly, ecologists seek to understand how and why these changes will mediate impacts on ecosystem function, and related theory can thus inform belowground dimensions of restoration efforts. In particular, microbial community assembly processes have been noted as an important driver of microbial community structure and function during natural and managed secondary succession.

Here we seek to empower restoration ecologists with microbial assembly and successional understandings that can generate actionable insights and vital contexts for ecosystem restoration efforts. To that end, we examine how the connection between environment, community structure, and function is fundamentally underpinned by the processes governing community assembly of microbial communities. We review important factors to consider in evaluating microbial community structure in the context of ecosystem recovery as revealed in studies of microbial succession: 1) variation in community assembly processes, 2) measurable microbial community attributes, and 3) linkages to ecosystem function. Ultimately, we provide guidance on how assembly processes may help unify variable results of empirical studies assessing biodiversity-ecosystem function and environment-ecosystem function relationships to reveal opportunities for guiding microbial mediated biogeochemistry in restoration.

Successional Trends in Community Assembly.

There is much debate surrounding the roles of microbial community succession and assembly in ecosystem restoration. Some insist upon unpredictable patterns in microbial communities through secondary succession and restoration [29-32]; more recently others highlight demonstrable patterns along these trajectories [21, 33, 34]. Underpinning these patterns are community assembly processes. Existing understandings from microbial succession on when and how community assembly is driven by more deterministic or stochastic processes, in turn informs strategies of when and how microbial communities may be influenced for restoration purposes.

Microbial community assembly is determined through the balance of deterministic and stochastic processes, each of which can operate across distinct spatial, temporal, and genetic variables [35-39]. Determinism is largely governed by the interplay of homogeneous vs. variable selective pressures; while stochasticity results from a combination of dispersal, drift, and dispersal limitation [37]. At the highest level, selection results from environmental conditions, or changes in those conditions through successional trajectories. Key factors influencing the selective pressures imposed on various microbial clades include temperature [40], moisture [41], salinity [42, 43], pH [44, 45], vegetation type [46-49], and resource availability [50-53]. Homogeneous selection through space or time results in specialized communities with low diversity, while variable selection can result in high diversity through niche-based processes [37, 38]. Similarly, variation in body size and dispersal traits (e.g., sporulation, flagella) can influence dispersal and dispersal limitation in taxon-specific ways [35, 36, 54-58]. In turn, the ratio of immigration/emigration influences community biodiversity. Differences in assembly between bacteria and fungi [59], heterotrophs and autotrophs [36], specialists and generalists [54], and abundant and rare taxa [60-63] influence community composition.

While there are multiple possible trajectories of assembly processes through succession [33], we present commonly observed patterns, as well as trajectories that may be beneficial for restoration efforts in Figure 1 and Box 1. We note that while we generally discuss assembly at the community-level, variation in assembly can also be assessed across microbial clades as discussed above [36, 60, 64-66]. Generally, there is an early period of stochasticity during secondary succession and restoration that is succeeded by increasing determinism [33, 67], although Dini-Andreote et al. [33] note that secondary succession may begin under a deterministic environment depending on disturbance type. Other factors that can influence assembly trajectories include priority effects whereby initial colonizers set successional trajectories despite similar environments [68-70] and life history strategies, with fast growing r-strategists having an advantage in early succession [71].

In the case of secondary succession, the type and strength of disturbance can impact the initial degree of stochasticity. Strong disturbances lead to a “blank slate” environment that can be easily colonized via immigration. Extreme disturbances can also result in low resource availability, limit microbial biomass, and limit the survival of sensitive species [21, 72]. In contrast, resilient community members remain after weaker disturbances, supporting competition and niche differentiation. As environmental stress declines through restoration, these attributes tend to recover, increasing selective pressures and opening new ecological niches [72-75].

Linkages between Microbial Assembly and Ecosystem Function.

The connections between successional trajectories in species composition and ecosystem functions are essential to promoting the long-term success of restoration efforts. Vital to this line of inquiry is understanding how communities that assemble through time evoke changes in community diversity, species and trait abundances, and interactions between community members that ultimately impact gene expression.

The biodiversity-ecosystem function (BEF) is a central tenet of ecosystem ecology and is increasingly recognized as an important fundamental of microbial systems [76-81]. BEF research posits that biodiversity supports enhanced rates of ecosystem functions through ecological mechanisms such as niche or resource use complementarity, mass or sampling effects in which more diverse communities include members with a trait of interest, and functional redundancy or insurance in which organisms or communities contain multiple copies of a trait of interest [82-84]; all of which may point to a role for rare species in supporting ecosystem functions [85, 86]. Yet, the nature of the BEF relationships can vary with assembly processes, ecosystem attributes, and the amount of redundancy in a community [rev. in 82]. In some cases, increases in diversity may even decrease ecosystem function; for example, through the dilution of traits of interest from immigration [54].

Community assembly therefore provides a framework for understanding the nuances of the BEF relationship. Determinism and stochasticity both denote ecological processes acting on organisms, or traits contained therein, that impact both their activities and overall community composition. For instance, selection can optimize microbial metabolism through species sorting [87, 88]. Communities with a history of consistent selection may be particularly well-adapted and contain efficient pathways for catalyzing biogeochemical processes and cell maintenance [54]. Alternatively, selection may exclude taxa that metabolize more scarce resources, resulting in decreased community metabolism [82, 89, 90]; and Graham et al. [35] have suggested that multiple competing selective pressures can optimize community function. Various stochastic processes can also alternatively increase or decrease ecosystem functions. Under high dispersal rates, communities may be more likely to contain species with more traits that are beneficial to a function of interest [91, 92] and allow for more niche complementarity [93]. This may be particularly important in early succession [33, 67]. Conversely, dispersal may add maladapted organisms to a community (i.e., mass effect or source-sink dynamics [94, 95]) resulting in decreased function, an effect that may vary with niche breadth [54]. Dispersal limitation can also inhibit the ability of organisms to reach their optional environment or decrease the diversity of immigrating organisms, lowering community function [54, 77, 96]. In total, it maybe be that a combination of diverse assembly processes acting on a varied suite of traits optimizes community functions [54].

Underlying the relationship between microbial diversity, community composition, and ecosystem function is the coupling of response and effect traits (Figure 2). Response traits determine species composition through interactions with the environment (e.g, spore formation, life history), while effect traits correspond to the functional roles of taxa (e.g., biogeochemical cycling, [97, 98]). The strength of the relationship between response and effect traits determines the impact of changes in community assembly on ecosystem functions. In turn, this is contingent on phylogenetic conservation of traits, or ecological coherence in which physiological diversity aligns with phylogenetic diversity [21, 99-101]. When determinism reigns, the coupling between effect and response traits varies depending on whether the environment selects for clades of organisms with optimal functional traits or acts on response traits that are unrelated to the ecosystem process of interest [82, 102-105]. When stochasticity reigns, community composition will largely depend on effect traits that facilitate or impede dispersal (e.g., spore formation), and thus response traits that dictate function may be decoupled from the environment. When a single response trait is dominant, community composition may be more easily manipulated by restorations efforts. For example, Knelman et al. [53] showed that nutrient addition to a nutrient limited glacial environment could dramatically advance succession.

Key Microbial Indicators for Assessing Assembly and Succession.

Because microorganisms respond quickly to changes in the environment, microbial communities are used in restoration ecology to assess the status of an ecosystem relative to a reference condition or to enhance ecosystem recovery through inoculations [14, 21, 106]. The return of soil microbial properties such as diversity and nutrient cycling are often considered to be indicative of restoration success [107]. More details on common metrics used to describe microbial communities, their relationships to community assembly and ecosystem function, and their implementation in restoration ecology are provided in Table 1. We provide a brief discussion of each below.

Diversity metrics are perhaps the most longstanding descriptors for microbial community composition. Indeed, many have pointed to microbial community diversity as a major driver of ecosystem health and soil fertility. Alpha- (within community), beta- (across local communities), and gamma- (across regional communities) diversity each serve as easy-to-measure assessments of ecosystem trajectories. At a finer level of resolution, trait-based approaches provide information on changes in response traits (e.g., changes in life history strategies) and effect traits (e.g., changes in carbon and nutrient cycling) through restoration [102, 104, 105]. For instance, fungal:bacterial ratios, ribosomal gene copy numbers, or shifts in bacterial and fungal composition are often leveraged to infer changes in r- vs. k- selection [14, 22, 71, 108-110]. Many studies also pair these metrics with changes in corresponding effect traits, particularly those related to biogeochemical cycles. Common observations include a shift from nitrogen cycling to C cycling as secondary succession proceeds [34, 65, 111, 112], greater C storage [113, 114] and aggregation [115, 116], and lower water stress [115, 116]. Finally, microbial community assembly is increasingly being studied by restoration ecologists. Most rely on neutral or null modeling approaches to infer the strengths of determinism (e.g., variable and homogenous selection via βNTI as proposed by Stegen et al. [37]) and stochasticity (e.g. RC_{bray} [37]).

Applications in Restoration Ecology.

The multitude of drivers and organismal interactions are a major challenge to evaluating and enhancing successes in restoration ecology. Given the large economic cost of restoration, it is vital that we garner a better understanding surrounding the trajectories and timeframes of restoration efforts. Without active intervention, ecosystem recoveries can occur exceedingly slowly [117, 118]. Belowground microbial communities present an opportunity to dramatically enhance and assess restoration outcomes [6, 108, 119]. For instance, there are many examples of restoration efforts focused solely on aboveground ecosystems that are unable to recreate reference conditions [7-9, 120-122], and microbial communities may be particularly important to facilitating the establishment of late successional species [6, 24, 123, 124].

Plant-microbial interactions are central to understanding the roles microorganisms play in restoration, particularly given the strong attention to management of vegetation. With some notable exceptions (e.g., mycorrhizal associations), it remains unclear how plants and the soil microbiome interact to drive ecosystem assembly and succession [14, 24], yet vegetation is an important factor in compositional and functional changes in microbial communities [6, 71, 125]. Plants have direct mutualistic and antagonistic relationships with soil microorganisms [126, 127] as well as indirect impacts through the transfer of phosynthate to decomposers and nutrient cyclers [128, 129]. Invasive species in particular have been noted to changed soil microbial community structure and function [130-132]. Conversely, inoculation with various microbes or whole soils has been shown to have bottom-up effects on plant establishment during restoration [24, 127, 133].

Given this context, there are interesting ways in which soil microbial communities may aid in restoration (Table 2). First, microorganisms may serve as an early indicator of recovery [14, 21]. With the relative affordability of amplicon sequencing, microbial community composition could provide value as part of rapid ecosystem function assessments [134]. A deeper understanding of microbial communities within the context of the ecological theory presented may also serve to help leverage microbes create “shortcuts” for restoration [14]. Targeted inoculations with microbiota have proven to override priority effects and aid in plant re-establishment under some circumstances [24, 64, 73, 135]. Inoculations that allow for faster plant re-establishment may inevitably provide shortcuts in which ecosystems bypass successional stages in route to a recovered state [14]. These strategies may provide the most value when coupled with habitat manipulations that support microbiota of interest [127, 133].

The discussion here is intended to provide an overview of the importance of microbial community structure and how it relates to changes that occur during ecosystem recovery. While it is clear that microorganisms provide essential functions in restoration ecology, new implementations of microbial ecology during restoration may help bolster management successes. For instance, management of belowground systems could be directed towards improving gamma diversity so as to maximize the sampling effect during early succession, towards facilitating niche diversity, or towards creating selective environments that maximize response-effect trait linkages. The vast potential of microorganisms for the benefit of ecosystem restoration remains largely untapped, and a greater understanding of the ecological context in which these organisms reside provides an avenue for more fully realizing their power.

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References.

1. Jacobs DF, Oliet JA, Aronson J, Bolte A, Bullock JM, Donoso PJ, Landhäusser SM, Madsen P, Peng S, Rey-Benayas JM (2015) Restoring forests: what constitutes success in the twenty-first century?, vol. 46. Springer, pp. 601-614.
2. Perring MP, Standish RJ, Price JN, Craig MD, Erickson TE, Ruthrof KX, Whiteley AS, Valentine LE, Hobbs RJ (2015) Advances in restoration ecology: rising to the challenges of the coming decades. Ecosphere 6: 1-25.
3. Perring MP, De Frenne P, Baeten L, Maes SL, Depauw L, Blondeel H, Carón MM, Verheyen K (2016) Global environmental change effects on ecosystems: The importance of land-use legacies. Global Change Biology 22: 1361-1371.
4. Suding KN (2011) Toward an era of restoration in ecology: successes, failures, and opportunities ahead. Annual review of ecology, evolution and systematics 42: 465-487.
5. BenDor T, Lester TW, Livengood A, Davis A, Yonavjak L (2015) Estimating the size and impact of the ecological restoration economy. PloS one 10: e0128339.
6. Koziol L, Bever JD (2017) The missing link in grassland restoration: arbuscular mycorrhizal fungi inoculation increases plant diversity and accelerates succession. Journal of Applied Ecology 54: 1301-1309.
7. Kindscher K, Tieszen LL (1998) Floristic and soil organic matter changes after five and thirty-five years of native tallgrass prairie restoration. Restoration Ecology 6: 181-196.
8. Sluis WJ (2002) Patterns of species richness and composition in re-created grassland. Restoration Ecology 10: 677-684.
9. Piper JK, Schmidt ES, Janzen AJ (2007) Effects of species richness on resident and target species components in a prairie restoration. Restoration Ecology 15: 189-198.

10. Grman E, Bassett T, Zirbel CR, Brudvig LA (2015) Dispersal and establishment filters influence the assembly of restored prairie plant communities. Restoration Ecology 23: 892-899.

11. Baker S, Eckerberg K (2016) Ecological restoration success: a policy analysis understanding. Restoration Ecology 24: 284-290.

12. Guo LB, Gifford RM (2002) Soil carbon stocks and land use change: a meta analysis. Global change biology 8: 345-360.

13. Hua F, Wang X, Zheng X, Fisher B, Wang L, Zhu J, Tang Y, Yu DW, Wilcove DS (2016) Opportunities for biodiversity gains under the world’s largest reforestation programme. Nature Communications 7: 1-11.

14. Harris J (2009) Soil microbial communities and restoration ecology: facilitators or followers? Science 325: 573-574.

15. Lynum CA, Bulseco AN, Dunphy CM, Osborne SM, Vineis JH, Bowen JL (2020) Microbial community response to a passive salt marsh restoration. Estuaries and Coasts 43: 1439-1455.

16. Sun Y, Wang S, Niu J (2018) Microbial community evolution of black and stinking rivers during in situ remediation through micro-nano bubble and submerged resin floating bed technology. Bioresource technology 258: 187-194.

17. Lin Q, Sekar R, Marrs R, Zhang Y (2019) Effect of river ecological restoration on biofilm microbial community composition. Water 11: 1244.

18. Igalavithana AD, Lee S-E, Lee YH, Tsang DC, Rinklebe J, Kwon EE, Ok YS (2017) Heavy metal immobilization and microbial community abundance by vegetable waste and pine cone biochar of agricultural soils. Chemosphere 174: 593-603.

19. Yang X, Tsibart A, Nam H, Hur J, El-Naggar A, Tack FM, Wang C-H, Lee YH, Tsang DC, Ok YS (2019) Effect of gasification biochar application on soil quality: trace metal behavior, microbial community, and soil dissolved organic matter. Journal of hazardous materials 365: 684-694.

20. Andersen R, Grasset L, Thormann MN, Rochefort L, Francez A-J (2010) Changes in microbial community structure and function following Sphagnum peatland restoration. Soil Biology and Biochemistry 42: 291-301.

21. Banning NC, Gleeson DB, Grigg AH, Grant CD, Andersen GL, Brodie EL, Murphy D (2011) Soil microbial community successional patterns during forest ecosystem restoration. Applied and environmental microbiology 77: 6158-6164.

22. Smith R, Shiel R, Bardgett RD, Millward D, Corkhill P, Rolph G, Hobbs P, Peacock S (2003) Soil microbial community, fertility, vegetation and diversity as targets in the restoration management of a meadow grassland. Journal of applied ecology 40: 51-64.

23. Van Der Heijden MG, Klironomos JN, Ursic M, Moutoglis P, Streitwolf-Engel R, Boller T, Wiemken A, Sanders IR (1998) Mycorrhizal fungal diversity determines plant biodiversity, ecosystem variability and productivity. Nature 396: 69-72.

24. Van der Bij A, Weijters M, Bobbink R, Harris JA, Pawlett M, Ritz K, Benetková P, Moradi J, Frouz J, Van Diggelen R (2018) Facilitating ecosystem assembly: plant-soil interactions as a restoration tool. Biological Conservation 220: 272-279.

25. Pande V, Pandey SC, Sati D, Pande V, Samant M (2020) Bioremediation: an emerging effective approach towards environment restoration. Environmental Sustainability 3: 91-103.

26. Beesley L, Moreno-Jiménez E, Gomez-Eyles JL, Harris E, Robinson B, Sizmur T (2011) A review of biochars' potential role in the remediation, revegetation and restoration of contaminated soils. Environmental pollution 159: 3269-3282.

27. Farrell HL, Léger A, Breed MF, Gornish ES (2020) Restoration, soil organisms, and soil processes: emerging approaches. Restoration Ecology 28: S307-S310.

28. Hamonts K, Bissett A, Macdonald BC, Barton PS, Manning AD, Young A (2017) Effects of ecological restoration on soil microbial diversity in a temperate grassy woodland. Applied Soil Ecology 117: 117-128.

29. Felske A, Wolterink A, Van Lis R, De Vos WM, Akkermans AD (2000) Response of a soil bacterial community to grassland succession as monitored by 16S rRNA levels of the predominant ribotypes. Applied and Environmental Microbiology 66: 3998-4003.

30. Kuramae EE, Gamper HA, Yergeau E, Piceno YM, Brodie EL, DeSantis TZ, Andersen GL, Van Veen JA, Kowalchuk GA (2010) Microbial secondary succession in a chronosequence of chalk grasslands. The ISME journal 4: 711-715.

31. Gros R, Jocteur Monrozier L, Faivre P (2006) Does disturbance and restoration of alpine grassland soils affect the genetic structure and diversity of bacterial and N2-fixing populations? Environmental microbiology 8: 1889-1901.

32. Jangid K, Williams MA, Franzluebbers AJ, Blair JM, Coleman DC, Whitman WB (2010) Development of soil microbial communities during tallgrass prairie restoration. Soil Biology and Biochemistry 42: 302-312.

33. Dini-Andreote F, Stegen JC, Van Elsas JD, Salles JF (2015) Disentangling mechanisms that mediate the balance between stochastic and deterministic processes in microbial succession. Proceedings of the National Academy of Sciences 112: E1326-E1332.

34. Knelman JE, Graham EB, Ferrenberg S, Lecoeuvre A, Labrado A, Darcy JL, Nemergut DR, Schmidt SK (2017) Rapid shifts in soil nutrients and decomposition enzyme activity in early succession following forest fire. Forests 8: 347.

35. Graham EB, Crump AR, Resch CT, Fansler S, Arntzen E, Kennedy DW, Fredrickson JK, Stegen JC (2016) Coupling spatiotemporal community assembly processes to changes in microbial metabolism. Frontiers in Microbiology 7: 1949.

36. Graham EB, Crump AR, Resch CT, Fansler S, Arntzen E, Kennedy DW, Fredrickson JK, Stegen JC (2017) Deterministic influences exceed dispersal effects on hydrologically-connected microbiomes. Environmental Microbiology 19: 1552-1567.

37. Stegen JC, Lin X, Fredrickson JK, Chen X, Kennedy DW, Murray CJ, Rockhold ML, Konopka A (2013) Quantifying community assembly processes and identifying features that impose them. The ISME journal 7: 2069-2079.

38. Vellend M (2010) Conceptual synthesis in community ecology. The Quarterly review of biology 85: 183-206.

39. Nemergut DR, Schmidt SK, Fukami T, O'Neill SP, Bilinski TM, Stanish LF, Knelman JE, Darcy JL, Lynch RC, Wickey P (2013) Patterns and processes of microbial community assembly. Microbiology and Molecular Biology Reviews 77: 342-356.

40. Waldrop M, Firestone M (2006) Response of microbial community composition and function to soil climate change. Microbial ecology 52: 716-724.

41. Brockett BF, Prescott CE, Grayston SJ (2012) Soil moisture is the major factor influencing microbial community structure and enzyme activities across seven biogeoclimatic zones in western Canada. Soil biology and biochemistry 44: 9-20.

42. Crump BC, Hopkinson CS, Sogin ML, Hobbie JE (2004) Microbial biogeography along an estuarine salinity gradient: combined influences of bacterial growth and residence time. Applied and environmental microbiology 70: 1494-1505.

43. Lozupone CA, Knight R (2007) Global patterns in bacterial diversity. Proceedings of the National Academy of Sciences 104: 11436-11440.

44. Lindström ES, Kamst-Van Agterveld MP, Zwart G (2005) Distribution of typical freshwater bacterial groups is associated with pH, temperature, and lake water retention time. Applied and environmental microbiology 71: 8201-8206.

45. Fierer N, Jackson RB (2006) The diversity and biogeography of soil bacterial communities. Proceedings of the National Academy of Sciences 103: 626-631.

46. Burke DJ, Hamerlynck EP, Hahn D (2002) Interactions among plant species and microorganisms in salt marsh sediments. Applied and Environmental Microbiology 68: 1157-1164.

47. Hamilton III EW, Frank DA (2001) Can plants stimulate soil microbes and their own nutrient supply? Evidence from a grazing tolerant grass. Ecology 82: 2397-2402.

48. Zak DR, Holmes WE, White DC, Peacock AD, Tilman D (2003) Plant diversity, soil microbial communities, and ecosystem function: are there any links? Ecology 84: 2042-2050.

49. De Vries FT, Manning P, Tallowin JR, Mortimer SR, Pilgrim ES, Harrison KA, Hobbs PJ, Quirk H, Shipley B, Cornelissen JH (2012) Abiotic drivers and plant traits explain landscape-scale patterns in soil microbial communities. Ecology letters 15: 1230-1239.

50. Eilers KG, Lauber CL, Knight R, Fierer N (2010) Shifts in bacterial community structure associated with inputs of low molecular weight carbon compounds to soil. Soil Biology and Biochemistry 42: 896-903.

51. Castle SC, Nemergut DR, Grandy AS, Leff JW, Graham EB, Hood E, Schmidt SK, Wickings K, Cleveland CC (2016) Biogeochemical drivers of microbial community convergence across actively retreating glaciers. Soil Biology and Biochemistry 101: 74-84.

52. Lladó S, López-Mondéjar R, Baldrian P (2018) Drivers of microbial community structure in forest soils. Applied microbiology and biotechnology 102: 4331-4338.

53. Knelman JE, Schmidt SK, Lynch RC, Darcy JL, Castle SC, Cleveland CC, Nemergut DR (2014) Nutrient addition dramatically accelerates microbial community succession. PloS one 9: e102609.

54. Graham EB, Stegen JC (2017) Dispersal-based microbial community assembly decreases biogeochemical function. Processes 5: 65.

55. De Bie T, De Meester L, Brendonck L, Martens K, Goddeeris B, Ercken D, Hampel H, Denys L, Vanhecke L, Van der Gucht K (2012) Body size and dispersal mode as key traits determining metacommunity structure of aquatic organisms. Ecology letters 15: 740-747.

56. Padial AA, Ceschin F, Declerck SA, De Meester L, Bonecker CC, Lansac-Tôha FA, Rodrigues L, Rodrigues LC, Train S, Velho LF (2014) Dispersal ability determines the role of environmental, spatial and temporal drivers of metacommunity structure. PloS one 9: e111227.

57. DeLong JP, Okie JG, Moses ME, Sibly RM, Brown JH (2010) Shifts in metabolic scaling, production, and efficiency across major evolutionary transitions of life. Proceedings of the National Academy of Sciences 107: 12941-12945.

58. Wu W, Lu H-P, Sastri A, Yeh Y-C, Gong G-C, Chou W-C, Hsieh C-H (2018) Contrasting the relative importance of species sorting and dispersal limitation in shaping marine bacterial versus protist communities. The ISME Journal 12: 485-494.

59. Wang K, Wang X, Fei H, Wan C, Han F (2022) Changes in diversity, composition and assembly processes of soil microbial communities during Robinia pseudoacacia L. restoration on the Loess Plateau, China. Journal of Arid Land: 1-15.

60. Chen W, Jiao S, Li Q, Du N (2020) Dispersal limitation relative to environmental filtering governs the vertical small-scale assembly of soil microbiomes during restoration. Journal of Applied Ecology 57: 402-412.

61. Yan W, Ma H, Shi G, Li Y, Sun B, Xiao X, Zhang Y (2017) Independent shifts of abundant and rare bacterial populations across East Antarctica glacial foreland. Frontiers in microbiology 8: 1534.

62. Xue Y, Chen H, Yang JR, Liu M, Huang B, Yang J (2018) Distinct patterns and processes of abundant and rare eukaryotic plankton communities following a reservoir cyanobacterial bloom. The ISME Journal 12: 2263-2277.

63. Pan C, Feng Q, Li Y, Li Y, Liu L, Yu X, Ren S (2022) Rare soil bacteria are more responsive in desertification restoration than abundant bacteria. Environmental Science and Pollution Research 29: 33323-33334.

64. Turley NE, Bell-Dereske L, Evans SE, Brudvig LA (2020) Agricultural land-use history and restoration impact soil microbial biodiversity. Journal of Applied Ecology 57: 852-863.

65. Hu L, Li Q, Yan J, Liu C, Zhong J (2022) Vegetation restoration facilitates belowground microbial network complexity and recalcitrant soil organic carbon storage in southwest China karst region. Science of The Total Environment 820: 153137.

66. Cao J, Pan H, Chen Z, Shang H (2020) Bacterial, fungal, and archaeal community assembly patterns and their determining factors across three subalpine stands at different stages of natural restoration after clear-cutting. Journal of Soils and Sediments 20: 2794-2803.

67. Ferrenberg S, O'neill SP, Knelman JE, Todd B, Duggan S, Bradley D, Robinson T, Schmidt SK, Townsend AR, Williams MW (2013) Changes in assembly processes in soil bacterial communities following a wildfire disturbance. The ISME journal 7: 1102-1111.

68. Elgersma KJ, Ehrenfeld JG, Yu S, Vor T (2011) Legacy effects overwhelm the short-term effects of exotic plant invasion and restoration on soil microbial community structure, enzyme activities, and nitrogen cycling. Oecologia 167: 733-745.

69. Vannette RL, Fukami T (2014) Historical contingency in species interactions: towards niche-based predictions. Ecology letters 17: 115-124.

70. Fukami T (2015) Historical contingency in community assembly: integrating niches, species pools, and priority effects. Annual review of ecology, evolution, and systematics 46: 1-23.

71. Nemergut DR, Knelman JE, Ferrenberg S, Bilinski T, Melbourne B, Jiang L, Violle C, Darcy JL, Prest T, Schmidt SK (2016) Decreases in average bacterial community rRNA operon copy number during succession. The ISME journal 10: 1147-1156.

72. Xiang X, Shi Y, Yang J, Kong J, Lin X, Zhang H, Zeng J, Chu H (2014) Rapid recovery of soil bacterial communities after wildfire in a Chinese boreal forest. Scientific reports 4: 1-8.

73. Calderón K, Spor A, Breuil M-C, Bru D, Bizouard F, Violle C, Barnard RL, Philippot L (2017) Effectiveness of ecological rescue for altered soil microbial communities and functions. The ISME journal 11: 272-283.

74. Hart SC, DeLuca TH, Newman GS, MacKenzie MD, Boyle SI (2005) Post-fire vegetative dynamics as drivers of microbial community structure and function in forest soils. Forest Ecology and Management 220: 166-184.

75. Guo Y, Hou L, Zhang Z, Zhang J, Cheng J, Wei G, Lin Y (2019) Soil microbial diversity during 30 years of grassland restoration on the Loess Plateau, China: Tight linkages with plant diversity. Land Degradation & Development 30: 1172-1182.

76. Cardinale BJ, Matulich KL, Hooper DU, Byrnes JE, Duffy E, Gamfeldt L, Balvanera P, O'connor MI, Gonzalez A (2011) The functional role of producer diversity in ecosystems. American journal of botany 98: 572-592.

77. Hooper DU, Adair EC, Cardinale BJ, Byrnes JE, Hungate BA, Matulich KL, Gonzalez A, Duffy JE, Gamfeldt L, O'Connor MI (2012) A global synthesis reveals biodiversity loss as a major driver of ecosystem change. Nature 486: 105-108.

78. Langenheder S, Bulling MT, Solan M, Prosser JI (2010) Bacterial biodiversity-ecosystem functioning relations are modified by environmental complexity. PloS one 5: e10834.

79. Bell T, Newman JA, Silverman BW, Turner SL, Lilley AK (2005) The contribution of species richness and composition to bacterial services. Nature 436: 1157-1160.

80. Hooper DU, Chapin III FS, Ewel JJ, Hector A, Inchausti P, Lavorel S, Lawton JH, Lodge D, Loreau M, Naeem S (2005) Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. Ecological monographs 75: 3-35.

81. Allan E, Weisser WW, Fischer M, Schulze E-D, Weigelt A, Roscher C, Baade J, Barnard RL, Beßler H, Buchmann N (2013) A comparison of the strength of biodiversity effects across multiple functions. Oecologia 173: 223-237.

82. Knelman JE, Nemergut DR (2014) Changes in community assembly may shift the relationship between biodiversity and ecosystem function. vol. 5. Frontiers Media SA, pp. 424.

83. Allison SD, Martiny JB (2008) Resistance, resilience, and redundancy in microbial communities. Proceedings of the National Academy of Sciences 105: 11512-11519.

84. Louca S, Polz MF, Mazel F, Albright MB, Huber JA, O'Connor MI, Ackermann M, Hahn AS, Srivastava DS, Crowe SA (2018) Function and functional redundancy in microbial systems. Nature ecology & evolution 2: 936-943.

85. Shade A, Jones SE, Caporaso JG, Handelsman J, Knight R, Fierer N, Gilbert JA (2014) Conditionally rare taxa disproportionately contribute to temporal changes in microbial diversity. MBio 5: e01371-01314.

86. Jousset A, Bienhold C, Chatzinotas A, Gallien L, Gobet A, Kurm V, Küsel K, Rillig MC, Rivett DW, Salles JF (2017) Where less may be more: how the rare biosphere pulls ecosystems strings. The ISME journal 11: 853-862.

87. Van der Gucht K, Cottenie K, Muylaert K, Vloemans N, Cousin S, Declerck S, Jeppesen E, Conde-Porcuna J-M, Schwenk K, Zwart G (2007) The power of species sorting: local factors drive bacterial community composition over a wide range of spatial scales. Proceedings of the National Academy of Sciences 104: 20404-20409.

88. Lindström ES, Langenheder S (2012) Local and regional factors influencing bacterial community assembly. Environmental Microbiology Reports 4: 1-9.

89. Grime J (1998) Benefits of plant diversity to ecosystems: immediate, filter and founder effects. Journal of Ecology 86: 902-910.

90. Loreau M, Hector A (2001) Partitioning selection and complementarity in biodiversity experiments. Nature 412: 72-76.

91. Tilman D, Lehman CL, Bristow CE (1998) Diversity-stability relationships: statistical inevitability or ecological consequence? The American Naturalist 151: 277-282.

92. Doak DF, Bigger D, Harding E, Marvier M, O'malley R, Thomson D (1998) The statistical inevitability of stability-diversity relationships in community ecology. The American Naturalist 151: 264-276.

93. Tilman D (1999) The ecological consequences of changes in biodiversity: a search for general principles. Ecology 80: 1455-1474.

94. Pulliam HR (1988) Sources, sinks, and population regulation. The American Naturalist 132: 652-661.

95. Shmida A, Wilson MV (1985) Biological determinants of species diversity. Journal of biogeography: 1-20.

96. Lindström ES, Östman Ö (2011) The importance of dispersal for bacterial community composition and functioning. PloS one 6: e25883.

97. Naeem S, Wright JP (2003) Disentangling biodiversity effects on ecosystem functioning: deriving solutions to a seemingly insurmountable problem. Ecology letters 6: 567-579.

98. Suding KN, Lavorel S, Chapin Iii F, Cornelissen JH, Díaz S, Garnier E, Goldberg D, Hooper DU, Jackson ST, Navas ML (2008) Scaling environmental change through the community-level: A trait-based response-and-effect framework for plants. Global Change Biology 14: 1125-1140.

99. Fierer N, Bradford MA, Jackson RB (2007) Toward an ecological classification of soil bacteria. Ecology 88: 1354-1364.

100. Philippot L, Andersson SG, Battin TJ, Prosser JI, Schimel JP, Whitman WB, Hallin S (2010) The ecological coherence of high bacterial taxonomic ranks. Nature Reviews Microbiology 8: 523-529.

101. Martiny AC, Treseder K, Pusch G (2013) Phylogenetic conservatism of functional traits in microorganisms. The ISME journal 7: 830-838.

102. Allison S (2012) A trait-based approach for modelling microbial litter decomposition. Ecology letters 15: 1058-1070.

103. Jiang L, Pu Z, Nemergut DR (2008) On the importance of the negative selection effect for the relationship between biodiversity and ecosystem functioning. Oikos 117: 488-493.

104. Malik AA, Martiny JB, Brodie EL, Martiny AC, Treseder KK, Allison SD (2020) Defining trait-based microbial strategies with consequences for soil carbon cycling under climate change. The ISME journal 14: 1-9.

105. Karaoz U, Brodie EL (2022) microTrait: A Toolset for a Trait-Based Representation of Microbial Genomes. Frontiers in Bioinformatics 2.

106. Hobbs RJ, Harris JA (2001) Restoration ecology: repairing the earth's ecosystems in the new millennium. Restoration ecology 9: 239-246.

107. Palmer MA, Zedler JB, Falk DA (2016) Foundations of restoration ecology. Springer

108. Bardgett RD, McAlister E (1999) The measurement of soil fungal: bacterial biomass ratios as an indicator of ecosystem self-regulation in temperate meadow grasslands. Biology and Fertility of Soils 29: 282-290.

109. Li C, Fultz LM, Moore-Kucera J, Acosta-Martínez V, Kakarla M, Weindorf DC (2018) Soil microbial community restoration in Conservation Reserve Program semi-arid grasslands. Soil Biology and Biochemistry 118: 166-177.

110. Spohn M, Novák TJ, Incze J, Giani L (2016) Dynamics of soil carbon, nitrogen, and phosphorus in calcareous soils after land-use abandonment–A chronosequence study. Plant and soil 401: 185-196.

111. Morriën E, Hannula SE, Snoek LB, Helmsing NR, Zweers H, De Hollander M, Soto RL, Bouffaud M-L, Buée M, Dimmers W (2017) Soil networks become more connected and take up more carbon as nature restoration progresses. Nature communications 8: 1-10.

112. Clemmensen K, Bahr A, Ovaskainen O, Dahlberg A, Ekblad A, Wallander H, Stenlid J, Finlay R, Wardle D, Lindahl B (2013) Roots and associated fungi drive long-term carbon sequestration in boreal forest. Science 339: 1615-1618.

113. Bailey VL, Smith JL, Bolton Jr H (2002) Fungal-to-bacterial ratios in soils investigated for enhanced C sequestration. Soil Biology and Biochemistry 34: 997-1007.

114. Malik AA, Chowdhury S, Schlager V, Oliver A, Puissant J, Vazquez PG, Jehmlich N, Von Bergen M, Griffiths RI, Gleixner G (2016) Soil fungal: bacterial ratios are linked to altered carbon cycling. Frontiers in Microbiology 7: 1247.

115. Rapparini F, Peñuelas J (2014) Mycorrhizal fungi to alleviate drought stress on plant growthUse of microbes for the alleviation of soil stresses, volume 1. Springer, pp. 21-42

116. Wilson GW, Rice CW, Rillig MC, Springer A, Hartnett DC (2009) Soil aggregation and carbon sequestration are tightly correlated with the abundance of arbuscular mycorrhizal fungi: results from long-term field experiments. Ecology letters 12: 452-461.

117. Knops JM, Tilman D (2000) Dynamics of soil nitrogen and carbon accumulation for 61 years after agricultural abandonment. Ecology 81: 88-98.

118. McLauchlan KK, Hobbie SE, Post WM (2006) Conversion from agriculture to grassland builds soil organic matter on decadal timescales. Ecological applications 16: 143-153.

119. Harris J (2003) Measurements of the soil microbial community for estimating the success of restoration. European Journal of Soil Science 54: 801-808.

120. Martin LM, Moloney KA, Wilsey BJ (2005) An assessment of grassland restoration success using species diversity components. Journal of Applied Ecology: 327-336.

121. Polley HW, Derner JD, Wilsey BJ (2005) Patterns of plant species diversity in remnant and restored tallgrass prairies. Restoration Ecology 13: 480-487.

122. Middleton EL, Bever JD, Schultz PA (2010) The effect of restoration methods on the quality of the restoration and resistance to invasion by exotics. Restoration Ecology 18: 181-187.

123. De Deyn GB, Raaijmakers CE, Zoomer HR, Berg MP, de Ruiter PC, Verhoef HA, Bezemer TM, van der Putten WH (2003) Soil invertebrate fauna enhances grassland succession and diversity. Nature 422: 711-713.

124. Frouz J, Prach K, Pižl V, Háněl L, Starý J, Tajovský K, Materna J, Balik V, Kalčík J, Řehounková K (2008) Interactions between soil development, vegetation and soil fauna during spontaneous succession in post mining sites. European journal of soil biology 44: 109-121.

125. Knelman JE, Legg TM, O'Neill SP, Washenberger CL, González A, Cleveland CC, Nemergut DR (2012) Bacterial community structure and function change in association with colonizer plants during early primary succession in a glacier forefield. Soil Biology and Biochemistry 46: 172-180.

126. Kardol P, Martijn Bezemer T, Van Der Putten WH (2006) Temporal variation in plant–soil feedback controls succession. Ecology letters 9: 1080-1088.

127. Wubs E, Van Der Putten WH, Bosch M, Bezemer TM (2016) Soil inoculation steers restoration of terrestrial ecosystems. Nature plants 2: 1-5.

128. Gorka S, Dietrich M, Mayerhofer W, Gabriel R, Wiesenbauer J, Martin V, Zheng Q, Imai B, Prommer J, Weidinger M (2019) Rapid transfer of plant photosynthates to soil bacteria via

ectomycorrhizal hyphae and its interaction with nitrogen availability. Frontiers in microbiology 10: 168.

129. Kaiser C, Kilburn MR, Clode PL, Fuchslueger L, Koranda M, Cliff JB, Solaiman ZM, Murphy DV (2015) Exploring the transfer of recent plant photosynthates to soil microbes: mycorrhizal pathway vs direct root exudation. New Phytologist 205: 1537-1551.

130. Ehrenfeld JG (2003) Effects of exotic plant invasions on soil nutrient cycling processes. Ecosystems 6: 503-523.

131. Liao CZ, Luo YQ, Fang CM, Chen JK, Li B (2008) Litter pool sizes, decomposition, and nitrogen dynamics in Spartina alterniflora-invaded and native coastal marshlands of the Yangtze Estuary. Oecologia 156: 589-600.

132. Van der Putten W, Kowalchuk G, Brinkman E, Doodeman G, Van der Kaaij R, Kamp A, Menting F, Veenendaal E (2007) Soil feedback of exotic savanna grass relates to pathogen absence and mycorrhizal selectivity. Ecology 88: 978-988.

133. Koziol L, Schultz PA, House GL, Bauer JT, Middleton EL, Bever JD (2018) The plant microbiome and native plant restoration: the example of native mycorrhizal fungi. BioScience 68: 996-1006.

134. Meyer ST, Koch C, Weisser WW (2015) Towards a standardized rapid ecosystem function assessment (REFA). Trends in ecology & evolution 30: 390-397.

135. Kardol P, Wardle DA (2010) How understanding aboveground–belowground linkages can assist restoration ecology. Trends in ecology & evolution 25: 670-679.

Figures and Tables.

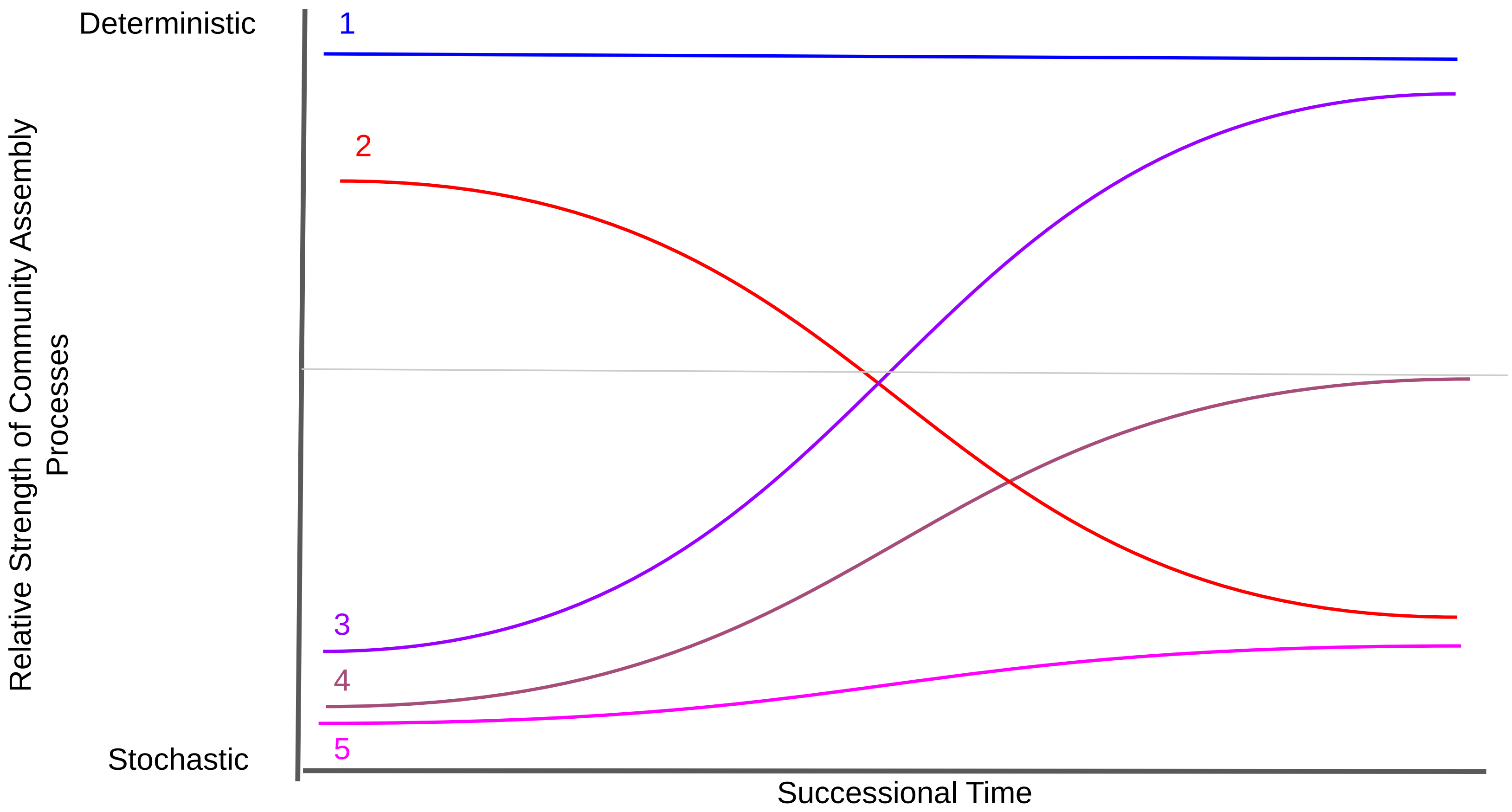

Figure 1. Example changes in community assembly through restoration. Placing management strategies in the context of community assembly can help to optimize restoration outcomes. The balance of assembly processes is denoted on the vertical axis, with the gray line denoting an equal balance of determinism and stochasticity. Scenario 1 (blue) represents a tightly regulated, low diversity system for targeted (but limited) functions, for example contaminant remediation. In scenario 2 (red), early colonizers in a deterministic set the stage for succession. Selection wanes as the ecosystem recovers and a more stochastic late-stage ecosystem supports diverse and multifunctional microorganisms. Scenario 3 hosts an initial community with a mix of diversity that progresses into a specialized community under increasing determinism. Likewise, scenario 4 begins with a similar community under high stochasticity but ends with an even balance of determinism and selection. Such a trajectory may optimize the balance between specialists and generalists for high rates of ecosystem functioning. Finally, scenario 5 represents the influence of priority effects in which early colonizers hold an advantage through succession. This may require targeted inoculations to change microbial communities.

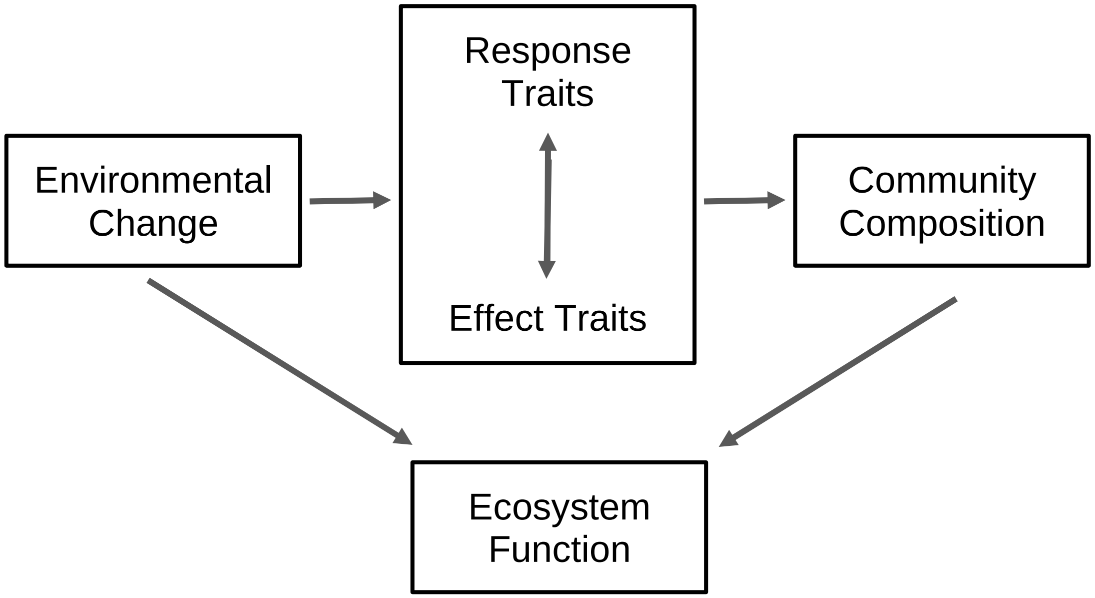

Figure 2. Relationships between environmental change, microbial traits, community composition, and ecosystem function. Changes in the environment impact the interplay between response and effect traits, which in turn influence microbial community composition. In turn, the environment and microbiome collectively determine ecosystem functions.

Box 1. Assembly-driven Considerations for Restoration Ecology.

Factors Influencing The Balance of Assembly Processes During Restoration

- Severity and Duration of Initial Disturbance
- Successional Stage
- Natural vs. Artificial Disturbance
- Strength of Environmental Pressures

Considerations for Restoration under Deterministic Microbial Assembly

- Environmental controls (pH, temperature, salinity, resource availability)
- Functional redundancy
- Niche Complementarity
- Response-effect trait linkages for traits of interest

Considerations for Restoration under Stochastic Microbial Assembly

- Metacommunity Composition
- Niche Breadth
- Priority and Mass/Sampling Effects
- Dispersal rate and/or limitations

Table 1. Common metrics of microbial community composition, relations to assembly processes and ecosystem function, and implications for restoration.

Genomics-enabled Variables	**Common Metrics**	**Assembly Process Implications**	**Ecosystem Function Implications**	**Restoration Implications**
Alpha Diversity	Shannon, Simpson, Chao1, Species Richness	• Elevated stochasticity (homogenizing dispersal) can lead to increased alpha diversity • The strength of selection (determinism) also influences alpha diversity, with strong selection in one direction generally leading to low alpha diversity	• High alpha diversity can lead to multifunctionality and/or low rates of a specific function through a dilution effect • Low alpha diversity may indicate specialized function or low rate of biogeochemical cycling	• Indicator of ecosystem health and multifunctionality
Beta and Gamma Diversity	Alpha Diversity Metrics plus Ordination Groupings, β-Dispersion	• Elevated stochasticity or determinism can lead to increased (dispersal limitation; variable selection) or decreased (homogenizing dispersal; homogeneous selection) beta- and gamma-diversity	• High beta and/or gamma diversity may bolster local biogeochemical functions through rescue effects • Comparative metrics can indicate changes in function across time or space	• Can be used to assess microbial trajectories through time and/or similarities to natural or restored ecosystems • Potential for enhancement of restoration through rescue effect
Community Composition	Species/trait (Relative) Abundances, Differential Expression and Gene Abundance	• Homogenizing dispersal or homogeneous selection can lead to more even species/trait distributions across communities	• Can be used as an assesment of genetic potential for a biogeochemical process of interest	• Can be used as early indicators of restorative success • Can be manipulated to support restoration outcomes
Response traits	Gene ratios, 16S rRNA gene copy number, Bacterial:fungal ratio; Resource Acquisition Traits; Resource Use Traits; Stress Tolerance Traits; Life History Traits	• The balance of assembly processes interacts with environmental conditions to determine the relative abundance of determine distributions of response traits	• Invoke and/or interact with effect traits that impact biogeochemical function	• Can denote successional stage and trajectory of community composition • Can be manipulated to support restoration outcomes
Effect traits	(Relative) Abundance of Specific Genes or Taxa related to Biogeochemical Processes	• The balance of assembly processes interacts with environmental conditions and response traits to determine the relative abundance of determine distributions of effect traits	• Under optimal environmental conditions, effect traits have a direct impact on function • Impact mediated by environment	• Can denote the trajectory of functional recovery through successional stages • Can be manipulated to support restoration outcomes
Stochasticity vs. Determinism	Neutral and Null Models, βNTI, RCbray	• Direct measurements indicating the balance of assembly processes	• The balance of assembly processes can reveal the nature of expected biodiversity-ecosystem function relationships	• Can denote successional stage and trajectories in composition and function • Can be manipulated to support restoration outcomes

Table 2. Examples of community assembly and management interventions.

Balance of Assembly Processes	Example Management Intervention	Reference
Deterministic Assembly; Strong response-effect trait linkage	Altering soil environment (homogeneous or variable selection)	Addition of a single nutrient drives poorly developed soil bacterial communities to resemble late succession community state (Knelman et. al, 2014)
Stochastic Assembly; Dispersal/Immigration limitation	Altering microbial immigration rates	Increases in immigration (soil addition) improves abundance of key microbes and removal of estrogens in wastewater treatment (Pholchan et al., 2013)
Stochastic x Deterministic Assembly: Priority Effects	Manipulating microbial colonization order	Inoculation order of phyllosphere with bacterial community members results in distinct end communities (Carlström et al. 2019)
Stochastic x Deterministic Assembly: Plant Microbe Interactions	Controlling presence/absence of specific microbes	Availability of ectomycorrhizal fungi (dispersal limitation) hinders success of exotic Pinaceae (Nuñez et al. 2009)

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