

# Species-rich networks and eco-evolutionary synthesis at the metacommunity level

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**Understanding how ecological and evolutionary processes interdependently structure biosphere dynamics is a major challenge in the era of worldwide ecosystem degradation. However, our knowledge of ‘eco-evolutionary feedbacks’ depends largely on findings from simple systems representing limited spatial scales and involving few species. Here we review recent conceptual developments for the understanding of multispecies coevolutionary processes and then discuss how new lines of concepts and methods will accelerate the integration of ecology and evolutionary biology. To build a research workflow for integrating insights into spatiotemporal dynamics of species-rich systems, we focus on the roles of ‘metacommunity hub’ species, whose population size and/or genetic dynamics potentially control landscape- or regional-scale phenomena. As large amounts of network data are becoming available with high-throughput sequencing of various host-symbiont, prey-predator, and symbiont-symbiont interactions, we suggest it is now possible to develop bases for the integrated understanding and management of species-rich ecosystems.**

By his famous metaphor of an entangled bank, Darwin<sup>1</sup> developed a viewpoint of how natural selection imposed by interactions among species could organize the web of life. Despite the potential interdependence of ecological and evolutionary processes, the belief that ecological processes occur at much shorter time scales than evolutionary processes has long hampered an integrated understanding of the ecology and evolution of interspecific interactions<sup>2–4</sup>. This situation is changing rapidly as experimental and field studies have come to indicate how adaptive evolution, arising through intraspecific genetic variation and natural selection, can alter population dynamics of interacting species<sup>5–7</sup> and patterns observed at the community or ecosystem level<sup>8–10</sup>. As a consequence, an increasing number of ecologists and evolutionary biologists are examining the ubiquity of ‘eco-evolutionary’ feedbacks in biological communities<sup>11–14</sup>. The viewpoint of intermingled ecological and evolutionary dynamics is essential especially in systems involving microbial species because rapid evolutionary changes of bacteria, fungi, and protists are potentially controlling the structure and functions of both aquatic and terrestrial ecosystems<sup>15–19</sup>.

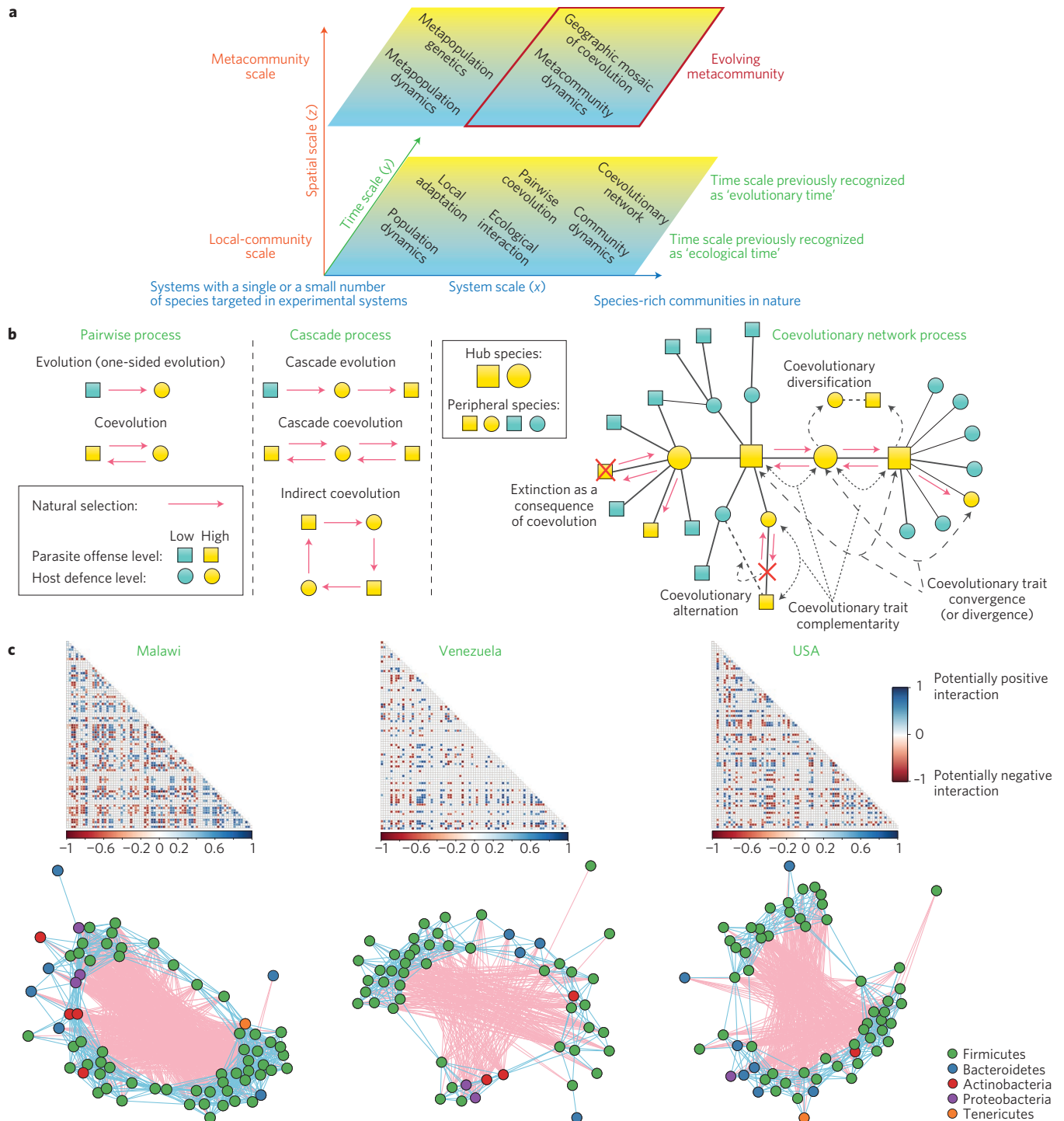
Although the concept of eco-evolutionary feedbacks has already contributed substantially to modern ecology<sup>2,4,12,14</sup>, we still lack a general framework for investigating eco-evolutionary dynamics in species-rich interaction networks. In addition, our understanding of eco-evolutionary feedbacks comes mostly from analyses of simple experimental systems and mathematical models depicting those species-poor systems with limited spatial scales<sup>5,20</sup>. Therefore, we remain ignorant of how eco-evolutionary dynamics can be important in (1) multispecies contexts and (2) spatial contexts<sup>18</sup> (Fig. 1a). An understanding of geographically structured processes of multi-specific interactions is fundamental both to community ecology and evolutionary biology<sup>21,22</sup>, but the two research disciplines have

developed mainly from different lines of empirical studies and theoretical backgrounds. The metacommunity concept in community ecology<sup>23–25</sup> and the ‘geographic mosaic’ concept in coevolutionary biology<sup>26,27</sup> share some key assumptions on interconnected dynamics of local communities through dispersal of individuals. However, most studies examine either an ecological or evolutionary aspect of spatial processes, although a small but growing number of studies simultaneously consider the ecology and coevolution of geographically structured interspecific interactions<sup>28,29</sup>.

Despite the potential importance of such an ‘evolving metacommunity’ viewpoint<sup>22,30</sup>, methodological constraints in evolutionary biology have precluded a comprehensive understanding of eco-evolutionary feedbacks in real metacommunities. Because evaluation of the strength of natural selection and the extent of microevolutionary response requires detailed information of intraspecific variation in both traits and fitness, it is often difficult to simultaneously investigate evolutionary processes shaping two or more species. Thus, even though community ecology has a long history of systematically analysing abundance and distribution of multispecific webs of interaction<sup>31,32</sup>, most empirical studies of evolutionary processes have targeted interactions involving only a few species<sup>27,33,34</sup> (but see refs<sup>28,29</sup>). The limitation in evolutionary biology led researchers to ‘community genetics’<sup>10,35</sup>, which provided a workflow of attributing community-level ecological properties to the evolutionary properties (genetic variation) of keystone species. However, finding and defining keystone species *per se* is often difficult when we try to investigate species-rich systems, especially those involving microorganisms.

In searching species whose ecological and/or evolutionary properties potentially influence whole-community dynamics, network theory<sup>36–38</sup> is expected to provide a standardized framework for

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**Figure 1 | Evolving metacommunities and species-rich networks.** **a**, Evolving metacommunity framework. The understanding that ecological and evolutionary processes can occur at the same time scale (y axis) has recently spurred eco-evolutionary feedback studies. The next challenge is to expand the concept along the axes of multispecies (x) and spatial (z) complexities. **b**, From studies of pairwise (co)evolutionary interactions to those of coevolutionary networks. Every pairwise evolutionary interaction (left) is embedded in cascade evolutionary processes (middle), ultimately forming coevolutionary networks (right). Host-parasite arms-race coevolution, for example, may result in the reduction of parasite mean fitness due to elevated host defence, causing the extinction or host shift (coevolutionary alternation<sup>27</sup>) of the parasite species. Arms races may also promote coevolutionary diversification through escape and radiation processes. The traits of coevolving species are expected to match each other within the network (complementarity<sup>27,44</sup>). Moreover, the traits of species on the same guild or trophic level can undergo convergent evolution through cascade evolutionary/coevolutionary events (convergence<sup>27,44</sup>). **c**, Inferring interaction networks based on high-throughput sequencing. For each gut microbial community dataset of human populations in Malawi, Venezuela, and USA<sup>100</sup>, potentially positive (blue) and negative (red) interactions between bacteria were inferred based on a latent variable model<sup>99</sup>. In the statistical model, the effects of the age and body mass index of host individuals were included as covariates to control correlated environmental responses among bacteria. To reduce computational time in the preliminary analysis, 40 human individuals were randomly chosen in each country: 80 most abundant bacterial operational taxonomic units (OTUs) were analysed in each dataset (Supplementary Methods).

**Box 1 | High-throughput sequencing for interaction network analyses.**

In examining communities involving tens or hundreds of species, DNA barcoding based on next-generation sequencing allows high-throughput analysis of network architecture in various types of interspecific interactions. DNA barcoding, a way of taxonomic identification of specimens based on DNA sequence information, has been used to promote the studies of prey–predator and host–symbiont associations<sup>55,75</sup>. Those studies have targeted prey DNA in predator gut contents or symbiont DNA in host tissue, enhancing our knowledge of interspecific associations that are impossible or difficult to observe by eye. Owing to recent advances in sequencing and bioinformatic technologies, we are now able to analyse hundreds of predator gut or host tissue samples in a single run of a next-generation sequencer<sup>51,52</sup> (Fig. 2a). Therefore, obtaining large datasets of victim–consumer, host–symbiont, or symbiont–symbiont associations is becoming increasingly easy in a wide range of biological communities<sup>51–54</sup>.

Although high-throughput DNA sequencing data do not provide any direct evidence of antagonistic or mutualistic interactions<sup>75</sup>, recently developed statistical frameworks help us infer

mutualistic and antagonistic interactions between species solely based on community datasets. In human gut microbiome studies, for example, potential ecological interactions between bacterial symbionts have been estimated using ‘co-occurrence’ patterns found in the high-throughput sequencing datasets of microbial communities<sup>53,54</sup>. Although pairs of species highlighted in these studies can include those merely sharing environmental preferences or niches, a recently proposed statistical procedure<sup>99</sup> allows us to separate interspecific interaction effects from niche sharing effects. Using the new Bayesian statistical method, we can control shared niche effects in a model, estimating potential interspecific interaction effects<sup>99</sup>. Our preliminary application of this method to human gut microbiome data<sup>100</sup> (Supplementary Methods) suggested that this statistical approach could be used for reconstructing networks of mutualistic and antagonistic interactions based on high-throughput sequencing datasets (Fig. 1c). Thus, ongoing advances in both molecular ecological and statistical methods are reorganizing the workflow of empirical studies that target complex webs of interactions in species-rich assemblages.

analysing various types of species-rich assemblages even without *a priori* information of the natural history of constituent species. Network science, in general, helps us understand the ways in which interactions between agents (for example, molecules, websites, human individuals, or species) organize the structure and dynamics of complex systems<sup>36–38</sup>. Since its application to community ecology<sup>37,39,40</sup>, network theory has made it clear that an understanding of the topology (architecture) of interaction networks is essential for scaling-up the effects of each species or pairwise interaction to community-level processes and consequences<sup>41,42</sup> (Fig. 1b,c; Box 1). Such studies have also proposed that a small proportion of topological ‘hub’ species in a network, considerably affect whole community properties such as resilience and tolerance to species extinctions<sup>40,43</sup>. Those discussions extend the notion that a small number of species at key topological positions organize community-level processes<sup>32</sup>, leading to the hypothesis that community-scale eco-evolutionary feedbacks are also driven, in large part, by those hub species.

Once a common framework for analysing both ecological networks and ‘coevolutionary networks’<sup>27,39,44</sup> (Fig. 1b) is established, we will be able to take the next steps and investigate how eco-evolutionary feedbacks are organized by ‘metacommunity hub’ species at the landscape or regional level. Metacommunity hub predators (or higher-order mobile consumers) moving across local communities are expected to connect different ‘energy channels’<sup>45</sup> within a metacommunity, thereby stabilizing or destabilizing large spatial-scale processes (see ref. <sup>46</sup>). Likewise, metacommunity hub parasites may synchronize and restructure coevolutionary processes of local communities<sup>47,48</sup>, thereby controlling the overall pace of host–parasite coevolution in the metacommunity<sup>49,50</sup>. Therefore, it remains a major challenge to investigate how those hub species serve as major pathways of eco-evolutionary feedbacks at the metacommunity level.

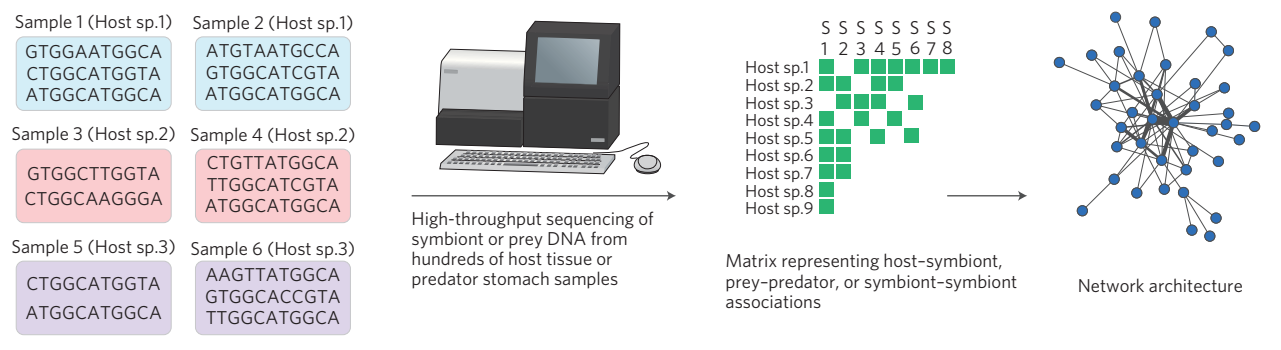
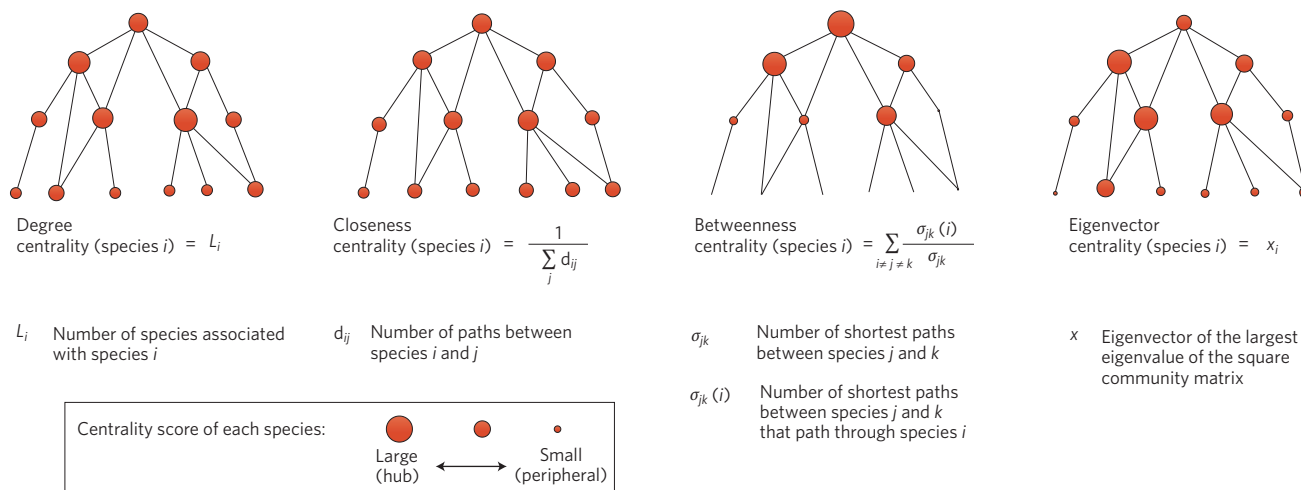
In this Perspective, we briefly review recent conceptual developments for the understanding of spatially structured ecological and/or coevolutionary processes, and we then discuss how empirical research based on species-rich network data will accelerate the synthesis of ecology and evolutionary biology at the metacommunity level. As large datasets of communities and interspecific associations are becoming available through high-throughput DNA sequencing<sup>51–56</sup> (Fig. 2a), we are now able to gain *a priori* insights into the network architecture and topological hubs of species-rich metacommunities before we design empirical research on eco-evolutionary feedbacks. By showing an example of workflow for

pinpointing topological hub species within a hyper-species-rich metacommunity-scale network involving microorganisms, we argue that the concept of coevolutionary network dynamics<sup>44</sup> helps us extend eco-evolutionary feedback studies from simple experimental systems to complex multispecific metacommunities in the wild (for example, multihost–multiparasite metacommunities<sup>19</sup>). Overall, we suggest how to integrate community ecological and coevolutionary insights by focusing on network hub species, which potentially have great impacts on landscape-, regional-, or global-scale ecosystem processes through eco-evolutionary feedbacks.

**Species-rich networks and spatial structure**

To promote studies of eco-evolutionary feedbacks in natural metacommunities beyond current limitations in eco-evolutionary syntheses (Box 2, step 0), we first emphasize the importance of expanding the scale of empirical investigations of evolutionary biology to that of community ecology in multispecific contexts (Box 1). In recent years, the conventional dichotomy between strict pairwise coevolution (that is, reciprocal adaptation in a pair of species) and ‘diffuse coevolution’<sup>34</sup> (that is, mostly non-reciprocal evolutionary interactions in a group of species) has been supplanted by more specific hypotheses on coevolutionary networks involving multiple species<sup>27,39</sup>. In addition, recent theoretical studies have modelled both pairwise and cascading evolutionary or coevolutionary events, predicting coevolutionary processes of species-rich assemblages within network theoretical frameworks<sup>44,57</sup>. Thus, in principle, every one-sided or reciprocal adaptation process is embedded within an entire web of interactions (that is, a coevolutionary network; Fig. 1b), and each interaction is seldom free from the influence of the evolutionary processes of adjacent interactions<sup>33,39,44</sup>.

The next step is then to consider how eco-evolutionary community processes are structured geographically. Community ecological studies have shown that stochastic and deterministic factors, such as priority effects<sup>58</sup> and phylogenetic clustering and overdispersion in community assembly<sup>59,60</sup>, can differentiate local species compositions, thereby causing geographic variation in interaction network architecture<sup>61</sup>. Spatial exchange of individuals can further reorganize local community dynamics, continuously restructuring evolving metacommunities. Dispersal of individuals among local communities, for example, may prevent local extinctions and alter local species compositions, controlling species diversity patterns at the metacommunity level (that is,  $\beta$ - and  $\gamma$ -diversity)<sup>23,24</sup>.

**a** Network analysis based on high-throughput sequencing data of interspecific associations**b** Scoring species with network centrality metrics

**Figure 2 | Flow of high-throughput sequencing and network analysis.** **a**, High-throughput sequencing analysis of host-symbiont, prey-predator, or symbiont-symbiont associations. **b**, Scoring species based on network centrality metrics. Degree centrality: the number of links (associated species) of a focal species in a network. Closeness centrality: a centrality metric measured based on the shortest path lengths between a focal species and all other species in a network. Betweenness centrality: the extent to which a given species is located within the shortest paths connecting pairs of other species in a network. Eigenvector centrality: an index of network centrality calculated based on the greatest eigenvalue of a community matrix. The size of a circle represents each species' centrality score.

Because community-scale outcomes of both ecological and evolutionary processes can depend on interaction network architecture<sup>44,62</sup>, evolving metacommunity processes can be also structured by geographic variation in network structure<sup>61</sup>. Due to 'G × G × E' effects<sup>27</sup> (genotype by genotype by environment) on the outcomes of interspecific interactions, both spatial genetic variation of interacting species and local environmental conditions can generate geographic variation in the direction and strength of natural selection on the traits mediating interspecific interactions<sup>28,63,64</sup>. Such geographic selection mosaics<sup>27</sup> then create geographically structured processes of host/prey defence and parasite/predator offense<sup>28,47,63</sup>, resulting in differences among local communities in network topology (Fig. 1b). Spatially structured coevolutionary processes, then, further restructure metacommunity-scale eco-evolutionary feedbacks<sup>27</sup>. Inflow of alleles selected in other local communities as well as hybridization and polyploidization<sup>33,35</sup> can provide novel genetic variation of coevolving traits in local communities, accelerating the rate of coevolution in recipient communities<sup>49</sup> (see ref. <sup>65</sup>). However, high levels of gene flow may overwhelm locally-selected alleles and hence perturb local reciprocal adaptation between interacting species (see ref. <sup>66</sup>), resulting in the mismatch of coevolving traits<sup>27</sup> (for example, local mismatches between host-symbiont compatibility alleles).

Thus, ecological processes controlling local species composition and (co)evolutionary processes organizing network topologies both generate the geographic differences in interaction network structure<sup>61</sup>. These processes, in turn, shape the ecological and coevolutionary processes at the metacommunity level. In this sense, ecological and coevolutionary processes are inevitably intermingled with each other at the metacommunity level through the causes and consequences of geographic variation in interaction network structure<sup>21,22,27</sup>. This perspective illuminates the importance of empirical studies that analyse geographic variation in network architecture<sup>61</sup> by focusing on spatial heterogeneity in environmental factors and ecological and evolutionary processes as well as G × G × E effects in interspecific interactions<sup>27,67</sup>.

### Metacommunity hubs

Through geographically structured eco-evolutionary feedbacks, different trophic levels (or guilds) can contribute differentially to metacommunity structure and dynamics. Webs of interspecific interactions often consist of species from at least two trophic levels that differ in the spatial scale of dispersal<sup>68</sup>. For example, many vertebrate and invertebrate predator species move across local prey communities, and bacterial (fungal) parasites in aquatic (terrestrial) ecosystems often have broader dispersal ranges than their



macroorganismal hosts<sup>15,69,70</sup>. Such asymmetry in dispersal abilities causes differences in the ranges of gene flow, thereby differentiating the spatial scales of local adaptation between interacting trophic levels<sup>48,70,71</sup>. In interactions between the pathogenic fungal species *Melampsora lini* and its host plant *Linum marginale*, for instance, pathogens potentially have a coevolutionary advantage over hosts, because the long-range dispersal of their spores provides local populations with novel virulence alleles<sup>48,50</sup>.

Effects to regional-level ecological and coevolutionary processes can vary not only between but also within trophic levels. Metacommunity-level foundation (or keystone) predators, for instance, may control local prey species compositions and enhance regional ecological stability<sup>72</sup> by preventing the outbreaks of competitively superior prey species in each local community (that is, apparent competition<sup>73</sup> at the metacommunity level). In addition, a few pathogenic species with broad dispersal ranges may spatially homogenize the level of virulence in multispecific pathogen–host interactions (see ref. <sup>49</sup>), potentially causing metacommunity-scale convergence of host resistance traits even without hosts' dispersal.

Overall, geographically differentiated processes of eco-evolutionary feedbacks could be continuously restructured by a small number of species that synchronize and restructure ecological and coevolutionary dynamics among local communities (Box 2, step 1). This proposition leads to the expectation that major pathways in evolving metacommunity processes derive from interactions driven by hub species within a 'metacommunity-level network'. Hereafter, we use the term metacommunity hubs to refer to species placed at key topological positions in networks at the metacommunity level. In this paper, network hubs are defined solely based on network topological data (Fig. 2b) in order to develop general research workflows for species-rich metacommunities without detailed natural history information of constituent species. This research strategy is crucial when we study species-rich microbial systems, for which detailed data of population size and geographic distribution are unavailable for most species.

Hereafter, we propose an empirical research workflow for investigating evolving metacommunity processes based on the promise that metacommunity hub species function as major pathways of feedbacks between ecological and coevolutionary dynamics. This reductionistic approach of attributing metacommunity-scale phenomena to the properties of a few species is similar to community genetics<sup>8,10</sup>, in which researchers investigate how variation in genes and traits of keystone, foundation, or dominant species control patterns at the community level. However, our empirical research framework is designed to examine not only the effects of the genetic structure of metacommunity hubs on metacommunity ecological processes (hereafter, 'metacommunity genetics') but also the relationships between ecological and genetic properties of metacommunity hubs and metacommunity-scale ecological and evolutionary processes as detailed below.

The bases of our research framework are summarized by two working hypotheses (Box 2, step 2). First, we posit that the structure of metacommunity-scale networks, which consist of interaction networks of multiple local communities, determines the outcomes of both ecological and coevolutionary processes as well as feedbacks between them. Second, we hypothesize that metacommunity hub species, which are placed at key topological positions within the metacommunity-level network, play major roles in synchronizing and restructuring eco-evolutionary dynamics at the regional or landscape level.

### Network analyses of metacommunity hubs

To fuel future empirical studies testing the hypotheses (Box 2, step 2), we illustrate a way for inferring the architecture of metacommunity-level networks and then finding topological hub species within the networks. Large community datasets are becoming easily

### Box 2 | Steps toward the understanding of eco-evolutionary feedbacks in natural metacommunities.

We propose the following steps toward the development of empirical research frameworks for future evolving metacommunity studies:

#### Step 0: Understanding current limitations

Although studies of simple experimental systems are rapidly reorganizing our knowledge of eco-evolutionary feedbacks, it remains difficult to investigate the interplay of ecological and coevolutionary processes in species-rich communities and metacommunities in the wild.

Although community (and metacommunity) genetics offers a basis for attributing ecological phenomena to the evolutionary processes of a few keystone or dominant species, finding keystone/dominant species within complex communities and metacommunities is, in itself, often difficult.

The number of species examined in coevolutionary studies is far less than that in community ecological studies, because measuring natural selection strength, response to selection, and/or population genetic structure often requires substantial research efforts even in an analysis of a pairwise interspecific interaction.

#### Step 1: Synthesizing current insights

Top predators, dominant primary producers, and super-generalist mutualists are often network hubs and they can drive whole-community ecological and evolutionary dynamics.

Species with broad ranges can synchronize or restructure metacommunity-level processes by interlinking local communities through dispersal and gene flow.

#### Step 2: Working hypotheses

Species in local communities are involved in a metacommunity-level interaction (association) network, whose topology determines the consequences of both ecological and coevolutionary processes and feedbacks between them.

Species placed at key topological positions in a metacommunity-level network play major roles in structuring eco-evolutionary dynamics at the regional or landscape level.

#### Step 3: Specific issues on evolving metacommunities

(i) Do allele frequency changes of a functionally important gene of a metacommunity hub species explain the population dynamics of other hub species across metacommunities? (ii) Do temporal changes in the  $F_{ST}$  of a hub species' functional gene drive the dynamics of the  $\beta$ -diversity of a focal metacommunity? (iii) Do abiotic environmental fluctuations drive the metatranscriptomic dynamics of local communities; (iv) thereby changing the architecture of local- and metacommunity-level interaction networks? What kinds of ecological and evolutionary characteristics (for example,  $\gamma$ -diversity, network nestedness<sup>37</sup> or modularity<sup>43</sup>, and coevolutionary rates at the metacommunity level) determine the robustness of metacommunities against invading species? (Roman numerals are linked to Fig. 4b).

available through next-generation sequencing, which allows high-throughput DNA-barcoding of prey–predator, host–parasite, host–symbiont, and symbiont–symbiont associations<sup>51–56</sup> (Fig. 2a). These methodological advances not only allow webs of interaction to be analysed more comprehensively (Fig. 1c) but also expand the target of network science to various types of interactions, which have been difficult to examine with conventional methods (for example, direct field observations). Moreover, such DNA-based analysis also

extends research platforms for classic study systems such as plant–pollinator interactions by identifying, for example, visitors to flowers based on bacterial community compositions specific to respective pollinator species<sup>74</sup>. Standardized protocols for high-throughput sequencing and subsequent bioinformatic procedures are making network topological analysis increasingly easy<sup>75,76</sup>, providing novel opportunities for investigating geographically hierarchical processes of multispecific eco-evolutionary feedbacks.

Imagine a situation in which a researcher has data on the network architecture of multiple local communities through high-throughput sequencing<sup>75–77</sup> (Fig. 3a). If the data include species that occur in two or more local communities between which they migrate, the local network topologies would be interlinked with each other by the presence of the shared species (Fig. 3b). Those species found in multiple local communities possibly constitute a metapopulation<sup>78</sup> within the examined region or landscape, potentially synchronizing or restructuring local processes and thereby continuously reshaping an evolving metacommunity<sup>48,71</sup>. In contrast, species unique to a single local community are unlikely to contribute directly to the synchronization of local ecological or coevolutionary processes, even if they play major roles within the local community.

Within the metacommunity-level network presented in Fig. 3b, species are expected to differ in their ability to synchronize or restructure ecological and coevolutionary processes among local communities. One straightforward way of evaluating topological properties of each species is to use network ‘centrality’ metrics (Fig. 2b). An important benefit of using simple network metrics is that both local- and metacommunity-level topological roles of each species can be evaluated solely based on network topological data. Conceptually, species in a metacommunity probably vary not only in their roles in interconnecting local community processes but also in their contributions to ecological and evolutionary phenomena within each local community. Therefore, by applying centrality analyses in parallel with a metacommunity-level network and to each local network, one can evaluate both regional and local topological properties of each species within a metacommunity-level network (Fig. 3c). Although this network-based approach does not provide any direct evidence of antagonistic or mutualistic interactions (see Box 1 and Fig. 1c), it can help pinpoint which species are probable focal points (hubs) for metacommunity structure and dynamics.

When metacommunity-level centrality scores are plotted against the centrality scores calculated within one of local communities (Fig. 3c), we can classify species into four categories on a two-dimensional surface; that is, (1) metacommunity hubs placed at the cores of both local- and metacommunity-level networks, (2) metacommunity connectors that may play major regional roles despite their minor local contributions, (3) local hubs whose topological influence is strong but confined to local processes, and (4) peripherals playing minor topological roles both locally and regionally.

Our example of two-dimensional centrality analysis implies that species potentially organizing local ecological and evolutionary processes as network hubs do not necessarily play important roles at the metacommunity level. Specifically, in the case of the belowground plant–fungus metacommunity network shown in Fig. 3 (Supplementary Methods), many possibly endophytic fungi showed statistical properties representing disproportionately large topological roles at the metacommunity level relative to their local topological roles (Fig. 3c). Considering that ecological and physiological roles of endophytic fungi have been far less understood than those of arbuscular mycorrhizal and ectomycorrhizal fungi, the metacommunity-hub methodological workflow helps us find potential ‘hidden’ keystone or foundation<sup>79</sup> species of metacommunity-scale dynamics out of many species with unknown natural history (see ref.<sup>54</sup>). Given that plants may use common genetic mechanisms for symbioses with diverse root-associated fungi and bacteria<sup>80</sup>, the population genetic structure of metacommunity-hub endophytes

may control the overall pace of host–symbiont coevolution at the metacommunity-level, determining the resistance and susceptibility of local- and metacommunities to invading pathogens or pests. Overall, the metacommunity-hub methodological framework allows us to take into account the complexity of real metacommunities beyond our current knowledge of keystone and foundation species, setting novel standards and opportunities for deepening our understanding of eco-evolutionary feedbacks in the wild.

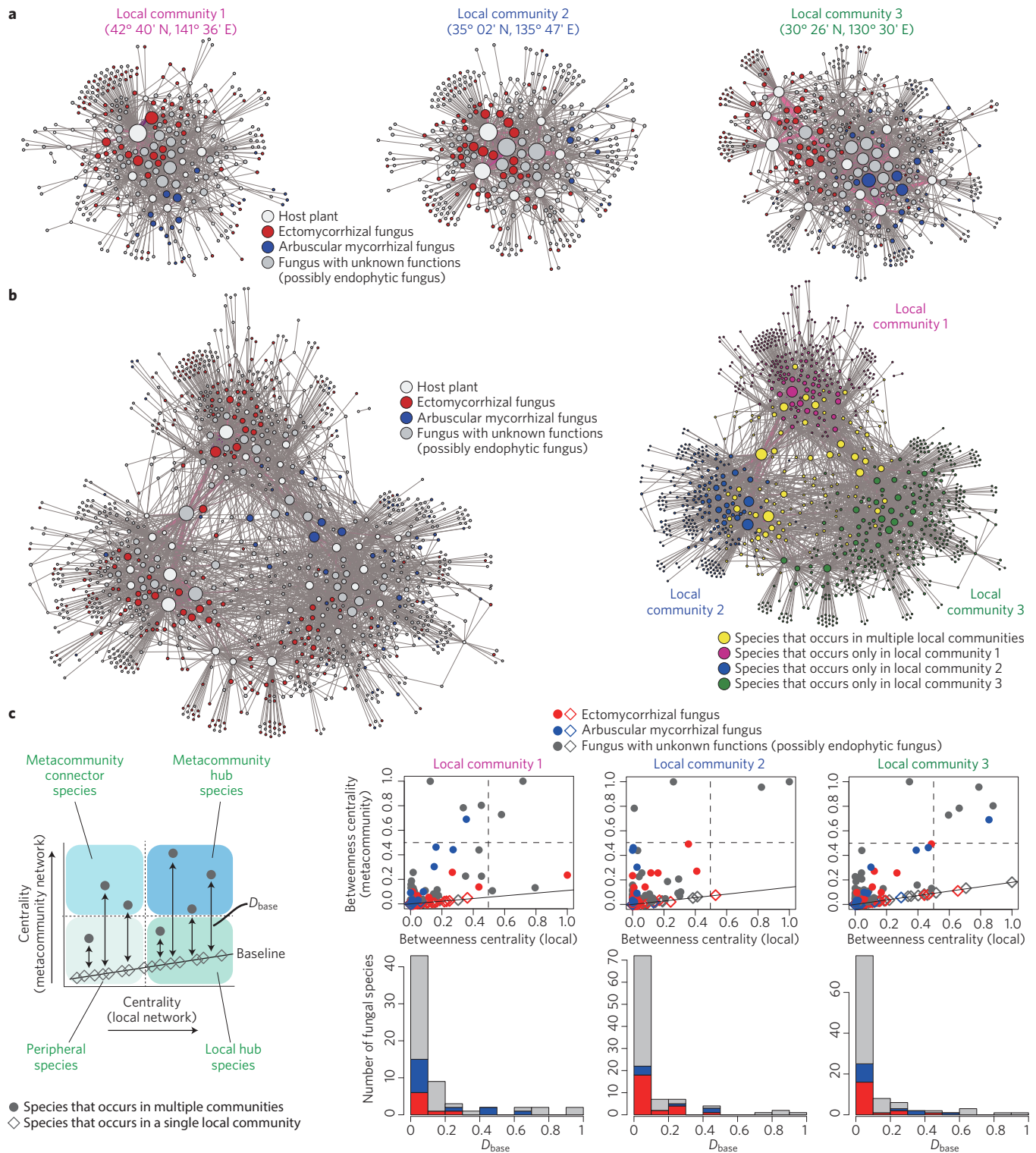
### Spatiotemporal eco-evolutionary dynamics

Once metacommunity hub (and connector) species are detected in network data, we will be able to analyse how those hubs work as interfaces between ecological and coevolutionary processes at the metacommunity level (Box 2, step 3; Fig. 4). In other words, by focusing on a small number of hub species out of hundreds of species in a metacommunity, we can infer how population dynamics and/or population genetic dynamics of hub species contribute to metacommunity-scale temporal dynamics. Recent advances in time-series data analysis<sup>81–84</sup> have the potential to aid these analyses. These methods have been used to estimate interspecific interactions based on population dynamics data of potentially interacting species (for example, time-series abundance data of prey and predators<sup>81,82</sup>), but they can also be used for inferring relationships between various biotic and abiotic variables<sup>81</sup>. Therefore, by using time-series analytical frameworks, it is possible to examine, for example, how the allele frequency of a functionally important trait of a hub species in a local community can drive population dynamics of other hub species in other local communities, and vice versa (Fig. 4b; Box 2, step 3).

Because microorganisms (for example, bacteria and fungi) generally have small genome sizes, draft whole-genome sequencing can be easily conducted for hub microbial species in various types of networks. Once such reference-genome data of hub species become available, single-nucleotide-polymorphism (SNP) variation of numerous genetic loci will be monitored for the target hub species based on (non-amplicon) metagenomic sequencing. Coevolutionary interactions in a pair of hub species can be then inferred by screening for pairs of functional genes showing interdependent SNP dynamics through time. We will also be able to examine how temporal variation in ecological interaction states (for example, infection rates) depend not only on temporal patterns in inferred coevolutionary traits and genes but also on changes in local abiotic environments, thereby detecting  $G \times E$  effects in the wild. Temporal genetic analysis also has the potential to reveal synchronization of intraspecific genetic variation between a pair of local communities, setting a basis for evaluating how gene flow contributes to metacommunity-scale processes. For example, we should be able to infer whether inter-population SNP variation of a focal hub species drives the temporal changes in the network structural properties or  $\beta$ -diversity<sup>85</sup> of a metacommunity (Fig. 4b; Box 2, step 3).

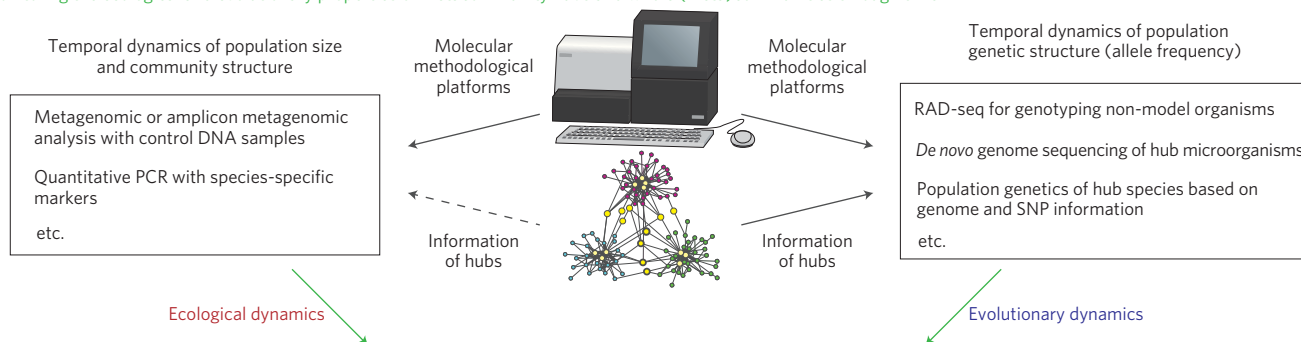
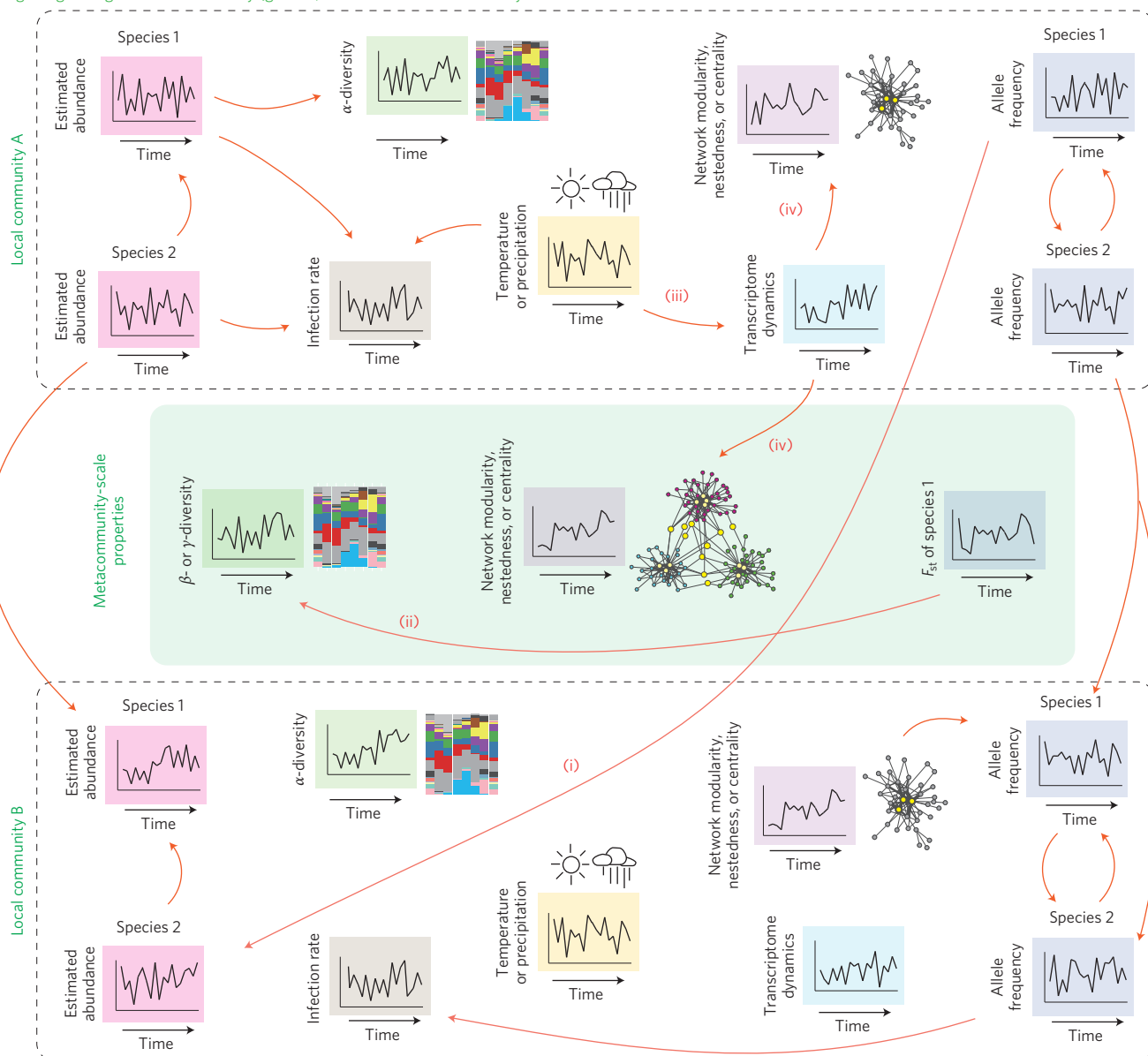
The benefits of those genetic profiling techniques would be doubled by combining them with emerging molecular ecological protocols that allow high-throughput analyses of community structure and transcriptomic dynamics. ‘Control DNA’<sup>86</sup> techniques, for example, can calibrate DNA concentrations over multiple (time-series) samples, thereby monitoring temporal changes in the abundance of each species in a community or metacommunity. Furthermore, as time-series modelling of transcriptomic profiles in wild conditions (that is, field transcriptomics) has become more common<sup>87</sup>, it will become possible to link the abiotic environmental dependence of metatranscriptomic dynamics with temporal changes in local- and metacommunity-level network architecture (Fig. 4; Box 2, step 3).

The combination of methods we have suggested here has limitations as well as benefits. For example, when analysing species-rich data, *a priori* information of network hub species helps us focus



**Figure 3 | Local community- and metacommunity-level networks.** **a**, Networks representing the associations of plants and their root-associated fungi in three forests across Japan<sup>95</sup>. Thicker links (highlighted in pink) between the circles indicate plant-fungal associations observed more frequently. **b**, Metacommunity-level network. By the presence of fungal species that appear in multiple local communities (yellow circles in the right network), the three local networks (**a**) were combined into a metacommunity-level network. **c**, Local- and metacommunity-level topological properties of each species. Each species can be plotted on the two-dimensional (2D) surface indicating network centralities within local community-level (**a**) and metacommunity-level (**b**) networks. The 2D surface can be used to screen for species potentially playing important metacommunity-level topological roles disproportionately to their local topological roles. Specifically, the points of those species are expected to deviate from the 'baseline', which represents how metacommunity-level network centralities increase with local-level centralities across species appearing only in a single locality. Centrality scores are standardized (minimum, 0; maximum, 1) in each network. Species (OTUs) with 0.5 or higher standardized centrality scores represented 1–2% in each local community. The histogram of the deviation scores ( $D_{base}$ ) is shown for each local community. See Supplementary Methods for methodological details.



**a** Monitoring the ecological and evolutionary properties of metacommunity hubs and whole (meta)communities through time**b** Integrating ecological and evolutionary (genetic) data within time-series analytical frameworks

**Figure 4 | Empirical study framework for spatiotemporal dynamics in metacommunities.** **a**, Basis for monitoring ecological and evolutionary processes through time. Once metacommunity hub species are pinpointed out of hundreds or thousands of species in a wild metacommunity, various molecular methodological platforms will allow us to track the genetic/population dynamics of those hubs. **b**, Integration of ecological and evolutionary time-series data. With time-series analytical methods, we can infer relationships between ecological and evolutionary processes. For example, we can examine whether the allele frequency dynamics of a functionally important gene of hub species 1 in local community A drives the population dynamics of hub species 2 in local community B. Moreover, we may be able to infer how the metapopulation genetic structure of species 1 controls the  $\beta$ -diversity of a metacommunity and vice versa. Roman numerals indicate specific hypotheses in Box 2, step 3.



on the genetic and population dynamics of species with potentially important roles (Fig. 3c), but the network centrality of each species itself can change through time (for example, through seasons). We may therefore need to redefine metacommunity hubs if there are major changes in interaction status<sup>67</sup> and/or network architecture<sup>88,89</sup> during the time-series observations. However, alterations of hub species, in themselves, are ecologically intriguing phenomena: by monitoring network centralities of multiple potential hubs, we may be able to evaluate how the dynamic nature of interaction networks drives local- and metacommunity-scale processes. In addition, although we have put emphasis on the use of basic network metrics such as betweenness centrality, which is intuitive and applicable to a wide range of network data, more sophisticated network-analytical methods will allow us to uncover the dynamical nature of interaction network architecture through time<sup>90</sup>.

## Conclusions

Biological communities are complex systems in which diverse types of agents (species) are continuously restructuring each other's quantitative (ecological) and qualitative (evolutionary or plastic) properties in spatially structured processes<sup>21,23,27</sup>. Although theories on species coexistence or coevolutionary network dynamics have been inspired mainly by interactions among macroorganisms (that is, animals and plants), mechanisms driving highly species-rich assemblages, especially those involving microorganisms<sup>77,91</sup>, have recently received much attention<sup>19,75,92–94</sup>. As a consequence, testing whether existing ecological, evolutionary, and eco-evolutionary theories are applicable to poorly explored (microbial) systems in nature remains a major challenge<sup>92,93,95</sup>. Another important challenge is to examine the working hypotheses (Box 2, step 2) and specific issues (Box 2, step 3) discussed herein by constructing species-rich experimental metacommunities in which we can manipulate the population density, genetic diversity, and dispersal of each species. For example, a set of spatially structured mesocosms with tens of annual plant species and hundreds of endophytic or pathogenic fungi will provide opportunities for testing how the spatially synchronized population dynamics and spatial genetic homogeneity of species with high network centralities determine the network-scale coevolutionary rates (for example, the frequency of plants' resistant alleles) or ecosystem properties (for example, plant biomass) of the metacommunity.

Understanding of eco-evolutionary feedbacks in metacommunities is important not only for basic science but also for applied environmental sciences. For example, as evident in recent global decline of amphibian populations and the emergence of antibiotic- or fungicide-resistant pathogens, the spread of infectious diseases across different regions or different types of habitat is threatening endangered species and degrading the ecosystem functions of both natural and agricultural fields worldwide<sup>15,17,19</sup>. In this context, it is increasingly important to develop theories on the key ecological and evolutionary processes that determine the robustness of local- and metacommunities against invading (spreading) species (Box 2, step 3). Furthermore, finding 'keystone communities'<sup>96</sup>, which play major ecological and evolutionary roles within a spatially explicit network linking local communities<sup>97,98</sup>, will become a major challenge in applied ecology. Overall, further integration of ecology and evolutionary biology is needed for biodiversity conservation and the management of sustainable natural and agricultural ecosystems. By integrating all the rapidly growing perspectives on eco-evolutionary feedbacks, metacommunity processes, and ecological and coevolutionary networks, our understanding of biosphere dynamics will be reorganized.

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## Author contributions

H.T. designed the study and wrote the first draft based on discussion with M.Y. and J.N.T.; M.Y. and T.Y. made significant inputs from the perspective of eco-evolutionary feedbacks and added some paragraphs to the first draft. H.T., P.R.G., J.M.O. and J.N.T.

revised the manuscript from the aspects of coevolutionary biology and ecological interaction networks based on discussion with all authors. A.M. added essential insights into the conceptual backgrounds of theoretical community ecology. All authors contributed to the final version of the manuscript.

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## Competing interests

The authors declare no competing financial interests.