



**QUEEN'S
UNIVERSITY
BELFAST**

Interchange of entire communities: microbial community coalescence

Rillig, M. C., Antonovics, J., Caruso, T., Lehmann, A., Powell, J. R., Veresoglou, S. D., & Verbruggen, E. (2015). Interchange of entire communities: microbial community coalescence. *Trends in Ecology & Evolution*, 30(8), 470-476. <https://doi.org/doi:10.1016/j.tree.2015.06.004>

Published in:
Trends in Ecology & Evolution

Document Version:
Peer reviewed version

Queen's University Belfast - Research Portal:
[Link to publication record in Queen's University Belfast Research Portal](#)

Publisher rights

© 2015, Elsevier. Licensed under the Creative Commons Attribution -NonCommercial-NoDerivs License (<https://creativecommons.org/licenses/by-nc-nd/4.0/>), which permits distribution and reproduction for non-commercial purposes, provided the author and source are cited.

General rights

Copyright for the publications made accessible via the Queen's University Belfast Research Portal is retained by the author(s) and / or other copyright owners and it is a condition of accessing these publications that users recognise and abide by the legal requirements associated with these rights.

Take down policy

The Research Portal is Queen's institutional repository that provides access to Queen's research output. Every effort has been made to ensure that content in the Research Portal does not infringe any person's rights, or applicable UK laws. If you discover content in the Research Portal that you believe breaches copyright or violates any law, please contact openaccess@qub.ac.uk.

Open Access

This research has been made openly available by Queen's academics and its Open Research team. We would love to hear how access to this research benefits you. – Share your feedback with us: <http://go.qub.ac.uk/oa-feedback>

1 Opinion

2 **Interchange of entire communities: microbial community coalescence**

3 Matthias C. Rillig^{1,2*}, Janis Antonovics³, Tancredi Caruso⁴, Anika Lehmann^{1,2}, Jeff R. Powell⁵,
4 Stavros D. Veresoglou^{1,2}, Erik Verbruggen⁶

5 *¹Freie Universität Berlin, Institut für Biologie, Plant Ecology, D-14195 Berlin, Germany*

6 *²Berlin-Brandenburg Institute of Advanced Biodiversity Research (BBIB), D-14195 Berlin, Germany*

7 *³University of Virginia, Department of Biology, Charlottesville, Virginia VA 22904, USA*

8 *⁴School of Biological Sciences and Institute for Global Food Security, Queen's University of Belfast,*
9 *Belfast BT9 7BL, Northern Ireland, United Kingdom*

10 *⁵University of Western Sydney, Hawkesbury Institute for the Environment, Richmond, NSW,*
11 *Australia*

12 *⁶University of Antwerp, Department of Biology, PLECO, Universiteitsplein 1 - 2610 Wilrijk, Belgium*

13

14 * Corresponding author: Rillig, M.C. (matthias.rillig@fu-berlin.de)

15

16 **Keywords:** communities; mixing; community coalescence; metacommunity; environment;
17 networks; biodiversity; global change

18

Abstract

Microbial communities are enigmatically diverse. We propose a novel view of processes likely affecting microbial assemblages which could be viewed as the Great American Interchange *en miniature*: the wholesale exchange among microbial communities resulting from moving pieces of the environment containing entire assemblages. Incidental evidence for such ‘community coalescence’ is accumulating, but such processes are rarely studied, likely because of the absence of suitable terminology or a conceptual framework. We provide the nucleus for such a conceptual foundation for the study of community coalescence, examining factors shaping these events, links to bodies of ecological theory, and we suggest modeling approaches for understanding coalescent communities. We argue for the systematic study of community coalescence because of important functional and applied consequences.

Great American Interchange *en miniature*?

Alfred Russell Wallace [1] was perhaps one of the first to consider what would happen when previously separated communities meet – in his case at a very large spatial and temporal scale, in what has become known as the *Great American Interchange*: the linking of North and South America by the appearance of the Isthmus of Panama. The result of such wholesale migration, mixing and joining of communities was likely a multifold of establishments, species exchanges and extinctions, massive effects at any rate. What if community encounter events like these were not exceptional singularities, but were to occur quite frequently, at time scales relevant to understanding community structure? Here we develop the idea that events reminiscent of the

40 *Interchange* could be common in microbial systems, and with potentially even greater degrees
41 of mixing. We think this is the case because in nature, pieces of the environment much larger and
42 more persistent than an individual microbe, and indeed containing entire local microbial
43 communities, are routinely moved (see Figure 1 and Box 1). Forces that move pieces of the
44 environment containing entire microbial assemblages include gravity (falling leaves), animals
45 (e.g. burrows and casts), growth of macro-organisms (plant roots encountering each other in the
46 soil), wind (dust movement), flow in liquids (natural or industrial water bodies mixing, movement
47 inside the human body) or human activities (horticultural outplanting, ploughing or movement
48 of wood). We propose the term *community coalescence* (see Glossary) to describe such
49 community interchange events (Box 1).

50 While the literature is replete with studies on the effects and importance of many of the events
51 mentioned above (e.g. litter fall), these reports have rarely addressed the microbial community-
52 level interactions. The field of microbial biogeography (see Box 2) has long debated the degree
53 of dispersal limitation among micro-organisms, and is now also beginning to explore how
54 environment, spatial processes, and biotic context shape local communities. Community
55 coalescence events are part of the dispersal process, but also much more, because such events
56 result in whole communities and their environments interacting. Therefore, it is important to ask
57 how they influence the resulting community, and how these consequences can be linked to and
58 illuminated by existing ecological theory. What is the empirical evidence on community
59 coalescence thus far? How can the problem of entire communities interacting be approached
60 from a theoretical perspective? What are functional consequences of community coalescence?
61 These are the questions we address here with the goal of stimulating research on this topic;

community coalescence is likely to be important not only in the everyday events of microbial ecology, but also of increasing importance as the inter-connectedness of biological systems increases with global change.

Factors influencing community composition resulting from community coalescence

While a number of empirical studies (see Box 1) and modelling exercises [2, 3] have addressed aspects of what we call community coalescence, there has been no systematic study of such phenomena, and this might in part be due to a lack of an applicable conceptual framework for classifying these events, estimating their frequency, or predicting their consequences. We believe such separate conceptual development is necessary because the coalescence of communities has features quite distinct from those described in other bodies of theory, in particular the processes envisaged in metacommunity theory [4]: (i) Metacommunity theory is concerned with dispersal of individuals among local communities, and not with their wholesale interchange. Thus in metacommunity theory, dispersal rate depends on the probability that local communities (e.g. on islands) receive immigrants from the metacommunity (e.g. continent) while coalescence is the encounter of entire local communities (e.g. an island community is translocated to another island or to the continent). (ii) Community coalescence also allows for and includes the movement and potential mixing of environments, for example aquatic environments [5], and not just the movement of communities between environments. (iii) Communities that coalesce do not necessarily belong to a metacommunity in the sense of exchanging species at a low rate, and having their structure affected by such an exchange.

Coalescence also occurs when there is physical relocation of habitats and accompanying changes of the spatial structuring of the habitat. An example would be the encounter of the leaf microbial communities and the soil biota; these would not normally be considered part of the same metacommunity.

Community coalescence can occur in a number of ways (see Figure 2), and these interaction modes could be captured by different types of theory. Coalescence events might differ in the degree to which different environments are involved in the coalescence, including the creation of 'mixed' environments or entry into one environment, the relative size of the interacting communities (mixing ratios), the nature of the contact interface, and aspects of the temporal nature of the coalescence events. Certain situations could then be grouped according to these interaction modes in order to derive predictions for general rules; for example, in the kissing situation the donated community would be experiencing the largely unaltered environment of the recipient, the added community would be relatively small compared to the recipient community, the contact interface would be a surface, and the interaction would be pulsed with relatively short duration.

Some of these situations can be linked to existing bodies of ecological theory. For example, if one community is moved to the environmental setting of another, environmental filtering [6] would likely benefit the subset of species that already inhabited the recipient environment. In cases where one community is added to another, priority effects [7] will be important, likely leading to invasion-resistance of the recipient community. The number of individuals partaking in the community transfer will also be important for the outcome; when the transferred communities

include only a small subset of the component species, metacommunity theory [4] might become more applicable.

It is likely that coalescing microbial communities will also contain predators and parasites [8], such that the ecology of trophic interactions could be brought to bear on the problem. For example, given that many predators are generalists, consuming a wide range of prey, the lack of specific adaptations to predators could result in altered top-down control of the coalesced community than in either of the two original communities. Conversely, during the coalescence, specialist pathogens and consumers might suffer disproportionately, as the density of their hosts would decline.

Network theory and other approaches to model and analyze coalescent communities

With these modes of interaction in mind, coalescence might be usefully modelled by using network approaches. Interaction matrices describe the dynamics of every species as a function of the other species, and in binary form the interaction matrix depicts the topology of interactions, for example in a food web. In the context of community coalescence, we could describe the topology of two (or more) initially non-interacting (e.g. physically separated) admixed communities, and investigate the network topology resulting from coalescence. The advantage of employing network theory to coalescence is that there is already a body of theory pertaining to this situation in other areas of science [9, 10]. Quite independently Kramer *et al.* [11] have used the term coalescence in the context of semi-independent neuronal networks that under some circumstances start to interact. Synchronization of networks [9] is also potentially

relevant to coalescence: when communities start to coalesce, there can be a transient period during which they maintain their individual temporal patterns but eventually become synchronized, with potentially destabilizing effects at the system level [12]. The study of temporal fluctuations following a coalescence event can therefore yield key insights important for understanding the assembly and stabilization of the resultant community. A fascinating aspect of the study of temporal fluctuations in networks is that communities coming in contact with one another maintain some internal temporal coherence (i.e. network modules [13]), at least for some period of time. This coherence suggests that these communities interact as internally integrated units rather than just as a collection of many species that suddenly interact with another collection of species, resulting in a coalescent process where species replacement occurs within these newly interacting integrated units rather than a more stochastic rearrangement of interactions within the entire new network. This type of network dynamic is an emergent property of the whole network, which arises from the fact that components of local communities can in some cases act as whole units with strong interactions within these units and weak interactions between [14]. We suggest that studying temporal synchronization [9, 10] in coalescing microbial populations is an exciting multidisciplinary perspective with which to document and understand such processes.

More classical network metrics such as (whole-network) modularity, connectance and nestedness [15, 16] could also be used to describe networks in response to coalescence. Interestingly, in network science modules are also called ‘communities’ [13] and can be qualitatively defined as relatively dense subsets of vertices (i.e. species in our case) that are more tightly connected internally than with the rest of the network. The quantitative definition of

modules is not a trivial task (e.g. [13, 17]) but by equating two interacting modules with two coalescing communities, ecologists can exploit network tools to investigate coalescence in terms of changes in network community structure. Furthermore, this type of interaction is not explicitly considered in current ecological models describing community assembly from a metacommunity perspective, possibly because in the last few decades community ecologists have often adopted the implicit idea of communities as taxonomic assemblages or functional guilds at a given spatial and temporal scale. In other words, community boundaries are generally defined based on the unit that was sampled (whether an area or volume at a given time) as opposed to the interactions occurring among members of the sample or the sampled units themselves. Therefore, the identification of modules during the coalescent process and how these modules interact has the potential to enhance ecological understanding at a profound level.

In this framework, expectations derived from simulations of coalesced communities [18-20] could serve as null models for comparison of predicted with observed outcomes. Current work on ecological networks (e.g. classical food webs) typically uses effects of single invasions or species removals to derive estimates of how stable those networks are [16], but different results might be expected when entire networks meet. Using model microbial communities with a known network architecture would be one approach to test how the outcome of coalescence varies with interaction frequency, size of communities, and environmental context (see Figure 2 and Box 1).

Other tools might be helpful in characterizing the patterns emerging from coalescence as well. The study of null models and β -diversity can be particularly promising [21-23], because changes in β -diversity reflect the effects of immigration dynamics and biotic interactions.

However, the analysis of coalescent events presents new challenges that require the validation of existing approaches and the development of new ones. For example, community dissimilarity patterns across the landscape can provide insight into the extent that exchange between local communities occurs and can be conceptualized in a metacommunity framework, [24]. But a coalescence framework is needed to determine the degree to which admixing influences the structure and functioning of the communities. There might be *a priori* expectations based on the original admixing communities where these can be identified and sampled; alternatively, network analysis could allow accounting for their composition in an *a posteriori* fashion. Importantly, however, we anticipate that coalescent events would result in complex outcomes and that careful consideration will need to be given to whether existing common metrics or null models can be used off-the-shelf or not [25].

Potential consequences of coalescence for community-level functionality

So far we have considered which factors might influence what communities resulting from coalescence events might look like in terms of composition or network structure. However, it is quite likely that community coalescence can also have strong functional consequences. We see three main topics that should be the focus of future research: (i) degree of environmental mixing;

(ii) dependence of functional consequences on traits of microbial species; and (iii) evolutionary implications of coalescence (horizontal gene transfer and adaptations).

First, environmental mixing is explicitly included in the concept of community coalescence, and therefore drastic changes in the environment during coalescence, i.e. changes in resources, abiotic factors and biotic interactants, will also have to be considered. Some types of community coalescence will lead to more drastic environmental changes with pervasive functional consequences, such as the addition of communities to a new environment, with near-equal mixing ratios (Fig. 2). Examples here would be predominantly from aquatic systems. Conversely, environmental shifts will be least important for community coalescence events involving relatively small additions of one community to another, with merely surfaces touching, and the larger community remaining in its 'home' environment (like a quick kiss). Likely, any drastic resource changes (e.g. nutrients and carbon) and altered abiotic conditions (e.g. pH and temperature) will lead to species losses, for example by exceeding tolerances or via competitive exclusion, with concurrent losses of functional traits from the resulting community.

The second aspect to consider is the trait space occupied by the communities prior to and after coalescence (this is in part dependent on the discussion of environments above). Trait-based approaches are increasingly being applied to microbial systems [26-28]. If the input communities occupy quite dissimilar trait space from each other, and if these are partially maintained after coalescence, then one could expect the resulting community to occupy an even wider trait space than either of the original communities, likely also representing altered functionality [28], including potentially greater productivity. The converse could be expected if input communities

207 are quite similar in trait space: then members might merely substitute for each other in the
208 resulting community, not causing wholesale functional changes, with similar productivity.

209 The third point to consider are evolutionary implications of coalescence. Here we see two main
210 avenues for systematic study: horizontal gene transfer made possible by transient coexistence,
211 and adaptations to coalescence events.

212 Community coalescence could permit organisms from highly diverging habitats (e.g. river water
213 and soil) and with dissimilar traits to at least transiently coexist, especially with recurring events
214 (see Fig. 2). This co-occurrence can permit horizontal gene transfer between very dissimilar
215 organisms, an issue of considerable importance in trying to quantify, for example, the rates of
216 transfer of antibiotic resistance (e.g. [29]). As such these transient communities can be
217 'incubators' for rapidly-evolving species which exhibit different trait combinations, potentially
218 resulting in altered ecosystem functionality.

219 A second evolutionary question is whether frequent coalescence events in microbial
220 communities have brought about adaptations in member species, which in turn have functional
221 consequence at the community level. For example, many parasites have evolved life-cycle stages
222 in the gut of the host as well as in the soil, and the transfer of parasite stages between these
223 habitats occurs as a part of the coalescence of soil and gut communities (see Box 1). Another
224 example is the exchange of endophyte microbial communities cycling between leaves and the
225 soil. Do adaptations to coalescing communities occur in these and other microbial groups?
226 Predictions from evolutionary ecology on traits related to within- and between species
227 interactions are strongly contingent on levels of mixing (e.g. [30]): traits related to cooperative

or mutually beneficial behavior are favored by spatial structure, and conversely ‘selfish’ non-cooperative behaviors are favored in well-mixed systems. This is because this structuring determines which individuals and/ or species are likely to iteratively interact over a prolonged period of time, allowing cooperation to evolve. Given the propensity of positive interaction in structured populations and communities, cycles of isolation followed by re-encounters in the form of coalescence events might have a profound influence on the evolution of traits of the constituent species and individuals.

Applied relevance

Microbial communities have an exceptional applied significance in many different fields from medicine and biotechnology to environmental remediation and horticulture. It is likely that an explicit consideration and conceptual treatment of coalescence involving microbial communities inhabiting the human body, some of which are in intense exchange with the environment (including other humans), could lead to a better understanding of their function in public health [29, 31] and open new directions in biomedical research (e.g. gut microbiome interactions [32]); in fact, some of the most intriguing empirical examples of coalescence so far stem from this area of public health (see Box 1). Community coalescence could also be eminently applicable to industrial processes, such as waste water treatment. Can community coalescence be used to ‘engineer’ microbial consortia [33] better suited to tasks than single communities? In agriculture, the coalescence concept could help frame situations where substrates (e.g. biochar, manures, compost and even crop seeds carrying endophyte communities) are added to resident soil

microbial communities. In the context of global change and ever increasing connectedness of global ecosystems, this concept can be very useful in capturing properties and dynamics of novel communities and ecosystems [34]. But some of the most exciting potential applications are likely to be completely unforeseeable until systematic study of these processes has commenced.

Conclusion

Our paper argues for the dedicated study of microbial community coalescence, which we anticipate will address a set of new research questions (see Box 3). This will require a joint effort from multiple disciplines and the empirical study of microbial communities that meet, of their functional properties, as well as the development of models to simulate their dynamics and evolution. Through this effort the concept of community coalescence can help better understand the complexity of microbial assemblages and open avenues for the targeted manipulation of such assemblages for human use in industry, medicine or environmental protection. While the examples we have used are microbial in nature, we think that general insights derived from microbial ecology might also be useful for understanding equivalent processes at larger timescales in macro-organisms, especially given the context of ever increasing connectedness of global ecosystems.

267

268 **Glossary**

269 **β -diversity:** the variation in the identities of species among sites [21].

270 **Community coalescence:** a joining of previously separate communities (or even ecosystems),
271 forming a new entity that is not easily separable into parts again; this new entity has distinct
272 properties from the parts it unites. The term 'coalescence' is also used in population genetics,
273 but in a quite different context to indicate that homologous genes in different populations were
274 at some point of necessity identical by descent, i.e. their history coalesces, and the genealogy of
275 one gene is sometimes termed its 'coalescent'. This history is usually inferred from DNA sequence
276 data.

277 **Connectance:** in ecological networks, the fraction of possible interactions that are actually
278 realized.

279 **Community:** a general and broad term for any recognized assemblage of organisms containing
280 multiple species that interact with one another due to their physical proximity.

281 **Horizontal gene transfer:** transfer of genes among unrelated species; postulated to occur by
282 vectors such as viruses or insects, or by direct uptake of plasmids or environmental DNA.

283 **Metacommunity:** a collection of local communities linked by dispersal of their component
284 species. The concept is derived from that of the metapopulation, which is a collection of
285 populations of one species linked by dispersal of individuals. Metacommunity dynamics includes
286 ecological 'rescue' of locally 'unfit' species, patch-dynamics (appearance and disappearance of

287 habitat patches), extinctions and recolonizations from the regional species pool, and processes
288 such as neutral drift (analogous to genetic drift) and species sorting (analogous to fitness
289 differences).

290 **Nestedness:** in ecological networks, this measures the tendency for species with few links to
291 exclusively interact with species with many links.

292 **Network theory:** describes interactions between multiple entities, which in ecology are typically
293 species. Using network theory, communities can be described in terms of direct and indirect
294 interactions among species.

295

Box 1. Evidence of microbial community coalescence

Below we outline several previous studies that can be used to build a case that community coalescence occurs frequently and has important consequences.

Encounter and mixing of aquatic communities. - Souffreau *et al.* [35] and Adams *et al.* [36] present an experimental and observational investigation of bacterioplankton community interactions. In these studies communities encounter each other (e.g. river and lake) and are mixed in a partially new environment. Some of these encounters occur at very rapid rates, namely the flux rates of rivers, and at the level of entire assemblages. Livingston *et al.* [8] studied dynamics of aquatic communities which were experimentally mixed under controlled conditions; this study also explicitly included trophic interactions.

Interacting microbial communities in roots. - Mummey *et al.* [37] examined segments of roots growing in the immediate vicinity of roots of another plant species. The root-colonizing fungal communities were more similar to that of a heterospecific neighboring plant than the typical community of the species to which the root belonged. This was interpreted as propagules of one fungal community ‘overwhelming’ those of another. Hausmann and Hawkes [38] found similar effects in controlled pot experiments. Given that plant roots in communities typically intermingle, this coalescence of root-borne or rhizosphere microbial communities could be commonplace.

Microbial communities in the human body. - Qin *et al.* [39], using a metagenomic study of liver cirrhosis patients, found evidence for invasion of microbes from the mouth into the gut. A

possible reason was a change in bile production in patients with disease, which permitted invasion by bacteria from the oral microbiome. It thus seems that entire microbial communities, occurring 'in series' in the digestive system, interact in complex ways and whose coalescence is under metabolic or environmental control.

Transfer of oral microbial communities by kissing. - Kort *et al.* [40] studied the exchange of bacteria after intimate kisses, including both observational and experimental data. They found substantial community exchange, leading to similarities among partners in oral microbiomes. Using tracer bacteria, the authors calculated an average transfer rate of 80 million bacteria per few-second kiss.

328

329 **Box 2. Microbial biogeography**

330 In the past decade, there has been a resurgence of interest in microbial biogeography, and
331 researchers have started to explicitly test and conceptualize whether ‘biogeographical rules’ also
332 apply to microorganisms [41-44]. In this field, the major issue has been establishing the relative
333 roles of dispersal limitation and environmental filtering as two fundamental factors that can
334 shape microbial community turnover [45]. It has been argued that the potentially large dispersal
335 distance of microbes precludes the ‘existence of microbial biogeography’ [46]. There is
336 substantial variation among microbial taxa in dispersal capacity (e.g. [47, 48]), and this debate,
337 not surprisingly, has largely settled in favor of at least ‘some’ dispersal limitation shaping
338 biogeography of microbes [49]. This has focused attention on the fact that interactions among
339 microbes are likely potent causes of community variation and deserving of more attention (see
340 e.g. [43, 50]). The idea of community coalescence adds a further dimension to these discussions
341 because it considers how whole communities and their environments interact with each other
342 and how this impacts on the dynamics of its members.

343

344

345 **Box 3. Outstanding research questions**

346 Have repeated and continuous coalescence events contributed to the high microbial diversity in
347 some habitats, like the soil?

348 Do 'hybrid' communities exhibit a broader functional range and higher productivity compared to
349 communities entering a coalescence event?

350 Will members of communities with a history of coalescence have a higher persistence upon
351 interaction with a 'naïve' community?

352 Can better mechanistic understanding of community coalescence help predict community-level
353 migration and/ or mixing as a result of global change?

354 Can we predict properties of coalescent communities using approaches derived from the study
355 of interacting networks?

356 Have microbes evolved specific adaptations to survive or profit from repeated coalescence
357 events? What form do these adaptations take? Are alternative life-forms and complex life-cycles
358 involved? When would antagonistic vs. mutualistic interactions be favored?

359 Is it possible to identify groups of microbes, or microbial traits, that are characteristic of
360 coalescent events and can these be used as indicators of the coalescent history of a community?

361

Figure legends

Figure 1. Encounters of entire microbial communities occur in many microbial systems. Examples where such community coalescences are likely occur include (A, B) interaction of aquatic and terrestrial systems, such as during flooding, in riparian zones or near ponds; (C) interaction of communities inside the digestive system (e.g., oral and intestinal communities); (D) mixing of communities inhabiting different water bodies in e.g. human-made industrial systems; (E) various soil inputs, such as animal casts or leaves falling on the soil surface; (F) human-induced movements of material, such as in horticulture or tree outplanting; (G) direct or indirect contact between humans, such as two people kissing (also see Box 1). Photographs from MC Rillig (A, C, D, E, F) and Wikimedia Commons (B: Niklas Tschöpe, G: anonymous).

Figure 2. Illustration of some factors that are likely to influence the outcome of community coalescence. These factors include environmental conditions (entry of communities into new environment vs. adding one community to another), the mixing ratios (equal vs. unequal community proportions), the interaction interface (communities coalesce via surface touching vs. wholesale mixing) or the temporal dynamics of community coalescence events (intermittent pulses vs. regular exchange). General factors can be linked to existing bodies of ecological theory (see text).

References

- 1 Wallace, A.R. (1876) *The geographical distribution of animals. With a study of the relations of living and extinct faunas as elucidating the past changes of the Earth's surface.* Harper and Brothers.
- 2 Gilpin, M. (1994) Community-level competition - Asymmetrical dominance. *Proc. Nat. Acad. Sci. U.S.A.* 91: 3252-3254
- 3 Wright, C.K. (2008) Ecological community integration increases with added trophic complexity. *Ecol. Complex.* 5: 140-145
- 4 Leibold, M.A. *et al.* (2004) The metacommunity concept: a framework for multi-scale community ecology. *Ecol. Lett.* 7: 601-613
- 5 Bandelj, V. *et al.* (2012) Fuzziness and heterogeneity of benthic metacommunities in a complex transitional system. *Plos One* 7: e52395
- 6 Kraft, N.J.B. *et al.* (2014) Community assembly, coexistence and the environmental filtering metaphor. *Funct. Ecol.* DOI: 10.1111/1365-2435.12345
- 7 Tucker, C.M. and Fukami, T. (2014) Environmental variability counteracts priority effects to facilitate species coexistence: evidence from nectar microbes. *Proc. R. Soc. B* 281: 1-9
- 8 Livingston, G. *et al.* (2013) The dynamics of community assembly under sudden mixing in experimental microcosms. *Ecology* 94: 2898-2906
- 9 Arenas, A. *et al.* (2008) Synchronization in complex networks. *Phys. Rep.* 469: 93-153
- 10 Munoz, M.A. *et al.* (2010) Griffiths phases on complex networks. *Phys. Rev. Lett.* 105: 1-4
- 11 Kramer, M.A. *et al.* (2010) Coalescence and fragmentation of cortical networks during focal seizures. *J. Neurosci.* 30: 10076-10085
- 12 Loreau, M. (2010) Linking biodiversity and ecosystems: towards a unifying ecological theory. *Philos. T. R. Soc. B.* 365: 49-60

407 13 Girvan, M. and Newman, M.E.J. (2002) Community structure in social and biological networks.
408 *Proc. Nat. Acad. Sci. U.S.A.* 99: 7821-7826

409 14 Krause, A.E. *et al.* (2003) Compartments revealed in food-web structure. *Nature* 426: 282-285

410 15 Palla, G. *et al.* (2005) Uncovering the overlapping community structure of complex networks in
411 nature and society. *Nature* 435: 814-818

412 16 Pascual, M. and Dunne, J.A. (2006) *Ecological networks: Linking structure to dynamics in food*
413 *webs*. Oxford University Press.

414 17 Fortunato, S. (2010) Community detection in graphs. *Phys. Rep.* 486: 75-174

415 18 James, A. *et al.* (2012) Disentangling nestedness from models of ecological complexity. *Nature*
416 487: 227-230

417 19 Pires, M.M. and Guimaraes, P.R., Jr. (2013) Interaction intimacy organizes networks of
418 antagonistic interactions in different ways. *J. R. Soc. Interface* 10: 1-7

419 20 Thebault, E. and Fontaine, C. (2010) Stability of ecological communities and the architecture of
420 mutualistic and trophic networks. *Science* 329: 853-856

421 21 Anderson, M.J. *et al.* (2011) Navigating the multiple meanings of beta diversity: a roadmap for the
422 practicing ecologist. *Ecol. Lett.* 14: 19-28

423 22 Pigot, A.L. and Etienne, R.S. (2015) A new dynamic null model for phylogenetic community
424 structure. *Ecol. Lett.* 18: 153-163

425 23 Rosindell, J. *et al.* (2012) The case for ecological neutral theory. *Trends Ecol. Evol.* 27: 203-208

426 24 Maurer, B.A. *et al.* (2013) Estimating metacommunity extent using data on species abundances,
427 environmental variation, and phylogenetic relationships across geographic space. *Ecol. Inform.*
428 13: 114-122

429 25 Gotelli, N.J. (2000) Null model analysis of species co-occurrence patterns. *Ecology* 81: 2606-2621

430 26 Aguilar-Trigueros, C.A. *et al.* (2015) Branching out: Towards a trait-based understanding of fungal
431 ecology. *Fungal Biol. Rev.* DOI:10.1016/j.fbr.2015.03.001

432 27 Aguilar-Trigueros, C.A. *et al.* (2014) Ecological understanding of root-infecting fungi using trait-
433 based approaches. *Trends Plant Sci.* 19: 432-438

434 28 Krause, S. *et al.* (2014) Trait-based approaches for understanding microbial biodiversity and
435 ecosystem functioning. *Front. Microbiol.* 5: 1-10

436 29 Mkrtchyan, H.V. *et al.* (2013) Could public restrooms be an environment for bacterial resistomes?
437 *Plos One* 8: e54223

438 30 Lion, S. and van Baalen, M. (2008) Self-structuring in spatial evolutionary ecology. *Ecol. Lett.* 11:
439 277-295

440 31 Meadow, J.F. *et al.* (2014) Bacterial communities on classroom surfaces vary with human contact.
441 *Microbiome* 2: 1-7

442 32 Seedorf, H. *et al.* (2014) Bacteria from diverse habitats colonize and compete in the mouse gut.
443 *Cell* 159: 253-266

444 33 Shong, J. *et al.* (2012) Towards synthetic microbial consortia for bioprocessing. *Curr. Opin.*
445 *Biotechnol.* 23: 798-802

446 34 Hobbs, R.J. *et al.* (2009) Novel ecosystems: implications for conservation and restoration. *Trends*
447 *Ecol. Evol.* 24: 599-605

448 35 Souffreau, C. *et al.* (2014) An experimental analysis of species sorting and mass effects in
449 freshwater bacterioplankton. *Freshwat. Biol.* 59: 2081-2095

450 36 Adams, H.E. *et al.* (2014) Metacommunity dynamics of bacteria in an arctic lake: the impact of
451 species sorting and mass effects on bacterial production and biogeography. *Front. Microbiol.* 5: 1-
452 10

453 37 Mummey, D.L. *et al.* (2005) Neighboring plant influences on arbuscular mycorrhizal fungal
454 community composition as assessed by T-RFLP analysis. *Plant Soil* 271: 83-90

455 38 Hausmann, N.T. and Hawkes, C.V. (2009) Plant neighborhood control of arbuscular mycorrhizal
456 community composition. *New Phytol.* 183: 1188-1200

457 39 Qin, N. *et al.* (2014) Alterations of the human gut microbiome in liver cirrhosis. *Nature* 513: 59-64

458 40 Kort, R. *et al.* (2014) Shaping the oral microbiota through intimate kissing. *Microbiome* 2: 41-41

459 41 Bell, T. (2010) Experimental tests of the bacterial distance-decay relationship. *Isme J.* 4: 1357-1365

460 42 Green, J.L. *et al.* (2004) Spatial scaling of microbial eukaryote diversity. *Nature* 432: 747-750

461 43 Hanson, C.A. *et al.* (2012) Beyond biogeographic patterns: processes shaping the microbial
462 landscape. *Nat. Rev. Microbiol.* 10: 497-506

463 44 Martiny, J.B.H. *et al.* (2006) Microbial biogeography: putting microorganisms on the map. *Nat.*
464 *Rev. Microbiol.* 4: 102-112

465 45 Baas Becking, L.G.M. (1934) *Geobiologie of Inleiding tot de Milieukunde*. W. P. van Stockum &
466 Zoon.

467 46 Finlay, B.J. (2002) Global dispersal of free-living microbial eukaryote species. *Science* 296: 1061-
468 1063

469 47 Ingold, C.T. (1971) *Fungal spores. Their liberation and dispersal*. Clarendon Press.

470 48 Young, K.D. (2006) The selective value of bacterial shape. *Microbiol. Mol. Biol. Rev.* 70: 660-703

471 49 van der Gast, C.J. (2015) Microbial biogeography: The end of the ubiquitous dispersal hypothesis?
472 *Environ. Microbiol.* 17: 544-546

473 50 Dickie, I.A. *et al.* (2012) Do assembly history effects attenuate from species to ecosystem
474 properties? A field test with wood-inhabiting fungi. *Ecol. Lett.* 15: 133-141

475