Movement-mediated community assembly and coexistence

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ABSTRACT

Organismal movement is ubiquitous and facilitates important ecological mechanisms that drive community and metacommunity composition and hence biodiversity. In most existing ecological theories and models in biodiversity research, movement is represented simplistically, ignoring the behavioural basis of movement and consequently the variation in behaviour at species and individual level. However, in an age where human endeavours modify climate and land use, the behavioural processes of organisms in response to this, including movement, become critical to understanding resulting biodiversity loss. Here, we draw together research from different subdisciplines in ecology to understand the impact of individual-level movement processes on community-level patterns in species composition and coexistence. We join the movement ecology framework with the key concepts from metacommunity theory, community assembly and modern coexistence theory using the idea of emergence: various behavioural aspects of movement scale up to local and regional patterns in species mobility and mobile-link generated patterns in abiotic and biotic environmental conditions, which in turn influence, at ecological time scales, mechanisms such as dispersal limitation, environmental filtering, and niche partitioning. We conclude by highlighting challenges and promising future avenues to data generation, data analysis and complementary modelling approaches and provide a brief outlook on how a new behavioural-based view on movement becomes important in understanding the response of communities to the ever-changing environment of the Anthropocene.

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I. INTRODUCTION

Current biodiversity loss severely reduces ecosystem resilience and threatens human well-being (Cardinale *et al.*, 2012; Hautier *et al.*, 2015). However, predicting how and where exactly biodiversity is lost is still difficult, as the drivers are diverse and observed trends vary across scales (Tylianakis *et al.*, 2008; McGill *et al.*, 2015). To unravel trends in biodiversity, we must take a closer look at the underlying mechanisms. A strong foundation to understanding local and regional diversity and their ongoing and their ongoing shifts constitute community assembly and coexistence theory (Valladares *et al.*, 2015; Bannar-Martin *et al.*, 2018). As the human impact on the Earth system accelerates (Steffen *et al.*, 2015), individual species do not only need to cope with a modified and highly dynamic environment but also interact with simultaneously affected species on both the same and other trophic levels. As a consequence, (quasi-)equilibrium situations in communities are being challenged, bringing the mechanisms that drive community dynamics into an urgent focus.

Many of the mechanisms that shape community assembly and maintain species coexistence at local and regional scales are mediated by organismal movement. This is apparent for dispersal-related mechanisms such as mass effects, colonization-competition trade-offs and dispersal limitation. In these mechanisms, organismal movement promotes diversity both directly through species' own mobility patterns and indirectly through mobile-link functions of the animal vectors that transport other organisms, their propagules and nutrients, or provide consumer effects (Lundberg & Moberg, 2003; Bauer & Hoye, 2014; Gounand *et al.*, 2018). More specifically, organismal movement can critically influence community assembly and species coexistence by, for example, reducing exploitation competition in spatiotemporally heterogeneous environments (Macandza, Owen-Smith, &

Cain III, 2012), locally strengthening predator effects on prey (Avgar, Giladi, & Nathan, 2008a), or modifying abiotic environmental filters (Shantz *et al.*, 2015).

Still, in many existing biodiversity assessments, movement is either ignored or only represented phenomenologically (e.g. by assuming certain dispersal kernels or space-use patterns). We know, however, from the field of movement ecology that movement is more complex (Nathan *et al.*, 2008a) and requires an individual-based perspective with individuals varying in phenotypes (e.g. personality), motivation, and locally experienced environments. Movement ecology has developed much technology and analytical tools to decipher how animals integrate information about their environment, experience, and innate states to make movement decisions (Kays *et al.*, 2015; Wilmers *et al.*, 2015; Hooten *et al.*, 2017). First efforts to join community- and landscape-level approaches have demonstrated that individual movement capacities and strategies are critical in determining spatial population structure and within-species niche specialization (Spiegel *et al.*, 2017; Schirmer *et al.*, 2019), how prey communities form in a landscape of fear (Teckentrup *et al.*, 2018), as well as the persistence of species and communities in fragmented landscapes (Brown *et al.*, 2017; González-Varo *et al.*, 2017). Yet, a full-fledged integration of movement ecology and biodiversity research is still in its infancy (Jeltsch *et al.*, 2013; but see Barton *et al.*, 2015).

To fill this gap, we provide a comprehensive overview of various possible pathways how organismal movement shapes community and metacommunity composition. As this requires merging different ecological subfields, and, respectively, their theories and concepts, we first briefly review relevant concepts from movement ecology and community ecology. Subsequently, we synthesize movement-mediated community assembly and coexistence, focusing on mechanisms for which specific movement processes are pivotal. In this part, we highlight how an integration of a more process- and behaviour-based view of organismal movement within community ecology can help us to better understand biodiversity patterns and their ongoing changes. In the last section, we outline a new framework for integrating the individual-based approach of movement ecology and the population- and species-based approaches of community ecology. We further describe current challenges and avenues for future research, emphasizing where we see the strongest needs and greatest potential for advancing our knowledge. With this, we intend to stimulate research at the interface of movement ecology and biodiversity research to make better use of the impressive amount of information generated in both disciplines and to move ecological research forward in the Anthropocene.

II. BACKGROUND

Although movement ecology has culminated into its own discipline only recently, a long tradition of observing and studying movements has brought forward important general insights and concepts. Likewise, community ecology has established a rich body of theory and concepts to understand patterns in community and metacommunity composition and their underlying processes. From this, we use the prominent frameworks of community assembly, modern coexistence theory, and metacommunity theory to investigate and evaluate where in these frameworks a deeper consideration of organismal movement may bring significant gains to our understanding. To accommodate readers that may not be familiar with all of these notions, we recapitulate the core concepts that we use for our review. We include a brief summary of the mobile link concept (Lundberg & Moberg, 2003), which systemizes the effects of actively moving animals on ecosystem functions and more generally emphasizes their role in connecting habitats in both space and time, a feature relevant for various aspects of community-levels processes.

(1) Movement processes

Although movement can be defined rather simply as the process by which organisms change their location in time, it is a process with many facets. It has biomechanical aspects, including the proximate physiological and physical processes that put an organism's stimulus to move into effect and define its locomotion. It requires a cognitive architecture, in which an organism integrates its motivation to move, information about the environment through perception or memory, and its navigation abilities to set and reach a destination. Movement further has an optimality aspect in the sense that it may ultimately impact fitness components such as survival or reproduction, which we expect to be reflected in actual movement decisions. To deal with this broad spectrum of elements of a movement process, Nathan and collegeagues (2008) introduced the movement ecology framework, which serves as a prism in breaking down movement into three basic components – internal state ("why move?"), motion capacity ("how to move?"), and navigation capacity ("where to move?") – that in relation to the environment shape the movement path of an individual or organismal unit (see upper panel of Fig. 1). Despite, or rather because of its simplicity, this framework provides a fundamental conceptual basis to understanding organismal movement.

Despite a great variety in short-term movement goals as well as taxa-, species-, and individual-specific strategies in how, where and when to move for accomplishing these goals, we use the "why move?" to differentiate between three broad categories of movement: (i) dispersal movements away from the natal site or a reproductive sites to (another) reproductive site, (ii) migratory movements, by which animals move regularly between breeding and non-breeding sites, and (iii) daily movements, which include all movements that occur outside dispersal or migratory phases and serve regular maintenance (e.g., foraging) or reproduction (e.g. mating and offspring rearing). Animals have different strategies in how to move on a daily basis, either restricting them to a relatively fixed, and possibly defended, area (station-keeping movements or range residency), or moving irregularly between transient core areas (nomadism). Nomadism can also be seen as large-scale movement pattern complementing migration (Milner-Gulland, Fryxell, & Sinclair, 2011; see also Teitelbaum & Mueller, 2019). In total, when complementing the process-based perspective on movement by a top-down view on the movement patterns that emerge from many movement bouts over long time spans (and up to lifetimes), we obtain four basic types of movement (Fig. 2; Mueller & Fagan, 2008; Barton *et al.*, 2015).

Broadly, the different movement types correspond to movement and possible community implications at different spatial scales. Here, we define scales not in spatial units *per se* but from the perspective of the moving individual. While station-keeping movements are local and within a population, dispersal movements are regional and connect populations at the metacommunity scale. Occasionally, dispersing organisms may move or be transported long distances even across regions. Migratory movements are typically interregional, crossing geographic regions (e.g. migrating ungulates), ecosystems (e.g. fish migrating between fresh water and the ocean), or even continents (e.g. many migratory birds), thus providing potential links at these scales. From a population perspective, migratory animals often migrate aligned with their population and thus migration does not necessarily imply large-scale mixing within a species. However, they encounter and interact with different (meta-)communities at their breeding versus non-breeding sites. Therefore, also from a metacommunity perspective migration can be considered interregional. Nomadic animals often stay within a region (e.g. bats, or birds during the non-breeding season) but may also move similar distances as migrants (e.g. nomadic gazelles), thus having the potential to link (meta)communities.

The movement types also operate on different time scales and thereby influence communities in fundamentally different ways (Amarasekare, 2008). Many movements such as foraging occur on shorter time scales than population dynamics (Fahse, Wissel, & Grimm, 1998), and therefore these movement processes influence community composition in aggregation, through the emergence of certain movement patterns via behavioural syndromes, where individual variability may be part of the pattern (e.g. Buchmann *et al.*, 2012). In contrast, dispersal impacts population dynamics more directly resulting in more immediate effects at the community level. However, individual dispersal events are still dependent on (behavioural) movement processes on short time scales during which an organism must draw on its movement capacities and, if moving actively, make movement decisions. Thus, whenever considering the implications of movement processes on community and metacommunity composition, we face the challenge of having to integrate time scales.

(2) Mobile links

Mobile animals may not only move themselves between sites and communities, but also confer mobility to other organisms or non-living material, or create spatiotemporal patterns in processes that affect the abiotic environment or the trophic web. Whenever animals act in this way, they are considered *mobile links* or *mobile linkers* (Lundberg & Moberg, 2003). Based on what they transport, three types of mobile linkers are distinguished. Genetic linkers transport organisms (e.g. zooplankton or soil fauna) or their propagules (e.g. eggs, seeds, spores), which may attach externally (e.g. in fur or feathers) or be ingested and later excreted (Viana *et al.*, 2013; Reynolds, Miranda, & Cumming, 2015; González-Varo *et al.*, 2017). Resource linkers transport nutrients and organic material, sometimes between ecosystems (Hannan *et al.*, 2007; Abbas *et al.*, 2012; Subalusky *et al.*, 2015). Lastly, process linkers provide either trophic effects, such as herbivory, predation and parasitism (Fuhlendorf & Engle, 2004; Avgar *et al.*, 2008a), or non-trophic effects (D'Souza *et al.*, 2015), for example disturbance via uprooting or trampling. The latter is similar to the concept of ecosystem engineers with a stronger focus on the movement of the 'engineering' species.

When considering the movements of mobile links, we must take care to distinguish between the scales at which their movements affect their own population dynamics and the scales at which they affect processes for other organisms and communities (often at other trophic levels). According to our organism-centered definition of scale (see section above, "Movement processes"), the same absolute spatial distance might represent different scales for mobile links and the interacting species. For example, frugivorous birds may move locally to forage in different trees and disperse seeds via endozoochory (Morales *et al.*, 2013), whereby local foraging movements of a genetic linker result in regional dispersal movements of a transported organism. Thus, the same movement process can have population- and community-level implications at different scales when different (sets of) species are considered. Therefore, for all but dispersal movements, we distinguish direct effects and mobile-link effects of how movement impacts communities and coexistence (Table 1).

(3) Community assembly, local and regional coexistence

The process by which local communities assemble is often conceptually viewed as a step-wise passing (or failing to pass) of species from a regional species pool through multiple filters (see lower panel of Fig. 1) (HilleRisLambers *et al.*, 2012; Kraft *et al.*, 2015). First, for a species to establish at a particular location, its dispersal abilities must be sufficient to reach the location (*dispersal limitation*). Second, abiotic environmental conditions must be suitable to allow survival and successful reproduction (*environmental filter*). Third, biotic interactions must allow persistence in the presence of other species when exploitation, interference or apparent competition but also trophic interactions pose further challenges (*biotic filter*). Often, both abiotic and biotic environmental factors together shape the outcome of competition and can be difficult to disentangle empirically (Cadotte & Tucker, 2017). Therefore, Kraft et al. (2015) advocate the use of environmental filtering *sensu strictu*, which applies when species cannot tolerate abiotic environmental conditions even in the absence of other species.

Coexistence theory can be seen as stepping in after environmental filtering *sensu strictu* to elucidate outcomes of the joint action of biotic interactions and the abiotic environment (HilleRisLambers *et al.*, 2012). One of the cornerstones of coexistence theory is the concept of the ecological niche. While Eltonian and Hutchinsonian niches are defined as species-specific properties, modern coexistence theory (MCT) focuses on *niche differences*, which are achieved, for example, by species being regulated by different limiting factors or responding differently to variation in common limiting factors (Chesson, 2000a; Letten, Ke, & Fukami, 2016; Barabás, D'Andrea, & Stump, 2018). This latter approach highlights the importance of stabilizing mechanisms that reduce niche overlap and induce negative frequency dependence of growth rates, thereby creating a rare species advantage. Niche differences are complemented by average *fitness differences* between species (recently termed competitive advantage by Barabás *et al.* 2018) that encompass the competitiveness of species and their adaptedness to the environment. Equalizing mechanisms, by definition, reduce fitness differences and the extent to which stabilizing mechanisms are necessary for coexistence (Chesson, 2000a; Barabás *et al.*, 2018). However, this separation should not mislead one to think about niche and fitness differences as being independent. Often, both equalizing and stabilizing mechanisms operate simultaneously and possibly stem from the same ecological process (Barabás *et al.*, 2018).

Although initially developed to explain coexistence locally in temporally varying environments, coexistence theory was soon extended to spatially varying environments (Chesson, 2000b; Barabás *et al.*, 2018). Within this framework, it can further help to elucidate coexistence in competitive metacommunities. Metacommunity theory commonly distinguishes the four paradigms neutral, patch-dynamic, species-sorting, and mass-effect. These paradigms take different, but not mutually exclusive, perspectives on how metacommunity structure is maintained. While the neutral paradigm attributes diversity to stochastic outcomes of emigration immigration, extinction and speciation, the other paradigms highlight the roles of habitat heterogeneity and environmental filtering (species sorting), spatial dynamics via dispersal (mass effects), and trade-offs between local competitive and dispersal abilities (patch dynamics) (Leibold *et al.*, 2004; Logue *et al.*, 2011). Shoemaker & Melbourne (2016) showed that within these paradigms (except, by definition, in the neutral model), species coexistence at the regional scale can arise from a combination of non-spatial coexistence mechanisms (fluctuation-independent mechanisms, relative non-linearities, and the temporal storage effect; see e.g. Barabás *et al.*, 2018) and specific spatial mechanisms (fitness-density covariance, spatial storage effect).

One of the difficulties in applying modern coexistence theory to empirical processes and patterns is that its coexistence mechanisms are aggregated and conceptual and can arise from a multitude of ecological processes and organisms' traits (Barabás *et al.*, 2018; Ellner *et al.*, 2018). Recent methodological advances may help to alleviate this problem in the future: Ellner *et al.* (2018) propose a framework, in which long-term species growth rates – crucial to evaluate rare species advantages – are decomposed not necessarily into the canonical coexistence mechanisms of MCT, but into any ecologically relevant mechanisms, for example local retention of seeds, plant-soil feedbacks, or facilitation processes in the context of plant species coexistence. With a similar focus on concrete ecological mechanisms, we here consider organismal movement and resultant processes and how they affect species coexistence. However, where possible, we also report how these effects fit into the equalizing-stabilizing paradigm of MCT.

III. MOVEMENT-MEDIATED COMMUNITY ASSEMBLY AND COEXISTENCE

In the following, we review current knowledge on the relevance of individual-level movement processes on short time scales for community processes and patterns on longer, ecological time scales. More specifically, we consider in turn the four basic movement types (Fig. 2), and how characteristics of the involved movement processes influence the community-assembly steps and coexistence mechanisms described above.

(1) Dispersal

Dispersal is key to metacommunity dynamics. Dispersal rates determine how strongly communities are connected and to which extent regional-scale diversity arises from spatial turnover through species sorting, local alpha diversities driven by mass effects, and heterogeneities in species dispersal (e.g., Logue *et al.*, 2011). From a local perspective, the metacommunity provides the regional species pool, from which local communities assemble, and a species' dispersal capacity determines whether it can colonize a suitable site and whether sink locations can be supported (local perspective of the mass effect). Thus, understanding dispersal processes and estimating dispersal rates and distances is paramount to understanding (meta)communities (Jønsson *et al.*, 2016). During recent years, it has been pointed out repeatedly that there are still methodological gaps in dispersal studies: they should more frequently embrace variability in dispersal between species (Heino *et al.*, 2015) and individuals (Cote *et al.*, 2010; Wey *et al.*, 2015), consider behavioural processes during the dispersal process (Auffret *et al.*, 2017), and quantify dispersal directly instead of using indirect proxies (Driscoll *et al.*, 2013; Keeley *et al.*, 2017). This calls for an integration of the movement ecology framework into dispersal studies (see e.g., McMahon *et al.*, 2014), linking it with the dispersal evolutionary ecology framework to account for the strong connection of dispersal with gene flow (Baguette, Stevens, & Clobert, 2014).

The movement ecology framework is particularly suitable to address questions about the transience stage of the dispersal process, although there exist links to the other stages (departure and settlement) (Baguette *et al.*, 2014). Transience is the most critical stage in determining final dispersal distances of an organism and hence the spatial scales at which dispersal limitation can manifest. Clearly, dispersal distances are influenced by motion capacities, which arise from the morphological and physiological traits of organisms or their dispersing propagules (De Bie *et al.*, 2012; McMahon *et al.*, 2014; Stevens *et al.*, 2014). In actively moving animals, dispersal distances tend to be larger with increasing body size and mass (Jenkins *et al.*, 2007; Stevens *et al.*, 2014), suggesting that an allometric scaling of movement (Carbone *et al.*, 2017) may hold for this particular movement type. For passive dispersal, the relationship between propagule size and dispersal distance is less clear (Jenkins *et al.*, 2007), possibly because of different vectors (abiotic and biotic). We discuss the effect of biotic vectors in sections below. Dispersal distances are further influenced by internal motivations. Differences have been observed, for example, between habitat specialist and generalist species, with specialists being less explorative and dispersing shorter distances than generalists (Stevens *et al.*, 2014; Dahirel *et al.*, 2015). Similarly, we also find differences within species among individuals with different personalities (i.e. behavioural dispersal syndromes; Cote *et al.*, 2010; Wey *et al.*, 2015).

During transience, dispersing organisms often cross unsuitable matrix, and their ability to survive and locate suitable habitat for settlement scales up, over many individuals, to affect dispersal rates (e.g. Lee & Bolger, 2017). While passively dispersing organisms usually cannot decide their exact dispersal routes, actively moving animals make movement decisions in relation to environmental or other types of information (Clobert *et al.*, 2009; Knowlton & Graham, 2010). Navigation capacities can be crucial in locating habitat patches. While direct visual cues are used when inter-patch distances are not large (Ibarra-Macias, Robinson, & Gaines, 2011; Kay *et al.*, 2016), more indirect cues, such as conspecific density, prevails for longer dispersal trips (Clobert *et al.*, 2009). Internal state can determine whether animals traverse hostile environments or barriers. For example, some studies have found that during dispersal movements, in contrast to daily movements such as foraging, the willingness to enter less preferred vegetation types is likely enhanced, which highlights the importance of collecting data from actual dispersal movements (Knowlton & Graham, 2010; Keeley *et al.*, 2017).

Species-specific heterogeneity in dispersal abilities has been investigated explicitly in the metacommunity paradigm ‘patch dynamics’ in form of the colonization-competition trade-off (CCTO; high dispersal ability is linked with low performance in competition and vice versa). Trade-offs in ecological traits are a constituent part of coexistence-enabling niche differences (Kneitel & Chase, 2004), and CCTO works this out in a spatial dimension. Although the regional-scale CCTO is a well-known hypothesis, the relevance in nature is not clear. While some studies that tested for this trade-off explicitly present evidence, mostly for passively dispersing organisms (Hanski & Ranta, 1983; Turnbull, Rees, & Crawley, 1999; Cadotte *et al.*, 2006), others failed to find support, possibly because of an insufficient ecological age of the studied system (Wilson, 2011; Pastore *et al.*, 2014). As a rare test on vertebrates, (Rodríguez, Jansson, & Andrén, 2007) found under field conditions that this mechanism appears to promote coexistence in a songbird guild (*Parus* spp.) in Sweden, where superior competitors were larger and inhabited predator-safe sites, whereas competitively inferior species were more mobile and could inhabit more isolated forest patches. Additionally, observed differences in dispersal distances in relation to dispersal syndromes as mentioned above might be related to CCTOs (Stevens *et al.*, 2014; Dahirel *et al.*, 2015; Cote *et al.*, 2017). While many studies classify CCTO as equalizing or stabilizing based on few heuristic arguments, a rigorous analysis by Shoemaker & Melbourne (2016) revealed that CCTO has an equalizing and a stabilizing component: the better disperser benefits from intraspecific aggregation (representing reduced interspecific competition), while the better competitor suffers from it, balancing out *a priori* fitness differences.

In addition to driving population dynamics and community composition within metacommunities, dispersal movements – with all their abovementioned intricacies – are further important in driving species range distributions (Holloway & Miller, 2017). In this way, dispersal influences the size of a metacommunity, that is over which spatial extent connectivity can be maintained and species exchanged, similar to the idea of a regional species pool supplying local communities. At this possibly inter-regional scale, capacities for long-distance dispersal (LDD) are especially important, although LDD events tend to be rare and hence can drive regional processes only on longer time scales. This makes LDD more difficult to observe and quantify directly (but see Griesser *et al.*, 2014), but indirect evidence comes from genetic analyses. Although LDD events have been occasionally identified in actively moving animals, such as highly mobile wolves (Vilà *et al.*, 2003), more studies on LDD are available for plants and invertebrates (Incagnone *et al.*, 2015) and invasive or otherwise harmful species (e.g. Ling *et al.*, 2009; Reynolds *et al.*, 2015; Ramos *et al.*, 2016). For plants, invertebrates and microorganisms, the mobility necessary for LDD can be conferred by large-scale wind or water currents but also highly mobile vectors (genetic linkers), especially migratory animals (Gillespie *et al.*, 2012); see next sections.

(2) Seasonal and life-cycle migration

Migration is a widespread phenomenon in animals. It has been studied widely, from an evolutionary and ecological perspective (Milner-Gulland *et al.*, 2011), and more recently also from an ecosystem perspective considering transport and trophic effects of migratory animals (Holdo *et al.*, 2011; Bauer & Hoye, 2014). We will consider in turn direct effects of migration within migratory animals' own trophic level and guilds and mobile-link effects that usually apply to organisms at other trophic levels.

(a) Direct effects

In our framework, the when and where of animal migrations directly affects regional species pools. While extinction and speciation drive species pools on relatively long timescales, migration produces inter-regional dynamics on much shorter timescales. According to the seasonal dynamics of migration, competition in communities tightens in pulses, with large consequences for species with strong resource niche overlap. When and where migratory species contribute to communities and elicit competition between residents and migrants or between multiple arriving migrants depends strongly on the environmental factors that drive migration (Milner-Gulland *et al.*, 2011; Teitelbaum *et al.*, 2015) but is also linked to the movement process of the migratory phase itself.

Most detailed movement data on migrations are available for birds, among which a fifth of all species is migratory (Somveille *et al.*, 2013). Spring arrival times of migrants are critical in competition for nest sites and territories and early arrival can be achieved either through fast migration or short migration distance (Kokko, 1999; Visser *et al.*, 2009; Nilsson, Klaassen, & Alerstam, 2013). Migration speed is related to flight mode, flapping being more energetic costly than soaring but also less dependent on weather conditions and less prone to off-route drift, hence being more suitable for a time minimization strategy during migration. Other factors in flight behaviour that support fast migration are the daily travel distance, which can be increased by higher speeds, longer flight duration, and particularly the total duration of stopovers during the journey, which can be reduced by night-time flight (allowing daytime foraging) or a combined flight-and-forage strategy (Nilsson *et al.*, 2013). Findings that birds employ such strategies predominantly during spring migration have been mostly linked to intraspecific competition, however, they may similarly apply to interspecific competition. For example, cavity-nesting bird species experience strong competition for a limited number of nest sites, such that early spring arrival of migrants can be beneficial for occupation of nest sites (Alerstam & Högstedt, 1981). However, early arrival also increases direct interference competition with residents (Ahola *et al.*, 2007). As arrival times are furthermore strongly linked to food availability, this creates a complex optimization problem, in which movement-related decisions are one means to secure competitiveness (Schaefer *et al.*, 2018).

In which regions or locations migratory species supplement resident communities depends mostly on movement-environment interactions but also, proximately, on navigation strategies. The regions between which migratory animals travel can be fairly fixed. However, some individuals may serve as innovators in establishing new migration routes and off-migration sites (e.g. wintering sites). These innovations may be driven by inexperienced individuals that have only crude navigation capacities and are therefore subject to high stochasticity in travel destination (Cresswell, 2014), or by experienced older individuals that can identify new sites with suitable habitat (Teitelbaum *et al.*, 2016). Observations of events, where new migratory routes lead to population-level effects in a newly established site, are difficult to make and usually only possible retrospectively. One such example is the over-wintering of south-central European blackcaps in the British Isles since the 1960s, representing migration in an entirely new compass direction (Bearhop *et al.*, 2005; Hiemer *et al.*, 2018). However we are not aware of any reports on novel competitive interactions between the blackcaps and resident species at these locations.

The evolution of seasonal migration as a strategy complementing residency has sparked much interest. Related to this is the question how the two strategies coexist thereby allowing species coexistence. Theoretical studies support the ubiquity of migration, showing that both strategies can invade each other in most scenarios of environmental seasonality (Holt & Fryxell, 2013). A possible explanation for this is that migrant and resident populations are regulated by different factors, predation playing typically a larger role for residents and resource availability being a stronger liming factor for migrants (Fryxell & Sinclair, 1988; Holdo *et al.*, 2011). Such different regulating factor have been put forward as an explanation for the high relative abundance of migratory ungulates in various ecosystems (Fryxell, Greever, & Sinclair, 2002). Similarly, if residents are limited by predation and food availability during the breeding season and migrants are limited by food availability during the non-breeding season, coexistence can occur in tropical bird communities even during periods of low food abundance (Johnson, Strong, & Sherry, 2006). In this sense, migration fosters niche differentiation between species, drawing both on spatial and temporal variation in environmental conditions. It would be interesting to investigate whether one could understand this conceptually in a similar way as coexistence mechanisms of MCT that draw on either spatial or temporal fluctuations in the environment.

(b) Mobile-link effects

As genetic, resource and process linkers, migratory animals couple ecosystems across biogeographic scales (Bauer & Hoye, 2014). From a metacommunity perspective, migratory genetic linkers mainly function over large scales, connecting (meta)communities across regions and continents (see Dispersal section). This has been investigated especially for freshwater organisms ("everything is everywhere" hypothesis: Incagnone *et al.*, 2015). Microorganisms as well as plant propagules can be transported by waterfowl both via endo- and ectozoochory. Although the effectiveness of biotic vectors over physical vectors may be case-specific (Incagnone *et al.*, 2015), birds have been identified as drivers of LDD in aquatic species (Viana *et al.*, 2013; Reynolds *et al.*, 2015). Because of their longer distances, migratory movements of waterfowl species are particularly important for LDD (Viana *et al.*, 2013). Given limited gut passage times, more important than migration distances *per se* may be the use of stopover sites, including temporary water bodies that constitute reservoirs of biodiversity (Incagnone *et al.*, 2015).

Further transport effects are provided by resource and trophic links. A classic example of resource links are spawning salmon that return in large numbers to freshwater streams, where they die. Their carcasses are carried away from streams by predators and scavengers and provide significant nutrient subsidies into riparian areas, lessening the effect of abiotic filters relative to biotic filters for primary producers, reduce species richness and shift community composition (Hurteau *et al.*, 2016). The significance of migration for this community-level effect lies in allowing a nutrient transfer between distant ecosystems. Via migration, salmon utilize the nutrients of marine environments for growth while using freshwater streams as relatively safe spawning habitat, where they ultimately deposit nutrients. Similarly, migrating sea turtles transport substantial amounts of nutrients large distances from foraging grounds to nesting grounds, where they fertilize dune plants (Hannan *et al.*, 2007). A slightly different case present migratory seabirds, which are known to critically enhance nutrient levels in the terrestrial systems on their breeding islands (Bauer & Hoye, 2014). Here, it is rather station-keeping movements during the breeding season that allow the nutrient transfer (see section below); however, migration is important in allowing the birds to utilize these specific regions during the breeding season. Similar considerations as for resource linkers hold for trophic linkers. Migratory animals can have strong effects on other trophic levels by exerting strong consumption, or serving as temporary prey (see Bauer & Hoye, 2014 and references therein). These effects occur usually at destination sites of migration (Popa-Lisseanu *et al.*, 2007), and more direct interactions between movement processes during migration and trophic-link effects remain to be investigated.

(3) Station-keeping movements

(a) Direct effects

Differences in the characteristics of station-keeping movements can allow competing mobile species to reduce both exploitation and interference competition as well as to use trade-offs in energy regulation to balance out competitiveness. A starkly contrasting dichotomy in foraging modes exists between ambush (or sit-and-wait) and actively searching predators. These two foraging modes arise as clusters of movement traits, possibly coevolved (Cooper, 2007), whereby active foragers typically show higher average movement speeds and spend more time moving than ambushing foragers. Compared to ambush hunting, active foraging often leads to higher prey encounter rates but incurs greater movement costs (Scharf *et al.*, 2006; Avgar *et al.*, 2008b). This trade-off might allow species with different foraging modes to balance out net energy gains (equalizing effect). When foraging strategies are additionally linked to different prey types, the contrast can also have a stabilizing effect on the predator species via resource partitioning (Nakano, Fausch, & Kitano, 1999). However, there might even be a third way in which dichotomic movement strategies promote coexistence when we additionally consider prey movements. Modelling studies suggest that predator foraging success depends not only on their own movement rates but also on the interplay their own and prey movements: higher encounter rates of active searchers rely on predators moving faster than prey, or prey moving with low levels of directionality (Scharf *et al.*, 2006; Avgar *et al.*, 2008b). Empirical studies in a spider-grasshopper system show that prey, in turn, adjust their movement rates to the mobility of their predators (Miller, Ament, & Schmitz, 2014). Thus, a predator's mobility level might induce prey mobility levels that support the opposite predatory strategy, such that a rare predator strategy can have an advantage (stabilizing effect).

Similar albeit less starkly contrasting foraging patterns exist in herbivores, which can also be linked to trade-offs between food intake and movement-related costs (including predation risk) and simultaneously lead to partially exclusive resource use. For example, two similar folivorous lemur species express different locomotion patterns, where the wider ranging species performs more energy-demanding leaps between trees but forages more selectively and takes higher quality food (Warren & Crompton, 1997). Another example are African ungulate guilds, in which different patterns in terms of within-patch displacements as well as movement rates and durations between patches are linked to spatiotemporal segregation of species (Macandza *et al.*, 2012; Owen-Smith, Martin, & Yoganand, 2015). Such partitioning in resource use via behavioural differentiation may operate on relatively small spatial scales, not being evident at home range scale but becoming only apparent when zooming in on movements with greater temporal resolution.

Spatiotemporal segregation at fine scales can also arise through active avoidance between heterospecific individuals. This can be effective in reducing interference competition between (meso-)predators (Nakano *et al.*, 1999; Vanak *et al.*, 2013) or to avoid a shared predator (Macandza *et al.*, 2012). Fine-scale avoidance occurs at the scale of individual movement decisions, and we expect this to be strongly influenced by internal state (e.g. risk-taking propensity) and navigation capacity (e.g. sensing and memory). Whether this mechanism in the long term may mainly reduce a dominant species' competitive advantage over sub-ordinate species or can also manifest in niche differentiation remains to be investigated.

(b) Genetic-link effects

Station-keeping movements further affect the dispersal movements of other organisms, thereby serving as genetic mobile links. Metacommunity affects for the transported organisms (e.g. whether dispersal rates promote species sorting or mass effects) depend most importantly on genetic linkers' movement rates and distances. While animals that travel longer distances on a daily basis, for example larger animals, tend to favour LDD, highly active species that frequently move between different foraging sites facilitate higher dispersal rates (Nathan *et al.*, 2008b; Schwalb, Morris, & Cottenie, 2015). Many animals concentrate their feeding in multiple, spatially distinct core areas within their home ranges, sometimes in fairly regular patterns (Berger-Tal & Bar-David, 2015). When such animals act as biotic vectors for organisms or their propagules, this may lead to the high dispersal rates necessary to maintain mass effects (Heymann *et al.*, 2017). Animals vary their mobility patterns, for example seasonally, such that realized dispersal might deviate from predictions based on general estimates of a vector's movement ability (Ismail *et al.*, 2017). Also, when assessing the dispersal potential of propagules via endozoochory, movement distances and patterns are not only important *per se*, but also in influencing the digestive processes. For example, movement distances of mobile linkers must be linked with gut retention times to obtain estimates of dispersal, but combining independent measures of the two is not enough, as mobility levels significantly affect retention times and hence both dispersal distance and propagule survival (Leeuwen *et al.*, 2016).

Although highly active mobile linkers have the potential to build strong links between certain patches, a single mobile-link individual or even species will unlikely be able to provide complete connectivity to a metacommunity. Each species, and even individuals within species, will link patches in correspondence to their resource requirements and preferences and in response to the available landscape structure, selecting different sites, and moving between sites with varying frequency and time lags (Carlo *et al.*, 2013; Morales *et al.*, 2013). On the one hand, when the link between an organism and its vector is strongly specific, this may promote differences in dispersal that scale up to a dispersal-colonization trade-off. On the other hand, when organisms can be transported by multiple vectors with differing movement behaviours, this can result in overall more evenly distributed dispersal patterns. This has been demonstrated for interactions between frugivorous birds and seeds, where a diverse frugivorous community with different space-use and movement patterns produces complementary seed rains (González-Varo *et al.*, 2017).

(c) Resource- and process-link effects

Foraging movement patterns of resource linkers and trophic linkers can have both local and regional effects by influencing the external environmental conditions that other organisms experience. Locally, repeated high nutrient input by resource linkers at local sites may affect the abiotic environmental filter that operates during community assembly. At the one end, intense nutrient loading can cause abiotic conditions that are not tolerated well by many species. For example, animal excreta enhance dissolved-oxygen depletion and ammonium levels in aquatic systems, which can be detrimental to fish (Wagner, 1978). At the other end, in extremely nutrient-poor systems, organic input from mobile links can decrease the strength of the environmental filter and allow greater diversity, which, for example, appears to occur for islands and surrounding shallow banks that receive nutrients through excreta from seabird colonies (Powell *et al.*, 1991). The emergence of spatially concentrated nutrient subsidies requires particular movement behaviours such as strong localized habitat selection or defecation, for example, as performed by grazers that evade high temperatures by spending repeatedly much time in the same riparian areas (Allred *et al.*, 2013; Earl & Zollner, 2017). Additionally, unidirectional "conveyor belts" for nutrients result from daily recurrent movements between areas of nutrient uptake and loss, e.g. feeding and resting places (Abbas *et al.*, 2012; Subalusky *et al.*, 2015). Even when vector movement is less regular, aggregated resource input can arise indirectly, for example, when predator-prey spatial interactions lead to clusters of prey carcasses (Bump *et al.*, 2009). Nutrient subsidy by mobile links also contributes to local community structuring through secondary effects. High site fidelity of aggregating meso-predatory fish attract grazers (trophic linkers) that provide strong herbivory pressure, suppress macroalgae and thereby facilitate coral settlement and survival (Shantz *et al.*, 2015). Note that, although local mobile-link effects can be strong enough to affect environmental filtering *sensu strictu*, often it creates changes in external conditions that interact with biotic factors (e.g. competition effects) to shape local communities.

Recurrence in movement patterns of resource and process links, especially herbivores that often act as both, also plays a role by creating spatial and spatiotemporal heterogeneity in external conditions. Such heterogeneity is the basis for species sorting in metacommunities but also for spatial variation in competitive abilities that supports the spatial storage effect and mass effects (Mouquet *et al.*, 2002; Sears & Chesson, 2007) or enhances the chance for coexistence via CCTO (Cronin, Loeuille, & Monnin, 2016). Additionally, recurrent movements by resource- or process links contributes to successional mosaics that are caused by spatiotemporal dynamics in disturbances (allogenic disturbance *sensu* Wilson, 2011). Which type of patterns occur, depends on the frequency of repeated visits to the same foraging sites, but also on feeding behaviour. When grazing or browsing is selective, frequent visits to the same preferred patches lead to arrested succession ("cultivation grazing", D'Souza *et al.*, 2015). Such patches maintain primary successional plant species, which can create a contrast to the surrounding landscape if this is dominated by later successional species (Olofsson, de Mazancourt, & Crawley, 2008). In contrast, generalist herbivores that provide strong disturbance but revisit areas more rarely rather create shifting mosaics of patches at different successional stages (Sommer, 1999; Fuhlendorf & Engle, 2004).

Another important aspect of trophic links' foraging movements can be their navigation capacities and the way in which they respond to cues. Predators, including herbivores, that exert density- or distant-dependent mortality, while being sufficiently prey-specific, contribute to negative frequency-dependent growth of their prey (pest pressure *sensu* Wilson, 2011; Janzen-Connell effect: Fricke, Tewksbury, & Rogers, 2014). Clearly, foraging behaviours of predators contribute to mortality patterns, as animals often focus search efforts where they expect high food abundance. However, it may not be as simple: for example, in contrast to solitarily foraging ants that only responded to resource density, socially foraging ants that also responded to cues from conspecifics were able to generate seed survival patterns in line with Janzen-Connell patterns (Avgar *et al.*, 2008a).

(4) Nomadism

Of the four movement types, nomadism is the least investigated. This may be due partly to conceptual difficulties in setting it apart from migration and station-keeping, which have been amended by Mueller & Fagan (2008), but also to challenges in tracking the movements of nomadic animals. Their large scale and irregularity render some methods more difficult, such as radio-tracking or the use of data loggers that need to be retrieved. However, reports of nomadism exist various taxa (Teitelbaum & Mueller, 2019), and we here synthesize currently known aspects of nomadism for community ecology.

(a) Direct effects

Similar to migration, nomadism can be seen as a strategy complementing residency that promotes niche differentiation between species, whereby nomads have shifted their foraging niche to unpredictably variable or ephemeral resources. For example, the movement behaviour and foraging niches of two sympatric wading birds, wood stork (*Mycteria americana*) and white ibis (*Eudocimus albus*), in the southeastern U.S. indicate that they have specialized on different strategies despite having similar feeding behaviour (Kushlan, 1981). Although inhabiting dynamic wetlands with high unpredictability in overall prey availability, wood storks use the same breeding colonies over long periods of time, facilitated by their strong flight abilities that allow them to selectively exploit the most stable water sources on a daily basis (Frederick & Ogden, 2006). White ibises, in contrast, rely on shorter daily foraging trips and more unpredictable water sources, which impels them to nomadism and relocation of their breeding colonies according to yearly fluctuating food availability (Frederick & Ogden, 2006). This example demonstrates that nomadism is not always linked to strong movement capacities and large movement distances over short terms. More generally, Allen & Saunders, (2002) suggest that nomadism is related to scale breaks in landscape and resource-availability patterns. In this sense, nomadic animals would be competitively inferior at each spatial scale on its own but able to switch back and forth between them, for example seasonally (Lenz *et al.*, 2015). As such, nomadism could act both to facilitate resource partitioning and equalize fitness across species.

(b) Mobile-link effects

Nomadism in frugivores and nectarivores can be central to their role as pollinators and seed dispersers. A straightforward benefit of nomadism is that it provides a chance for pollination or dispersal events over longer distances than most station-keeping movements. Additionally, nomadic foraging can be essential in facilitating seed dispersal in highly patchy habitats. For example, trumpeter hornbills (*Bycanistes bucinator*) that are nomadic during the non-breeding season visit fruiting trees much further into the agricultural landscapes than during the breeding season when they remain in larger, continuous forest areas. They thus provide important connectivity for small forest patches in the agricultural matrix and ease dispersal limitation (Lenz *et al.*, 2015). A further critical aspect of nomadic foraging for seed dispersal can be its underlying navigation mechanism. To locate unpredictable resources, nomadic animals cannot rely on innate fixed orientation mechanisms, as are known to be important in migration. Instead, they rely on sensory stimuli from the environment, whereby sociality and large group sizes are important in facilitating effective search (Milner-Gulland *et al.*, 2011). Large group size, in turn, has been found to be crucial for effective seed dispersal by fruit bats, as strong intraspecific interactions force individuals to carry fruits away from the tree (Eby *et al.*, 1999; McConkey & Drake, 2006).

The link between nomadism and high group abundance may also be important for other ecosystem effects of such animals. Large herds of herbivores exert strong effects on plant communities, through trophic and non-trophic (e.g. disturbance) effects. While ecosystem effects of natural nomadic movements of herding ungulates such as gazelles (Mueller *et al.*, 2011) remain to be investigated, movements of domestic livestock or wild game in rangelands have received more attention. In systems where management objectives focus on increasing livestock productivity through steady-state management that confines movements, vegetation tends to become homogenized, accompanied by a shift towards pioneer or unpalatable species (Little, Hockey, & Jansen, 2015; Fuhlendorf *et al.*, 2017). More recent approaches recognize the importance of maintaining or reinstating spatiotemporal grazing regimes through nomadic-like movements in order to preserve shifting-mosaic patterns of vegetation structure and resulting diversity of the species that locally use these habitats (Augustine & Derner, 2015; Fuhlendorf *et al.*, 2017).

IV. COMMUNITY PERSPECTIVE

The biggest hurdle in integrating movement and community ecology arises from a difference in perspective. The movement ecology framework (Nathan *et al.*, 2008a) highlights movement as an individual-level behavioural process, with variation in inner states and movement capacities and also in relation to the individually experienced environmental conditions. In contrast, community assembly and coexistence theory usually average out individuals and focus on populations that are characterized by their means, for example long-term average population growth rates (Chesson, 2000a). Consequently, within this perspective, movement is usually represented by few species-level characteristics, such as average movement rates or distances, or dispersal kernels. The conceptual differences between movement ecology and community ecology likely also arise because of the large range in time scales that they cover. While movement processes occur within individual lifetimes, community-level effects play out over many generations. To truly integrate movement and community ecology, we must reconcile the individual-based and population-based perspectives.

We propose that we can link the community assembly and coexistence framework, including metacommunity dynamics, with the movement ecology framework by using the concept of emergence. Emergence refers to the fact that any structure and dynamics at the population or higher level emerges from the behaviour and decisions made by individual organisms. Using averages to capture this emergence works well under certain conditions, in particular in well-mixed populations and homogeneous environments, but fails under heterogeneous and dynamic conditions. Observed patterns are linked to the conditions under which they were observed; however, to predict the response to new conditions, we need to understand the responses of individual organisms to their environment (Grimm, Ayllón, & Railsback, 2017).

In our framework, two types of patterns emerge from movement (Fig. 1, middle part). First, *mobility* encompasses population-level movement patterns that emerge from movement processes within individual lifetimes. This also applies to passive mobility conferred by genetic links and abiotic vectors. As illustrated in detail above, species' mobilities, at ecological time scales, influence their dispersal rates within metacommunities, their degree of dispersal limitation at local sites, their differences in competitiveness, and niche differences (Table 1). Similarly, out of movement processes of mobile resource and process linkers emerge patterns in abiotic and biotic external factors (Fig. 1, Table 1), where biotic external factors include competitors, disturbance regimes, or predation pressure. At the community level, these abiotic and biotic conditions modify environmental filters (both *sensu strictu* and in interaction with biotic filters) and likewise affect competitive biotic interactions by serving as limiting factors to species in the focal community. Importantly, intra- and interspecific interactions occur on both time scales. Within individual life times, i.e. at the individual level, organisms can interact, for example by avoiding each other or by seeking each other out, both within and across trophic levels. These interactions, when viewed across many individuals, scale up to species level interactions in ecological times, i.e. the population-level effects that species have on their own growth rates and those of other species. Therefore, understanding the effects of individual-level interactions on movement processes is essential because they in turn lead to the emergence of species-level interactions that determine coexistence and patterns of diversity.

Adopting the behaviour-based perspective on movement also opens the door to a better incorporation of variation in the environment, in individuals, and in environment-individual interactions into community ecology. Movement processes depend strongly on external factors, and will change in space and time as environmental conditions change. In addition, considerations of individual trait variation (ITV) and personality have recently started to perforate the classic mean-field approach (Turcotte & Levine, 2016; Spiegel *et al.*, 2017). While it is not clear whether variation among individuals generally facilitates or hampers coexistence (Bolnick *et al.*, 2011; Hart *et al.*, 2016), intraspecific trait variation is omnipresent, particularly in movement-related traits, and these differences affect the manifestation of intra- and interspecific interactions (Wolf & Weissing, 2012; Spiegel *et al.*, 2017; Schirmer *et al.*, 2019). Given the multiple sources of trait variation among individuals, it is important to scrutinize assumptions of well-mixed populations, to investigate how variation in movement processes scales up to variation in mobility and mobile-link generated patterns, and to incorporate this variation at the community level.

V. CURRENT CHALLENGES AND AVENUES FOR FUTURE RESEARCH

(1) Generating new data

Currently, the biggest leap in data acquisition is possible in the quantification of movement processes. Improvements in animal tracking technology, such as GPS, allow us to observe individuals' movements with increasing accuracy and resolution (Kays *et al.*, 2015; Weiser *et al.*, 2016), while auxiliary data from bio-logger sensors (e.g. accelerometers, thermometers, and microphones) provide us with an increasingly comprehensive picture of the conditions that animals experience during their movements (Wilmers *et al.*, 2015). However, due to the weight of animal-borne devices, these technologies are still limited to larger and medium-sized animals (Kays *et al.*, 2015). To date, movement data of small vertebrates or insects are mostly obtained through mark-recapture (e.g., Perry *et al.*, 2017) or by direct observation of marked moving individuals (Kay *et al.*, 2016; Brown *et al.*, 2017), which limits the scope and quantity of such data. Promising new approaches are automated radio-telemetry systems (Taylor *et al.*, 2017), image-based tracking (Dell *et al.*, 2014), and radar monitoring (Shamoun-Baranes *et al.*, 2014), the latter two methods not requiring any animal-borne tags and thus being suitable for small invertebrates (Augusiak & Van den Brink, 2015). However, radar- and image-based methods still have to solve the problem of distinguishing species and individuals (Dell *et al.*, 2014; Shamoun-Baranes *et al.*, 2014). Machine-learning based classification of multiple simultaneously moving individuals might help to overcome this challenge (Pennekamp, Schtickzelle, & Petchey, 2015). Additionally, stable isotope signatures can be used to indirectly infer information on movements. This method works well for large-scale movements such as migration across continent-wide so-called isoscapes (Courtiol & Rousset, 2017), but may also be sufficient for tracking the origin of smaller organisms with limited motion capacities (Dammhahn, Randriamoria, & Goodman, 2017).

Our limitations in tracking organisms becomes even more pronounced for those that disperse mainly passively, such as plants and microorganisms. As indirect methods of studying dispersal in passively moving organisms, metabarcoding and other high-throughput molecular techniques have become standard practice (Choudoir *et al.*, 2018). More direct methods would involve the collection of wind-dispersed organisms in air samples (Fernández-Rodríguez *et al.*, 2014) and the collection of dispersal stages directly from dispersal agents (Reynolds *et al.*, 2015). These techniques allow for extensive analyses of communities, but obtaining individual-level data is a challenge for microbes: for fungi and other modular organisms, there is not a clear definition of ‘individual’. In bacteria, clonal organisms with often very high cell division rates, following an individual cell may not even be desirable.

Despite the relative ease with which we can track larger animals, we still see gaps in the design of studies. While comparative studies can reveal movement-related differences between species, which may foster coexistence within their communities (Owen-Smith *et al.*, 2015; Conners *et al.*, 2015) or within communities that they serve as mobile links (Morales *et al.*, 2013), post-hoc comparisons are difficult, because results of movement analyses often depend strongly on data collection methods (e.g. sampling intervals: Rosser *et al.*, 2013). Therefore, we advocate to record movements of multiple species with the same protocol. Furthermore, simultaneous multi-individual and -species tracking is necessary to better understand interactions at the movement level. For example, interference competition can be reduced if competitors avoid each other in their fine-scale movements. Although this has been suggested as coexistence mechanism, few studies have investigated it (Vanak *et al.*, 2013). Exploring interactions, however, requires sufficiently detailed tracking data. A recent promising development aimed at closing these gaps is the ATLAS system, capable of tracking multiple individuals of relatively small species (down to 7 g bats) in the same region at high spatiotemporal resolution (Weiser *et al.*, 2016). Moreover, most tracking studies on macroorganisms focus on station-keeping movements while paying less attention to dispersal. One reason may simply be greater investment required, for example, when only a small portion of individuals in a species disperse and thus many individuals need to be tagged. However, information on animal responses to habitats during foraging cannot always be transferred to dispersal movements (Keeley *et al.*, 2017), thus explicit observation of dispersal processes is desirable. Here, the forthcoming ICARUS tracking system (http://www.orn.mpg.de/ICARUS) will hopefully enable large-scale tracking of dispersing individuals of relatively small vertebrates.

At the interface of movement and community ecology, openly available, rich databases offer new opportunities for the integration of the two fields. Movement data can be found on platforms such as movebank (Kranstauber *et al.*, 2011) and OzTrack (Dwyer *et al.*, 2015), while plant and animal occurrence data can be found, for example, on the Global Biodiversity Information Facility (GBIF) or on regional databases. Other databases such as LEDA (Kleyer *et al.*, 2008) or 3D Dispersal Diaspore Database (Hintze *et al.*, 2013) offer information about plant dispersal features (e.g. seed characteristics) which help to integrate biodiversity data with species' mobilities (through pollen or seeds) or mobile links' mobilities (pollinators and dispersers). However, massive heterogeneity of the data in terms of quality, scales and types of measurements makes them difficult to integrate. Moreover, many classical data collection methods are species specific and limited to specific movement or activity patterns, and hence may distort our knowledge of biodiversity. For example, light capture of nocturnal insects only attracts phototactic species while species that avoid light or reduce activity at illumination are underrepresented (Eccard *et al.*, 2018). We therefore advocate an integrative framework for linking different data types and standardizing data collection, for example, through an increased collaboration among taxon specialists and comparative sampling designs for biodiversity monitoring that guarantee a consistent long-term application of sampling methods. Such joint efforts will allow us to better connect movement and community processes.

(2) Performing novel experiments

While the technical options to observe organismal movement in the field are rapidly increasing, identification of both underlying mechanisms of specific movement patterns and their consequences at the community level is still challenging. In principle, sound scientific experiments are the best option to unravel links between causes and consequences. However, performing reproducible experiments on movements in natural environments is difficult. One reason is the gap in timescales between short-term movement processes and possible consequences at the level of populations or communities. Other problems include the protection status of many larger animals, which limits the possibility for manipulation, or logistic and financial challenges to conduct *in situ* landscape-scale experiments.

We have gained an opportunity for such experiments under laboratory conditions with the ability to track small multicellular organisms such as insects and zooplankton (e.g. using camera systems: Dell *et al.*, 2014; Colangeli *et al.*, 2018). The small spatial scale, the relative ease with which these organisms can be reared in the laboratory, and their short generation times render manipulations in controlled conditions possible. For example, we can use such set-ups to study movement patterns across major feeding types (e.g. primary producers, consumers, predators), or to investigate links between physiology and movement ecology (e.g. changes in movement characteristics of zooplankton with increasing temperature or changing resources). In addition, experimental micro-landscapes can be designed to investigate effects of movement on coexistence of multiple species and even be extended to the community-level. For example, microfluidic systems can be tailored to reflect fine-scale habitat characteristics to study movement within spatial features as would occur in a soil matrix (Aleklett *et al.*, 2018). The small scale allows us to measure community effects of movement in experiments, with the potential to scale up or at least compare those movement effects to communities at larger scales.

Even in real landscapes certain aspects of the small-scale laboratory experiments could be performed, using local multi-species tracking systems such as automated telemetry systems or ATLAS (see above). These systems allow for tracking many organisms of different species at a high temporal and spatial resolution. Ideally, they can be combined with manipulations of land-use (e.g. mowing of grasslands or illumination to create risk landscapes or disturbances; Hoffmann *et al.*, 2018) or landscape elements (e.g. through paid experimental management by farmers). This approach of combining and systematically comparing different scales could be described as an “allometry of movement ecology”. It would stimulate the hybridization of well-established but currently separate disciplines.

(3) Developing statistical tools

While we collect more detailed data on movements, another challenge is to keep up with statistical and computational tools to process and analyze these data. Movement data are complex, having a space and time dimension, and to do movement justice as a behavioural process requires sophisticated models. While this is met with a steady output of new methods for analyzing the various components of movement (Hooten *et al.*, 2017), we see two key directions in which advancement is required. First, tracking technology has improved to a point where we can observe movement paths at resolutions of multiple locations per minute, down to 1 Hz and lower (Weiser *et al.*, 2016). To go beyond descriptive analyses, or to avoid having to subsample data, we need to advance our inferential methods to handle high-resolution and highly autocorrelated data. Conceptually most promising is a switch to continuous-time movement models (Blackwell *et al.*, 2016). Applying these models is computationally more challenging than simpler methods based on discrete-time models, for example step-selection functions, however implementation in statistical software will pave the way for more frequent application (Calabrese *et al.*, 2018).

Second, when interested in communities, considering species interactions is imperative, including at the movement level. There exist methods to detect pairwise interactions between individuals (dynamic interaction indices; Long & Nelson, 2013), behavior of individuals with respect to the spatial distribution of their conspecific population (e.g., Delgado *et al.*, 2014), or coherent responses between individuals within a group (Calabrese *et al.*, 2018). However, we still lack flexible methods for investigating differential responses among conspecifics, heterospecifics, and the environment, for example, when responses are one-sided, vary with respect to different individuals, or when the environment mediates interactions.

(4) Modelling emergent mobility and its consequences

Our ambition for a stronger integration of disciplines at the movement-community interface goes hand in hand with the need to cross levels of organization and scales along various axes. Here, computer-based simulation models, especially mechanistic, individual-based models (IBMs, also referred to as agent-based models), are a powerful tool because they allow us to let population level features, such as growth rates, population structure, or spatial distribution, emerge from the adaptive behaviour of the individuals (Grimm & Railsback, 2005). Despite their great promise, IBMs of communities in which movement is based on first principles do not yet exist and will require integration of new data and experiments (see above). Mobility is still often represented via movement parameters that characterize fairly simple movement models such as correlated random walks, informed by observed turning angle and step-length distributions. Over the last two decades, however, the interaction of movement and habitat features is increasingly taken into account (Kramer-Schadt *et al.*, 2004), while explicitly linking movement decisions to established energy budget theories is a very recent development (Malishev, Bull, & Kearney, 2018). Here, IBMs might profit from mechanistic optimal annual routine modelling that determines the behavioural decision rules underlying movement based on energy and health budgets, taking evolutionary considerations into account (Schaefer *et al.*, 2018).

Presently, IBMs of communities are rarely linked to the theoretical concepts of modern coexistence theory, but they allow for measuring emerging population growth rates and determining niche differences. Here, a major obstacle to integrating the individual and population level lies in the different mindsets of researchers modelling from one or the other perspective. Coexistence theory is rooted in phenomenological population models, which lack a mechanistic description of the competition parameters. Carroll *et al.* (2011) suggested to define fitness and niche differences based on per capita growth rates from no-competition and invasion scenarios, which can be computed in simulation models (Chu & Adler, 2015). Recently, Ellner *et al.* (2018) proposed linking long-term growth rates to ecological processes via numerical simulations as a workaround of the typically only analytically considered mathematical equations of MCT. Similar approaches could be used to link outcomes of behavioural-based IBMs to community-level coexistence mechanisms. Another approach has been put forward by Jeltsch *et al.* (in press), who suggest to extend the toolbox of population viability analysis, which often employs IBMs, to communities (termed coviability analysis). We advocate a further development and application of such approaches to make simulations more mechanistic in the sense that we look closer at how community-level patterns arise from movement processes through community-level mechanisms.

As simulation models are increasingly being developed, they face challenges with respect to calibration, validation, and balancing complexity. IBMs typically have many parameters and complex structures, and some degree of freedom as to which parameter values and sub-model formulations to use. We can tie data into these decisions through pattern-oriented modelling (POM), in which various observed patterns are used as filters to reject unrealistic parameter combinations or submodels of specific key behaviours (Grimm & Railsback, 2012). Since patterns at the individual and higher levels are linked to each other, a lack of sufficient data at one level can be compensated by a set of distinctive patterns at the other level. In this way, we can use a set of community-level patterns (e.g. species richness, rank abundance, spatial distribution) to parameterize individual-level movement parameters. This can be performed in a statistically rigorous way through techniques like Approximate Bayesian Computation (Hartig *et al.*, 2011) and POM-information criterion (Piou, Berger, & Grimm, 2009).

When many species are considered, key for IBMs to be manageable in terms of parameterization, runtime, and analysis is to find generic representations of individuals of different species, and a generic representation of interactions between individuals. To limit the number of different species to be considered, trait-based approaches have proven to be useful, where species are replaced by functional types that are characterized by certain trait combinations. These types can be imposed, based on observed trait combinations, or let emerge via community assembly from a pool of all possible trait combinations. Most existing realistic individual-based models of communities are forest or vegetation models, but a combination with animal functional types seems possible and promising (Hirt *et al.*, 2018; Teckentrup *et al.*, 2018).

(5) Communities under environmental change

As demonstrated above, movement processes are an integral part of community assembly and several key coexistence mechanisms. As a result, community composition is expected to respond to altered movements in the wake of an increasing human footprint on the environment (Harris *et al.*, 2009; Tucker *et al.*, 2018). Climate change and human land use are among the main global environmental change drivers (Tylianakis *et al.*, 2008). At an individual level, they modify how, when and where organisms move, as movement processes across taxa and scales are tightly linked to the environmental conditions that organisms experience.

Climate change can affect any component of the movement process. In the most direct way, climate warming influences motion capacity via the thermal sensitivity of physiological processes involved in locomotion (Gibert *et al.*, 2016). Indirectly, climate change affects dispersal capacities of organisms that disperse via abiotic vectors such as water and wind, for example by modifying ocean circulation patterns with significant effects for many marine taxa (Wilson *et al.*, 2016). Also at smaller scales, regional changes in wind speed impact the transport of plant propagules, affecting both average dispersal distances and the chance of long-distance dispersal events (Bullock *et al.*, 2012). Dispersal behaviour is further expected to change due to evolutionary pressures under climate change (Travis *et al.*, 2013). Climatic conditions also contribute to the environmental cues that drive migration. Over the last decades, migratory patterns of many species have been observed to change, involving shifts in timing, reduced extent of migrations, or increased proportions of sedentary individuals in partial migrants, with climate change likely being a key driver (Seebacher & Post, 2015). Some migratory animals may even switch their movement type, becoming nomadic in response to reduced predictability of environmental conditions (Harris *et al.*, 2009).

With increasing anthropogenic land use, biodiversity has become seriously threatened by habitat loss and degradation, often accompanied by fragmentation. At the landscape scale, fragmentation may hinder dispersal by increasing the distances required to reach new habitat patches and posing challenges to the transience phase. For example, orientation in agricultural matrix can be hampered especially for non-flying animals such as small reptiles in high crop types (Kay *et al.*, 2016), and sublethal doses of insecticides can negatively affect insects' cognitive abilities, including their memory and navigation capacities (Tison *et al.*, 2016). In addition, strong habitat specialists may perceive matrix as barrier and move greater distances to take detours (Knowlton & Graham, 2010). Yet this cannot be generalized and requires consideration of species' mobility (Kniowski & Gehrt, 2014) or internal state (Keeley *et al.*, 2017). Another obstacle to movements are roads and railways, and their effect on mobility depends on movement-related factors such as familiarity with passage locations (Ascensão *et al.*, 2014). At the other extreme, the removal of historical dispersal barriers through human trade and transport activities is problematic with respect to invasive species and disease spread (Hulme, 2009). Non-human biotic vectors, that is genetic linkers, may likewise act as primary introducers (Reynolds *et al.*, 2015), but also play a critical role in secondary dispersal once introduced (Moravcová *et al.*, 2015).

With a heightened awareness of the importance of movement for other ecological processes and higher-level patterns (Jeltsch *et al.*, 2013; Bauer & Hoye, 2014; Barton *et al.*, 2015; Jønsson *et al.*, 2016), more research focuses on the links between environmental change, movement processes, population and species persistence, and community dynamics. However, few studies connect all of these components. Therefore, we need a framework that joins the different parts of the story, and we hope to contribute to this with our framework of movement-mediated community assembly and coexistence.

VI. CONCLUSIONS

(1) Any component of individual-level movement processes, as summarized in the movement ecology framework, can scale up to significant effects at community level. That is, details of how animals move (motion capacity), how they orient in space and time (navigation capacity), and how they make movement decisions in response to external stimuli (e.g. (micro)habitat selection, fine-scale individual interactions) and internal state (e.g. movement propensities and frequencies) matter for metacommunity dynamics, the different states of community assembly and species coexistence mechanisms. Although all movement components work in unison, often one or two components may be critical in their effect at the community level.

(2) Despite an increasing awareness of the importance of movement for other ecological processes, there remains a gap between studies that investigate the details of movement, which are typically single-species studies, and studies that examine community composition, in which movement is often considered simplistically at species level. This gap is likely due to large differences in time scales between individual movement processes and community-level effects. The studies that go furthest in bridging the gap typically employ computer simulations.

(3) To achieve a true integration of individual-based and community-based perspectives, we need concepts that link both perspectives and bring together new observations, experiments, and computational tools:

(i) We must recognize the emergence of species' mobility from individual-level movement processes.

(ii) We recommend to make use of improvements in direct and indirect tracking methods to extend movement-process studies to small taxa and to track multiple individuals of a community concurrently.

(iii) Facilitated by tracking technology, experiments can be set up with the same design both in the laboratory with microorganisms and in the field with macroorganisms to test causal links between movement mechanisms and community-level patterns.

(iv) We urge for an advancement of statistical methods to keep up with the analyses of newly available rich data sets.

(v) We expect computer-simulation models to increase in their applicability in extrapolating insights from short-timescale observations and experiments to ecological timescales through complexity-reducing trait-based approaches and improved links with data.

(4) In addition to increasing awareness for the many ways in which movement processes affect the mechanisms that drive community composition, we hope to achieve two main goals: to encourage community ecologists to consider more explicitly the complexities of movement processes and to stimulate movement ecologists to perform more multi-species analyses within and across trophic levels and link these to community-level mechanisms.

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TABLES

Table 1. Community-level impacts of movement. For each movement type, specific components and characteristics of the movement process scale up to patterns in mobility or abiotic and biotic external factors, which in turn affect metacommunity dynamics (i.e. the extent to which species sorting, mass effects and patch dynamics occur), the different steps of community assembly, and coexistence mechanisms (see also Fig 1).

Movement type	**Community-level impact**	**Relevant movement features**	
		Emergent mobility or environmental pattern	**Movement characteristics**
Dispersal	**Direct effects**		
	Regional species pool	Frequency of long-distance dispersal events	Adaptation to long-distance dispersal (including distance)
	Metacommunity dynamics	Dispersal rate Dispersal distance	Motion capacity Orientation mechanism Habitat selection Internal state (e.g. exploration behavior)
	Dispersal limitation		
Migration	**Direct effects**		
	Regional species pool dynamics	Arrival time	Movement mode Travel speed Daily travel distance Stopover duration
		Route & destination sites	Orientation mechanism Habitat selection
	Niche differences	Migration versus residency	
	Mobile-link effects		
	Metacommunity dynamics (genetic links)	Dispersal rate Dispersal distance	Migration distances Use of stopover sites
	Dispersal limitation (genetic links)		
	Abiotic environmental filter (resource links)	High or pulsed nutrient input	Migration as strategy
	Biotic filter (process links)	Pulsed predation*	Migration as strategy
Station-keeping movement	**Direct effects**		
	Niche differences: Resource partitioning	Differentiation in mobility Spatio-temporal segregation	Movement rates and distances (within & between foraging arenas) Residence time (Micro)habitat selection Plasticity in movement strategy
	Interference and apparent competition	Spatio-temporal segregation	Fine-scale interspecific interactions (avoidance & attraction)
	Fitness similarity: Energy trade-offs	Differences in mobility	Locomotion pattern Movement rates Movement distances

	Mobile-link effects		
	Metacommunity dynamics (genetic links)	Dispersal rate Dispersal distance	Recurrence in movement Movement rates Movement-physiology interactions
	Environmental filter (resource links)	Local high-intensity space use and nutrient input	Recursive movement Residence time (Micro)habitat selection Fine-scale interspecific interactions (e.g. predator-prey)
	Metacommunity dynamics Successional mosaics Abiotic-biotic filter (resource & process links)	Environmental spatial heterogeneity	Recurrence in movement Inter-patch movement rates
	Niche differences: Negative frequency-dependent growth (process links)	Distance- & density-dependent predation pressure	Orientation: response to cues
Nomadism	**Direct effects**		
	Niche differentiation: Resource partitioning	Nomadism as strategy	Motion capacity
	Fitness similarity	Scale differences in foraging	Nomadism as strategy
	Mobile-link effect		
	Dispersal limitation (genetic links)	Dispersal rate Dispersal distance	Movement distances Habitat selection Navigation: orientation mechanism
	Successional mosaics (process links)	Spatiotemporal disturbance pattern	Nomadism as strategy

[*] includes herbivory and parasitism

FIGURES

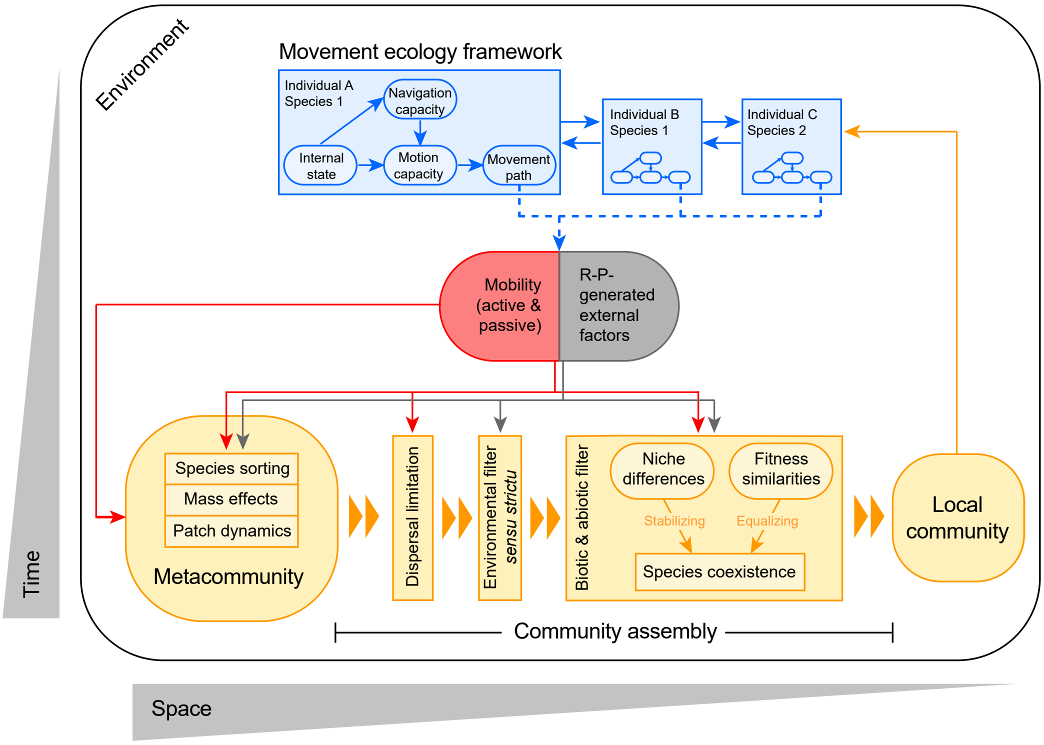


Figure 1. The movement ecology framework for interacting individuals (upper part in blue), unified with major concepts from metacommunity theory, community assembly and coexistence theory (lower part in yellow). Square boxes depict processes, and rounded shapes represent patterns. In movement ecology, movement is seen as a behavioural process. In contrast, in community ecology, movement typically appears as species-level mobility, which emerges (dotted arrows) from the underlying movement processes of individuals, either as active mobility or passive mobility conferred by genetic mobile links and abiotic vectors. In addition, movements by resource and process links scale up (dotted arrows) to influence abiotic and biotic environmental conditions (R-P-generated external factors) that drive metacommunity- and community-level processes. Note: We omit all factors at the community level that are not directly related to movement.

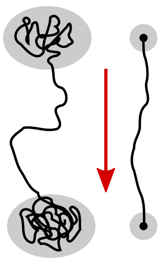
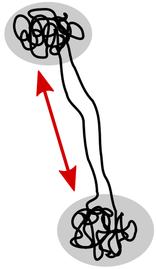
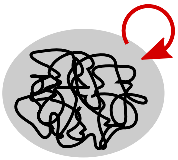
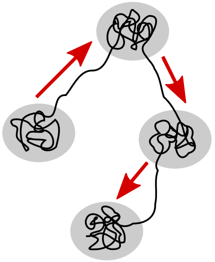
Movement type Long-term pattern	Characteristic features and function	Spatial scale
Dispersal 	*Uni-directional movement away from the natal and towards the reproductive site (natal dispersal; once per lifetime) or movement between multiple sites of reproduction (breeding dispersal; multiple times per lifetime).* Dispersal is an important mechanism for maintaining genetic diversity, both for actively and passively moving organisms. Passively dispersing organisms often have a specific life-cycle stage (e.g. spore, egg, seed) that is adapted to being transported by abiotic vectors (e.g. wind or water) or biotic vectors (genetic mobil links).	Direct effect: • Regional • Interregional
Migration 	*Bi-directional movements between distinct breeding and non-breeding sites, which are often long-distance in relation to body size.* Migrating animals use seasonally changing resources or escape seasonal risks (seasonal migration; one to multiple times per lifetime), or complete their life cycle in different habitats, e.g. aquatic and terrestrial (life-cycle migration; once per lifetime). Outside the actual migratory phase, individuals may perform station-keeping or nomadic movement within their breeding and non-breeding range.	Direct effect: • Regional • Interregional Mobile-link effect: • Regional • Interregional
Station-keeping movement 	*Daily movements within a restricted area (home range).* Range-resident animals preform station-keeping movements throughout their lifetime, possibly excepting a dispersal phase. Although home ranges can be dynamic in space and time, they are typically used throughout the reproductive lifetime of an individual. We also refer to station-keeping movements when migratory animals perform their daily movements such as foraging outside the migratory phase in restricted areas.	Direct effect: • Local Mobile-link effect: • Regional
Nomadism 	*Undirected movements between irregularly shifting transient core areas (multiple times within months, a year, or a lifetime).* Nomadic animals typically use resources that irregularly change in space and time. Nomadic movements between transient core areas are interspersed with daily local movements. In this way, some nomadic animals cover large distances during their lifetime. Nomadism may also occur seasonally, e.g. only during the non-breeding season.	Direct effect: • Loca • Regional Mobile-link effect: • Regional

Figure 2. The four basic types of movement, which can be distinguished by different patterns that the underlying movement processes generate over an organism's life time (picograms) but also serve different ecological functions. The movement types occur at different spatial scales, where they have direct effects on moving focal species and their competitors, and may further confer mobile link functions to other organisms (typically at other trophic levels) at scales that differ from those of the direct effects. Pictograms adapted from Barton et al. (2015).