Filling the Information Gap in Meta-Ecosystem Ecology

Chelsea J. Little[1,2,*], Matteo Rizzuto[3*], Thomas M. Luhring[4,†], Julia D. Monk[5,†], Robert J. Nowicki[6,†], Rachel E. Paseka[7,†], James C. Stegen[8,†], Celia C. Symons[9,†], Frieda B. Taub[10,†], Jian D. L. Yen[11,†]

[*]equal contribution: correspondence to chelsea.little.does.ecology@gmail.com and matteomrizzuto@gmail.com

[†]listed alphabetically

[1] Biodiversity Research Centre, 2212 Main Mall, University of British Columbia, Vancouver, BC, Canada, V6T 1Z4

[2] Department of Zoology, 2212 Main Mall, University of British Columbia, Vancouver, BC, Canada, V6T 1Z4

[3]Department of Biology, 232 Elizabeth Avenue, Memorial University of Newfoundland, St. John's, NL, Canada, A1B 3X9

[4]Department of Biological Sciences, Wichita State University, 1845 Fairmount Street, Wichita KS, USA 67260

[5]School of the Environment, Yale University, New Haven, CT, USA, 06511

[6]Elizabeth Moore International Center for Coral Reef Research and Restoration, Mote Marine Laboratory, 24244 Overseas Highway, Summerland Key, FL, USA, 33042

[7]Department of Ecology, Evolution, and Behavior, University of Minnesota, Saint Paul, MN, USA, 55108

[8]Pacific Northwest National Laboratory, Richland, Washington, USA

[9]Department of Ecology and Evolutionary Biology, University of California, Irvine, Irvine, CA, USA, 92697

[10]School of Aquatic and Fishery Sciences, University of Washington, Seattle, WA, USA 98195

[11]School of BioSciences, University of Melbourne, Melbourne, Australia

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Abstract

Fluxes of matter, energy, and information over space and time contribute to ecosystems' functioning. The meta-ecosystem framework addresses the dynamics of ecosystems linked by these fluxes, however, to date, meta-ecosystem research focused solely on fluxes of energy and matter, neglecting information. This is problematic due to organisms' varied responses to information, which influence local ecosystem dynamics and can alter spatial flows of energy and matter. Furthermore, information itself can move between ecosystems. Therefore, information should contribute to meta-ecosystem dynamics, such as stability and productivity. Specific subdisciplines of ecology currently consider different types of information (e.g., social and cultural information, natural and artificial light or sound, body condition, genotype, and phenotype). Yet neither the spatiotemporal distribution of information nor its perception are currently accounted for in general ecological theories. Here, we provide a roadmap to synthesize information and meta-ecosystem ecology. We begin by defining information in a meta-ecological context. We then review and identify challenges to be addressed in developing information meta-ecology. Finally, we present new hypotheses for how information could impact dynamics across scales of spatio-temporal and biological organization.

Glossary

Agent: An interpreter of information (Sharov 2010); in an ecological context, agents exist at multiple levels of organization (cells, organisms, populations, etc.).

Aggregate Response to Information: Information reception and processing by a group, population, or community without the additional step of transmission between individuals *[analogous to aggregate risk (*Robson *et al.* 1999)*].*

Ecosystem Function: The flow of energy, matter, and information through the biotic and abiotic compartments of an ecosystem (Díaz *et al.* 2015).

External Information: Abiotic or biotic information an agent [organism] perceives from its environment; also known as *condition dependence* in the context of dispersal (Clobert *et al.* 2009).

Idiosyncratic Information Transfer: Information transmitted through a group (or part of a group) from one individual, which has processed or interpreted it, to (an)other individual(s) *[analogous to idiosyncratic risk* (Robson *et al.* 1999)*]*.

Internal Information: Information intrinsic to the agent [organism], for example genetic information, phenotypic traits, or body condition; also known as *phenotype dependence* in the context of dispersal (Clobert *et al.* 2009).

Meta-ecosystem: A group of ecosystems connected by cross-boundary flows of energy, matter, and information (Loreau *et al.* 2003b) — an arrangement that is ubiquitous in nature.

Meta-ecosystem dynamics: The dynamic flows of energy and material through trophic compartments of a meta-ecosystem, and their influence on its temporal stability in space.

Perceptual range: The distance at which an agent can perceive or detect information (Lima & Zollner 1996).

Semiotic information: Something that decreases an agent's [individual's] uncertainty about the state of the world (O'Connor *et al.* 2019); syntactic information as it is interpreted by an agent.

Syntactic information: The non-random arrangement of matter or energy in space or time (O'Connor *et al.* 2019).

Trophic compartment: A group of functionally-similar abiotic resources or producer or consumer organisms [comprising multiple taxa], used in ecosystem models.

Meta-Ecosystem Ecology: The Information Gap

Interactions between organisms and the environment are structured in space (Lovett *et al.* 2005). Ecosystems are not isolated or self-contained (see **Box 1**), but rather intrinsically open and connected. Ecological frameworks increasingly incorporate connections among ecosystems. This is evident in metapopulation (Hanski & Gilpin 1991; Moilanen & Hanski 1998; Ovaskainen & Saastamoinen 2018), metacommunity (Leibold *et al.* 2004; Leibold & Chase 2017), and landscape (Wiens *et al.* 1993) ecology. One such framework is *meta-ecosystem* ecology (see the **Glossary** for a definition of italicized terms), which integrates the movement of organisms with a landscape ecology perspective on movement and cycling of matter and nutrients, considering both flows among *trophic compartments* and within and among ecosystems (Loreau *et al.* 2003b). Conceptualizing the world as a network of meta-ecosystems has helped our understanding of the importance of cross-ecosystem fluxes to biodiversity, *ecosystem function*, stability, and spatiotemporal dynamics, as well as the importance of spatiotemporal overlap in regulating those fluxes and their feedbacks (Gounand *et al.* 2018a; Schiesari *et al.* 2019). For example, theoretical work has shown that resource flows between ecosystems often destabilize meta-ecosystems, while exchanges of consumers biomass can stabilize them (Marleau *et al.* 2010; Gounand *et al.* 2014), and that explicitly incorporating nutrient fluxes can affect predicted biodiversity in meta-ecosystems (Gravel *et al.* 2010). Empirical work has complemented meta-ecosystem theory with case studies. For example, in coastal ecosystems, trophic and non-trophic interactions depend on not only the magnitude, but also the temporal intermittency of pulsed subsidies from upwelling (Menge & Menge 2013), and resource fluxes from marine to terrestrial systems can be interrupted by changes in recipient ecosystems' community composition, altering their internal nutrient stocks and fluxes (Young *et al.* 2010).

Box 1: Information in Open Ecosystems

The simplest conception of an ecosystem is as a Closed Ecological System (CES) with internal cycling of materials and no material exchanges with other ecosystems or the broader outside world, apart from energy (light) inputs and heat outputs (Taub 1974). Similar to how meta-populations differ from isolated populations because the former allows for emigration and immigration of individuals (Levins 1969), meta-ecosystems differ from CESs because they allow for transfer of materials across ecosystem boundaries. Material transfer across ecosystem boundaries is so common that meta-ecosystems are nearly ubiquitous and are often simply referred to as ecosystems. Why is this important? Studies of CESs indicate that isolating ecosystems limits chemical cycling, contributing to the potential of ecosystem collapse, most obviously the loss of grazers (Taub & McLaskey 2013, 2014; Taub 2019). Based on these results, one emergent property of meta-ecosystems is that the fluxes of matter, energy, and information across ecosystem boundaries confers stability through a material version of the "rescue effect" (*sensu* Stacey *et al.* 1997), which allows them to complete elemental cycling. Indeed, theoretical work has shown that consumer dispersal between high- and low-productivity ecosystems stabilizes them (Gounand *et al.* 2014).

It is likewise interesting to compare information in CESs versus meta-ecosystems. Energy and materials are required to store, transmit, interpret, and reproduce information (O’Connor *et al.* 2019): for example, issuing a vocal call, displaying a visual phenotype, or reproducing genetic material all require energy. Thus, in a truly closed system (adiabatic), the finite supply of energy and materials in the CES would constrain information use and storage; conversely, constraints to organismal use of information could limit the efficiency of energy and material cycling, jeopardizing the stability of the CES. In a meta-ecosystem, not only can organisms use information arising from outside their local context because the system is open, but energy and material subsidies can support the storage and use of that information. Thus, as for other ecosystem dynamics, considering the effects of cutting off cross-ecosystem fluxes serves as an illustration for why spatial connections between ecosystems are important in an information context.

Meta-ecosystem ecology thus addresses flows of organisms and materials among ecosystems, but what of another essential component of life — information? Life is the interaction of energy and matter shaped by the influence of information (Fong 1973; Miller 1978; O’Connor *et al.* 2019). Matter is the building block: the raw materials from which structures are made. Energy is contained in matter, and life requires energy to grow and survive. Information is the non-random arrangement of energy and matter over space and time. Its interpretation reduces uncertainty about current and future states of a system. Cells, individual organisms, populations, and ecosystems contain, transmit, respond to, and copy information; information allows life to reproduce, adapt, and evolve. Fundamental interactions between organisms and their environment(s) depend on stocks and flows of all three building blocks of life. These interactions occur at multiple spatio-temporal scales, bridging landscapes and ultimately establishing biological pathways that span from local to global scales (Doughty *et al.* 2016; Gounand *et al.* 2018a, b; Schiesari *et al.* 2019).

As a field, ecology has not yet grappled explicitly with the dynamics of information in linked ecosystems. This is despite the fact that the movement of information necessarily accompanies the movement of energy and matter, and that information flow and information use by organisms both mediate and contribute to spatial feedbacks in ecological dynamics (Gil *et al.* 2018; O’Connor *et al.* 2019). Furthermore, the measurement of information is relevant both to organisms (e.g., through signals and cues; O’Connor *et al.* 2019) and to those studying biological systems (e.g., the use of Shannon entropy to study trophic or species diversity [Rutledge *et al.* 1976; Pueyo *et al.* 2007; Harte 2011] or genetic similarity as a measure of population isolation [Holsinger & Weir 2009]). Despite the widely-appreciated importance of information in ecology, multiple operational definitions of "information" inhibit its coherent integration into ecological concepts (O’Connor *et al.* 2019), including meta-ecosystem research. Not accounting for information results in blind spots and contributes to a lack of predictability. For example, many of the mechanisms leading to “ecological surprises” (Doak *et al.* 2008; Filbee-Dexter *et al.* 2017) result from the omission of information sensing and responses by organisms.

Among the reasons that information is currently absent from the meta-ecosystem framework is that individuals — the units that ecologists most often consider to respond to information — are not always explicitly modeled. A general limitation in the meta-ecosystem framework may be that meta-ecosystems are typically depicted with flows of resources and/or biomass among trophic compartments within and between ecosystems (Gravel *et al.* 2010; Gounand *et al.* 2014; Marleau *et al.* 2014), with the dynamic of interest being the stocks and flows of these trophic compartments, not individuals (but see Earl & Zollner 2017; Bampoh *et al.* 2019). However, trophic compartments can be difficult to measure empirically, and many ecologists are interested in interactions between units at other levels of biological organization, e.g. populations or individuals. Furthermore, by ignoring biological mechanisms operating within trophic compartments, the indirect effects of organismal behavior, life history, or development on the size of these same compartments and the fluxes between them are mostly unaddressed (Massol *et al.* 2017; Gounand *et al.* 2018a). Crucially, all of these mechanisms depend on information use by the organism(s). In meta-ecosystems, information — and organisms' responses to it — may affect the way that perturbations are propagated across levels of biological organization and ecosystem boundaries. Predicting the potential spatial 'cascade' of perturbations is a key promise of meta-ecosystem theory (Gounand *et al.* 2018a), yet it may be greatly hindered by omitting interactions between organisms (or groups of organisms) and information.

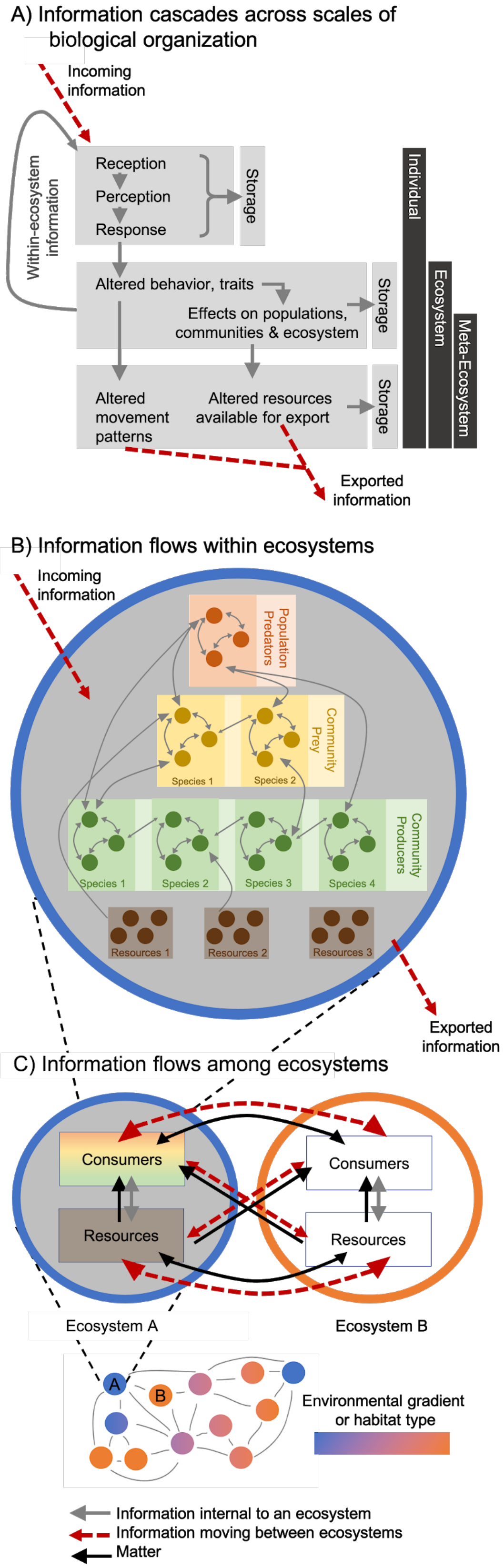
Here, we review current knowledge of information in ecosystems and identify a path towards including this third building block in the meta-ecosystem framework. We begin by discussing information and its definition as used in the ecological literature. We then briefly review evidence of how information influences ecosystem dynamics through organismal behavior, development, and life history. Next, we discuss challenges that must be addressed before the effects of information can be quantified in theoretical and empirical meta-ecosystem research. Finally, we highlight key frontiers in an information-based meta-ecosystem ecology and make initial hypotheses about how its incorporation could alter assumptions and predictions about meta-ecological dynamics.

What is information?

If information is important and neglected, what is it, and why has it been so challenging to incorporate into ecological frameworks? Here, we adopt a broad definition: information is something that decreases an individual's uncertainty about the state of the world (Anderson 2008). Within this broad definition of information lie other precisely-defined concepts. A key distinction is in treating information in terms of its quantity (*syntactic information*) or quality (*semiotic information*) (Donaldson-Matasci *et al.* 2010; O'Connor *et al.* 2019). Syntactic information is the information generated by the arrangement of matter or energy (or "objects" more generally) in space and time, such as the time of sunrise, the rhythm and pitch of animal vocalizations, or even the number of species in an area. By contrast, semiotic information is the meaning associated with syntactic information and it may be measured as the fitness value of syntactic information. For example, consider a sign warning of a specific danger. Two observers (*agents*) may receive the same syntactic information (the sign's contents) but assign different semiotic information to it based on how much that syntactic information influences fitness (e.g., one agent might not understand the sign). This example illustrates that, while related, syntactic and semiotic information differ both fundamentally and in their measurement. A consequence of these differences is that semiotic information involves an interpretative agent, while syntactic information does not (Short 2007). For example, the proverbial tree that falls when no one is around will generate syntactic information (a rearrangement of matter and energy in space and time) but, with no agent to interpret it, it will not generate any semiotic information.

Ecologists often view individual organisms as agents that take in and process information, with less focus on how information functions at higher levels of organization. Another distinction is between *internal* and *external information*. Internal information includes genetic material, body condition, and traits, and may be perceived by an organism (e.g., hunger, water stress, reproductive status) or hard-coded (e.g., genetic and trait information). External information such as environmental conditions or biotic interactions, by definition, requires perception by an organism to elicit a response. While nature is full of potential external information, this information can only affect (meta-)ecosystem dynamics through organismal responses if there is an agent to perceive it; otherwise, this information never becomes "realized" (*sensu* Wagner & Danchin 2010). The effects of individual agents processing information can spread through levels of biological organization to affect populations, communities, ecosystems, and meta-ecosystems (**Figure 1**). Multiple agents in a population or community may respond to the same information. *Idiosyncratic information transfer* from one individual to another or simultaneous, *aggregate response to information* by many agents (analogous to idiosyncratic and aggregate risk; Robson *et al.* 1999) can amplify the effects of information on ecosystem dynamics to different degrees. Through behavioral modifications, individual-level responses can thus generate information that cascades through other individuals to have consequences for populations (e.g., schooling), communities (e.g., trophic cascades), and ecosystems (e.g., alteration of the environment) (Beschta & Ripple 2006; Schmitz *et al.* 2010).

Understanding how individual responses to information cascade to higher levels of organization is thus a promising research avenue through which to understand ecosystem and *meta-ecosystem dynamics*. Although often transferred with energy or matter, information (particularly semiotic information) possesses unique properties that may require different methods of study than energy or matter. For example, semiotic information is not conserved like energy or matter; its value differs among individuals, and — although it can be transferred by energy or matter — information can also be transferred by the absence of energy or matter (e.g., the sudden absence of a normally common predator can carry meaning). These consequences of information transfer are highly context-dependent, often depending on an individual agent's response to a cue (O'Connor *et al.* 2019), thus making them difficult to study in traditional ecological frameworks. Nevertheless, the consequences of information flux in ecosystems have been clearly established (Schmitz *et al.* 2010) and information should be viewed as a critical but distinct currency that flows among ecosystems similarly to matter and energy (**Figure 1**). Through its effects on individuals, the processing of information can alter energy and matter transfer at all levels, from genes to ecosystems.



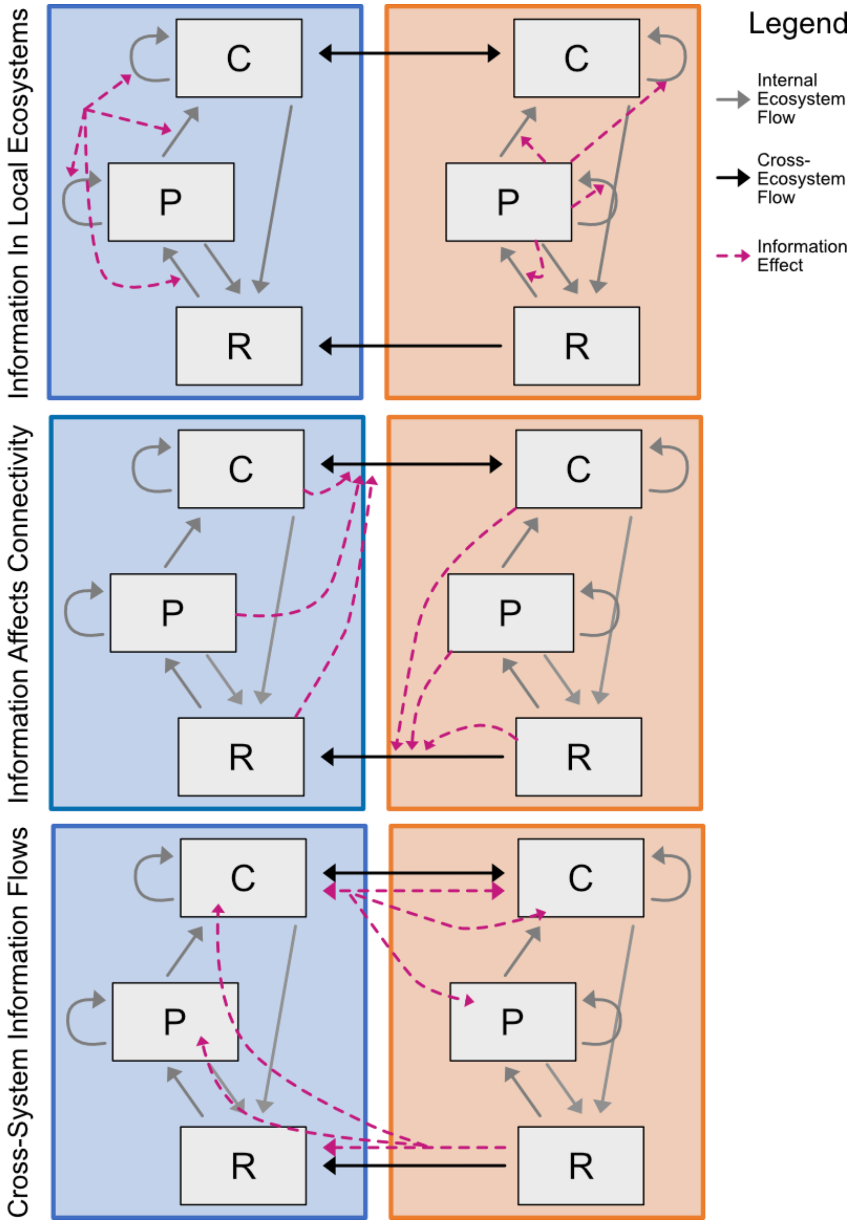
< Figure 1. In a meta-ecosystem framework, information is exchanged within ecosystems and across ecosystem boundaries. A) Once information arrives in an ecosystem, it can impact every level of biological organization, and/or be stored to influence future dynamics. Individuals act as receivers, and their response can ultimately affect ecosystem dynamics and the connectivity of ecosystems across the landscape. B) Within ecosystems, individuals are exchanging information within and between species (gray arrows) and receiving information from the abiotic environment. Information can also enter from, or leave to, another ecosystem (red arrows). C) Meta-ecosystem studies often consider matter and energy exchanges among ecosystems (black arrows); however, there is also information exchanged between ecosystems (red arrows).

Information in meta-ecosystems

The flow of information within and among ecosystems can be envisioned as a web overlaid on a meta-ecosystem, indicating the information that accompanies flows of matter and energy (**Figure 1**). Information can influence meta-ecosystem dynamics in three ways: (1) by affecting local ecosystem dynamics by eliciting changes in the behavior, life history, and development of individuals; (2) by influencing movement of organisms and materials, altering meta-ecosystem connectivity; and (3) by arriving in an ecosystem from an external source and influencing local ecosystem dynamics (**Figure 2**).

Information influences local ecosystem dynamics

Organisms respond to semiotic information to potentially increase their fitness via life history, behavioral, and developmental responses (Schmitz *et al.* 2010). The sum of individual organisms' states and interactions (Schmitz *et al.* 2010; Massol *et al.* 2011) generate the high-level processes such as production, respiration, and nutrient cycling that are the focus of ecosystem ecology. Therefore, information scales from individual-level effects to ecosystem-level consequences (Massol *et al.* 2017; Gounand *et*



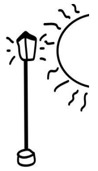
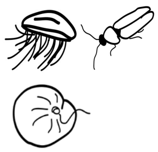
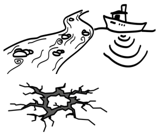
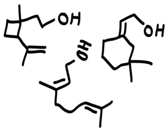
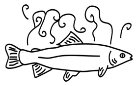
< Figure 2. The effects of information on a conceptual two-patch meta-ecosystem model with bidirectional movement of consumers (C) and unidirectional movement of resources (R), and negligible dispersal by producers (P). Empirical meta-ecosystems are characterized by a variety of movement types, including of producers and between dissimilar trophic compartments, for example producers from one ecosystem to detritus/resources in another, however here we select a few flows for simplicity. *(Top panel)* Within each patch, abiotic (shown in blue ecosystem) and biotic (shown originating from producers in orange ecosystem) information influence how energy and/or biomass are transformed from the resource to producer to consumer compartments before being recycled back into resources (straight arrows), and the population/community dynamics of producers and consumers (semicircular arrows). (*Middle panel)* Information about resources, producers, and density of other consumers inform cross-ecosystem movement of consumers (shown in blue ecosystem) and the quality, quantity, timing, and duration of cross-ecosystem resource flows (shown in orange ecosystem). (*Bottom panel*) Information moves among ecosystems with movement of organisms (shown in orange ecosystem) and resources (shown in blue ecosystem), affecting organisms in the recipient ecosystems. Information effects are shown in one or the other of patches for visual clarity but, in reality, all mechanisms occur across the meta-ecosystem.

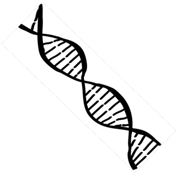
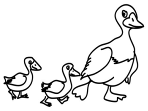
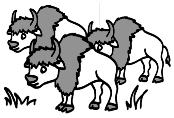
al. 2018a) (**Table 1**), which manifest through one to few agents (e.g., individuals or a population within a species), or many agents (individuals from diverse taxa) (Schaefer *et al.* 2004). For example, information can alter energy flux (Barnes *et al.* 2018) through behavioral responses: internal information in snails (hunger levels) in the rocky intertidal alters their behavioral response to predator cues (external information). Thus, a combination of internal and external information determines whether snails contribute to trophic energy flux by staying put and being preyed upon, or transport biomass to another habitat patch by fleeing the tide pool (Gravem & Morgan 2016). Life history responses to information can influence growth and production. For example, plant seeds use genetic and epigenetic information to interpret stimuli such as day length, water availability, or fire as indicators of whether future conditions are suitable for germination or whether dormancy should continue (Baskin & Baskin 1998; Karban 2008). Developmental responses to information can also alter energy flux and nutrient cycling, for example when tadpoles perceive predator presence and develop tail muscles at the expense of longer guts, leading to less efficient nutrient extraction and thus slower growth (Relyea & Auld 2004) and altered consumer nutrient recycling via excretion/egestion (Liess *et al.* 2015). Information also mediates microbial contributions to ecosystem dynamics, for example, by catalyzing the formation of (Hall-Stoodley *et al.* 2004) and dispersal from (McDougald *et al.* 2012) biofilms, which alter how bacteria and other microorganisms contribute to carbon and nutrient cycling. These ecosystem effects can form feedback loops as altered information elicits further behavioral, life history, or dispersal responses (Earl & Zollner 2017; McInturf *et al.* 2019).

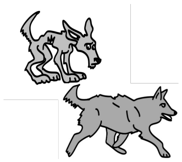
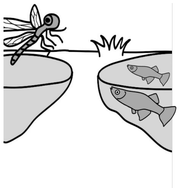
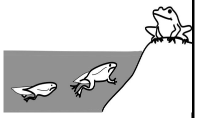
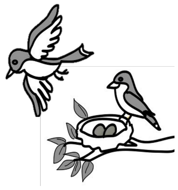
Information influences ecosystem connectivity

Ecosystem heterogeneity in space and time influences the ability of organisms to survive and reproduce. This heterogeneity, in turn, makes up information that can alter the functional connectivity of ecosystems by altering the movement of organisms. Examples of informed organismal movement between ecosystems abound (**Table 1**). For instance, phytoplankton respond to light, and move nitrogen and phosphorus with them (Salonen *et al.* 1984; Villareal *et al.* 1993). Information affects organisms' dispersal, migration, and foraging patterns at all stages of the movement process. Travelling organisms continuously receive and process information. For example, animals moving across heterogeneous landscapes in search of resources (e.g., food items, refugia from predators, mating partners) move faster when they encounter low-quality habitat, increasing rates of range expansion (Crone *et al.* 2019). This continuous collection of information by the organisms from their environment and their internal state can potentially initiate, halt, or alter their movement among ecosystems (Nathan 2008). Many of these dynamics have also been well documented in plants, where information influences flowering and fruiting, seed dormancy, germination, and nectar production (Rathcke & Lacey 1985; Baskin & Baskin 1998; Veits *et al.* 2019). Thus, heterogeneity in information landscapes generates continuous change in the flow of information to agents. These informational changes can alter organism behavior and movement, with profound consequences. Information therefore affects organismal abundance and genetic composition in connected ecosystems across a landscape, and ultimately influences the transfer of materials and information among ecosystems (see **Figure 3**), which in turn may feed back to reinforce ecosystem heterogeneity (Monk *et al.* 2020).

Table 1. Ecological effects of varying types of information, and how movement between ecosystems depends on and conveys information.

Types of Information Flows					
	Syntactic Information	**Proximity and Scale**	**Similarity of patches**	**Source**	**Ecological Effects of Information/Transport**
	Light	Local, possibly regional	High and/or low	Abiotic or artificial origin	Light is a cue for development (Fankhauser & Chory 1997) and behavior (Karban 2008); visibility affects trophic interactions (Gliwicz 1986) and perceived risk thereof (Palmer *et al.* 2017), thus altering behavior; navigational aid and indicator of spatial positioning (Ragni & Ribera D'Alcalà 2004) (**Box 2**)
	Light	Local, possibly regional	High and/or low	Biotic origin	Bioluminescence can function as a cue in enabling or preventing trophic interactions (Young & Mencher 1980; De Cock & Matthysen 2003; Haddock *et al.* 2010)
	Sound/ Sonic signaling	Local and possibly regional	High and/or low	Abiotic or artificial origin	Sonic information about climate, weather, and fire influence behavior and animal navigation (Paterson *et al.* 2013) (**Box 2**)
	Sound	Local and possibly regional	High and/or low	Biotic origin	Alarm calls, mating calls, and other vocalizations inform behavior (Seyfarth *et al.* 2010); used for navigation (Haddock *et al.* 2010)
	Chemicals	Local and possibly regional	High and/or low	Abiotic or artificial origin	Chemicals produced abiotic processes, including those synthesized by humans, are used as indications of habitat quality or as navigational cues (Dittman & Quinn 1996; Atema *et al.* 2002; Hinojosa *et al.* 2018) **(Box 2)**
	Info-chemicals	Local and possibly regional	High and/or low	Biotic origin	Indicates resource availability or presence of con- or hetero-specifics (Hay 2009) (including reproductive status; Thomas 2011); trophic interactions/risk (Paterson *et al.* 2013; Karban

					*et al.* 2014); navigational cues (DeBose & Nevitt 2008) (**Figure 2**)
	Magnetic Fields	Local to global	High and/or low	Abiotic	Used to navigate at multiple scales (Wiltschko & Wiltschko 1988; Hays 2013)
	Genetic information	Local to global	High	Biotic	Feedbacks from genetic adaptation to ecosystem processes (Ousterhout *et al.* 2018; Abdala-Roberts *et al.* 2019); changes in population dynamics due to (mal)adaptation after alleles introduced (Weeks *et al.* 2017; Kyriazis *et al.* 2019)
	Cultural information	Local to regional	High and/or low	Biotic	Organismal behavior transmitted to new individuals via observation or learning alters behavior, life history, movement patterns, and trophic interactions (Helfman & Schultz 1984; Gil *et al.* 2018; Jesmer *et al.* 2018)
Biotic Flows (Note: the organisms moving transmit the types of information described above; below, we primarily describe their information use)					
Photo	**Flow Information**	**Proximity and Scale**	**Similarity of patches**	**Types of Information**	**Ecological Effects of Information/Transport**
	Movement of mobile consumers foraging in many similar patches	Local to Regional	High	Received: external information determines foraging pattern	Consumers bring resources from other patches to “home” patch (Lai *et al.* 2017), and can affect dynamics in other ecosystems directly (trophic interactions) or indirectly (by leaving information about their presence; Grostal & Dicke 1999)
	Movement of mobile consumers across multiple ecosystem types	Local to regional	Low	As above	Similar as above, but for consumers foraging in multiple ecosystem types (field/forest, or riverside/ terrestrial, or use of ice to access aquatic habitats in winter) (**Figure 2**)

	Condition-dependent dispersal	Local to regional	High: Organism must be able to live in both source and target patch	Received: internal information on body condition, genetic information	An individual's own body condition or phenotype can influence dispersal propensity and distance, thus affecting (meta-)population processes and resource flows (Bowler & Benton 2005; Clobert *et al.* 2009; Endriss *et al.* 2019). Dispersers convey information as they travel and may bring it to new patches.
	Context-dependent dispersal	Local to regional	High: Organism must be able to live in both source and target patch	Received: internal and external information	An individual's perception of biotic and abiotic conditions can alter dispersal propensity and distance traveled (Bowler & Benton 2005; Clobert *et al.* 2009; Endriss *et al.* 2019); ecological effects and conveyance of information as above
	Life History Movement	Local	Typically low (life stages live in different ecosystem types)	Received: external and possibly internal information	Amphibians use information to navigate and select breeding pools (Buxton *et al.* 2017b); conspecific density and predator cues alter timing of metamorphosis and emergence to a new ecosystem (Relyea & Auld 2004)
	Migration Settlement Decisions	Continent / global	High to low	Received: external and internal information	Animals use a variety of information sources to decide where to settle after migration, e.g. infochemicals (Dittman & Quinn 1996) or social information (Doligez 2002)

In addition to abiotic information and structural cues, both conspecific (Greene & Stamps 2001) and heterospecific (Goodale *et al.* 2010) presence and performance can provide information about habitat quality (Parejo *et al.* 2005). For example, birds alter movement between ecosystems based on external information about the quality and quantity of conspecific offspring (Doligez 2002). Female frog pond visitation may depend on information about male body size, condition, and overall attractiveness inferred from male frogs' songs (Bernal *et al.* 2006; Akre *et al.* 2011; Ziegler *et al.* 2016). Perceived predation risk can similarly shape prey distribution as highlighted in the 'landscape of fear' concept (Gaynor *et al.* 2019). For example, frogs preferentially oviposit in fishless ponds where survival of their offspring is higher (Buxton *et al.* 2017b), while dolphins, dugongs, and other megafauna alter their habitat use patterns at landscape scales in response to predictable cycles of predation risk by tiger sharks (Heithaus *et al.* 2012). Because of this attunement to predictable informational cues, "ecological traps" can

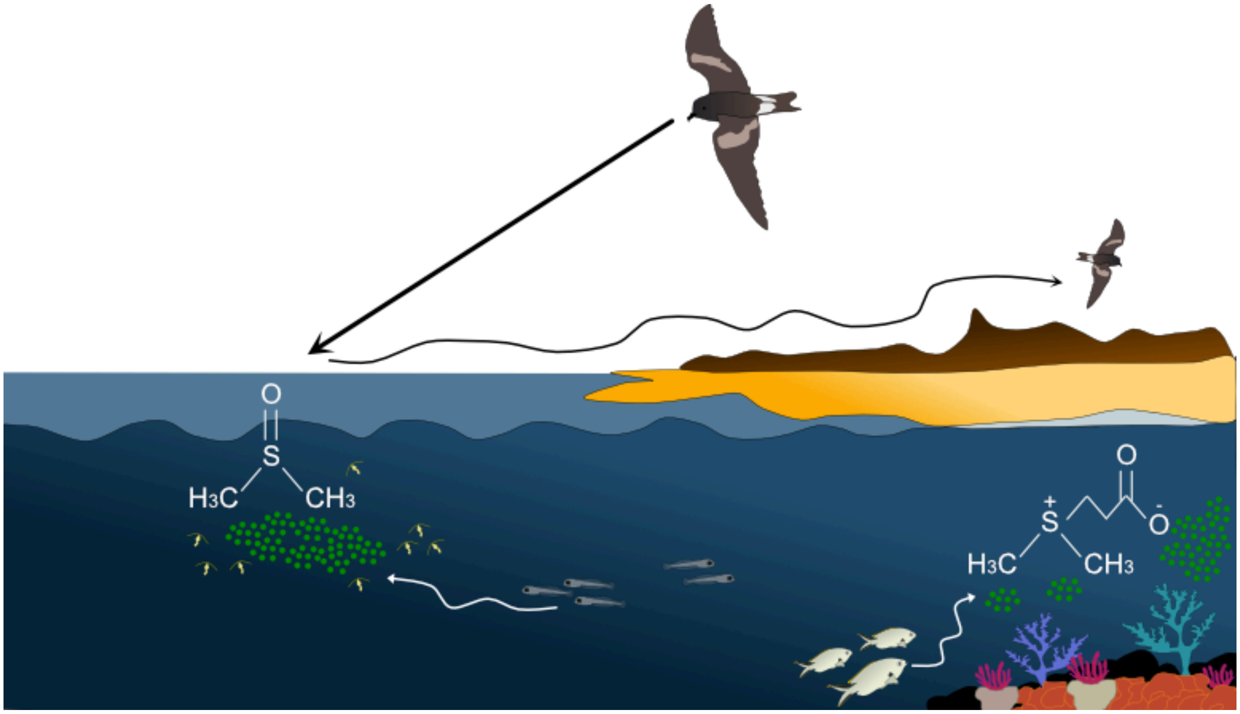


Figure 3. Dimethyl sulphide (DMS, left) and the other chemical compounds in its biochemical pathway (such as dimethyl sulfoniopropionate, DMSP, right) are released by marine phytoplankton after senescence or consumption by grazers (Stefels *et al.* 2007). High DMS concentrations convey information about areas with high productivity due to large phytoplankton populations and can also indicate the presence and activity of zooplankton grazers. This information is used by a variety of taxa in the marine food web. Grazing dinoflagellates and autotrophic and heterotrophic bacteria can orient to DMSP over the scale of nanometers in order to graze or use it as a source of sulfur (Seymour *et al.* 2010). At intermediate scales, some larval reef fish detect and respond to DMS (Atema *et al.* 2002) and juvenile fish to DMSP (DeBose *et al.* 2010). By contrast, seabirds that forage over hundreds to thousands of kilometers can detect even fairly low DMS concentrations and use them as signposts to orient to high-productivity areas for foraging (Nevitt 2008). After seabirds consume prey located using DMS, they fertilize multiple ecosystems: while at sea, their excretions recycle iron, promoting marine productivity (Savoca & Nevitt 2014), while in their breeding colonies the seabirds collectively excrete thousands of tons of marine-derived nitrogen and phosphorus into terrestrial ecosystems (Otero *et al.* 2018). The estimated role of DMS, DMSP, and other infochemicals is likely conservative, as there is evidence that turtles (Endres & Lohmann 2012) and seals (Kowalewsky *et al.* 2006) respond to these infochemicals, but this has not yet been linked to movement. This example also illustrates the potential for disruption of meta-ecosystem information webs in the Anthropocene: plastic debris in the ocean also emits DMS, attracting seabirds without providing the forage they seek (Savoca *et al.* 2016).

develop when cues indicating a favorable habitat become less reliable, leading an organism's evolved habitat preferences to result in reduced fitness (Schlaepfer *et al.* 2002). For example, migratory shorebirds often establish breeding territories on beaches in late winter, when beaches are empty, and birds perceive abundant available habitat near intertidal feeding zones, only to experience high chick mortality due to heavy human recreational activity during midsummer when chicks hatch (DeRose-Wilson *et al.* 2018). These ecological traps are often associated with human alteration of the environment and show how humans can influence meta-ecosystem dynamics via effects on information (Gates & Gysel 1978; see also **Box 2**).

Organismal responses to information affect meta-ecosystem connectivity not only through the movement of living organisms, but also through effects on resource subsidies. Plant detritus and animal carcasses are vital resource flows in meta-ecosystems (Gounand *et al.* 2018b). The effects of such subsidies on recipient ecosystems depend on their quantity, quality, timing, and duration (Marcarelli *et al.* 2011; Schindler & Smits 2017; Subalusky & Post 2018). All of these characteristics depend on organismal use of information. For example, senescence is a phenological life history process which depends on genetic but also environmental information, and thus determines the timing and duration of terrestrial plant detritus subsidies to aquatic ecosystems, and aquatic insect subsidies to terrestrial ecosystems (see also **Box 2**). Genetic information is one determinant of development, leading to intraspecific trait variation which can alter the quality (e.g. stoichiometry) of detritus subsidies and therefore their effects on ecosystems (Crutsinger *et al.* 2014). Meanwhile, the same mechanisms through which animal movement emerges from information use, also contribute to determining when and where animals die. In cases where carcasses are deposited across ecosystem boundaries (e.g. mass drownings of wildebeests or other terrestrial animals, whale carcasses falling to deep ocean habitats), animal use of information affects the quantity and timing of these resource subsidies to any particular location. By influencing this most basal type of connectivity, information plays a fundamental role in shaping the structure and function of meta-ecosystems.

Box 2: Anthropogenic Information & Information Disruption in Meta-Ecosystems

Artificial information from human sources is pervasive and can have non-trivial effects on natural information pathways. For example, an increasing portion of the world, up to 23% of the non-polar land mass as of 2016 (Falchi *et al.* 2016), is subjected to artificial light at night (ALAN). Light is both a resource for primary producers, and thus a driver of ecological (*sensu* Vellend 2010) and evolutionary selection, and information that is used by individuals to time life-history events or determine behavior. Preliminary evidence suggests that ALAN can change the timing of flowering, budburst, and leaf fall in trees (Bennie *et al.* 2016), influence species composition and phenology in grasslands (Bennie *et al.* 2018), and destabilize nocturnal pollination networks—which in turn can influence diurnal ones as well (Knop *et al.* 2017). Such effects can elicit indirect, bottom-up effects altering ecosystem connectivity, for instance by reducing the resources available for herbivores (Bennie *et al.* 2015). Some man-made habitats (e.g., hedgerows, road verges) consistently exposed to high amounts of ALAN are increasingly recognized as important for biodiversity conservation and ecosystem connectivity; might their role be altered under exposure to excess anthropogenic information? How far through the food web, or distance in space, might these effects travel? These are important questions to acknowledge as conservation efforts are made to reduce ALAN and policies begin to address this and other types of pollution in natural environments (Davies & Smyth 2018).

Organisms in meta-ecosystems can potentially perceive information from a variety of sources near and far, both in their home environments and as they move over the landscape. ALAN is an example of how far the response to one type of information can cascade: through trophic levels, space, and time. This is particularly true in aquatic-riparian meta-ecosystems. ALAN entering stream ecosystems affects multiple trophic levels, from the composition and respiration rates of microbial sediment and phytoplankton communities (Hölker *et al.* 2015) to the composition of invertebrate communities (Sullivan *et al.* 2019). ALAN also affects trophic flux by shifting the magnitude of predation through several mechanisms. Within the aquatic ecosystem, light affects predators' behavior and ability to find prey: for instance, ALAN increases sculpin predation on migrating juvenile salmon (Tabor *et al.* 2004). Meanwhile, ALAN can also shift prey availability for terrestrial predators by altering the timing and reducing the quantity of insect emergence from streams (Manfrin *et al.* 2017). This can have mixed consequences: some terrestrial communities have shown reduced food chain length and reduced reliance on aquatically-derived energy (Sullivan *et al.* 2019), though elsewhere ALAN increased aquatic insect emergence and terrestrial predator abundance (Manfrin *et al.* 2017). ALAN effects on terrestrial ecosystems also cascade to aquatic ecosystems by delaying the timing of autumn leaf drop, thus altering the terrestrial-to-aquatic resource flux mediated by plants' phenological responses to light information (Sullivan *et al.* 2019). As these examples show, even a single type of anthropogenic information can substantially alter connectivity across ecosystem boundaries, with profound effects on the functioning of those ecosystems.

ALAN is one of many types of anthropogenic information pollution. Noise pollution is now recognized as a grand challenge in aquatic ecosystems globally (Kunc *et al.* 2016; McWhinnie *et al.* 2017) and is pervasive even in terrestrial protected areas (Buxton *et al.* 2017a), raising the question of their efficacy for conserving ecological interactions. Synthetic chemicals are another increasing aspect of anthropogenic global change with the potential to disrupt natural information pathways. For example, six million metric tons of pesticides are applied per year globally (Bernhardt *et al.* 2017), yet there has been minimal focus on their indirect effects as information, which may be associated with sublethal effects separate from their direct effects as toxins. We currently do not know how these multiple types of anthropogenic information affect meta-ecosystems, for example whether exposure to multiple types of information pollution has synergistic or antagonistic effects, or what attributes of recipient ecosystems (including size, trophic complexity, and connectivity) may predict their response to anthropogenic information. Crucially, however, efforts to investigate the influence of these pollutants on natural systems have happened largely in isolation from each other. We see value in developing a unified approach rooted in their role as information entering meta-ecosystems from artificial sources. Such a framework could help characterize the impacts of information pollution and predict its consequences, while still retaining relevant details about each type of anthropogenic information.

Information originating outside an ecosystem has local impacts

Previous reviews highlight how information influences population, community and ecosystem properties, but they largely focus on information that is produced and acted on within a single ecosystem (Schmidt *et al.* 2010; Gil *et al.* 2018). However, information arriving from outside an ecosystem's boundaries can also have strong effects on organisms and ecosystem dynamics. Light, environmental conditions, and weather serve as information across regional scales, entering many ecosystems. Resources or detritus exported by one ecosystem, a typical flow considered in meta-ecosystems (Loreau *et al.* 2003b), also provide/contain information about the exporting ecosystem. Vocalizations or infochemicals (e.g. pheromones, kairomones) comprise information about resource, habitat, or individual quality that cross ecosystem boundaries. Information can also arrive in the form of mobile, dispersing, or migrating individuals with a myriad of indirect and direct effects (**Table 1**). Given the many ways information can cross ecosystem boundaries, a regional perspective on information may better explain dynamics within and across ecosystems than a sole focus on information produced locally.

Further research is needed to understand when arriving information will have important effects on local dynamics. The successful transmission of information depends both on the ability of information to flow between disparate ecosystems, and on the ability of organisms in receiving ecosystems to detect and process new information. The former may at times be mediated by ecosystem proximity, and the latter by ecosystem similarity. Similar ecosystems may be connected by a dispersal-based exchange of individuals that decays with distance (e.g. zooplankton dispersal among ponds, seed dispersal among plant patches). Agents mediate information transfer: as individuals disperse, they move information about their ecosystem of origin and, upon establishment in an ecosystem, they provide signals/cues that alter local dynamics. More dissimilar ecosystems may be largely characterized by resource-based exchanges (e.g. leaf fall into lakes, the emergence of insects from ponds). However, the flow of information between dissimilar ecosystems can also have large impacts on organismal behavior and movement. For example, anthropogenic light and noise pollution is often produced in human population centers but can be detected by organisms outside the urban environment (Francis & Barber 2013). This photic and phonic information can subsequently divert animal movement at local (e.g. reversing sea turtle hatchlings' movement direction) and continental scales (e.g. disrupting bird migrations) (Longcore & Rich 2004; Bourgeois *et al.* 2009; Francis *et al.* 2009; McLaren *et al.* 2018; see **Box 2** for further discussion of anthropogenic information).

The Challenge of Accounting for Information

Although the flow of information among ecosystems directly impacts the exchange of organisms and materials among them, and thus ecosystem structure and dynamics (**Table 1**), the role of information is not explicitly incorporated into meta-ecosystem frameworks. Organismal life history, developmental, and behavioral responses to information requires at least two things: the information itself and its perception. There is a large body of research regarding the latter — how detection/perception of information affects fitness, life history, behavior, and/or development (DeBose & Nevitt 2008; Schmidt *et al.* 2010; Wagner & Danchin 2010) — which could, for instance, be built into individual-based models of ecosystem dynamics. The distribution and movement of information itself, however, is much less addressed and lacks an obvious starting point for inclusion in meta-ecosystem research. Thus, predictions in ecosystem ecology could likely be improved by quantifying information and its flow between ecosystems (O'Connor *et al.* 2019). Yet, there are also clear challenges to incorporating information into theoretical and/or empirical meta-ecosystem research, and these perhaps partly explain why information is lacking from the field to date. Here, we identify several of these challenges — which range from practical to philosophical — as we situate information use in existing hypotheses about spatial ecology and develop new predictions (see also **Box 3**).

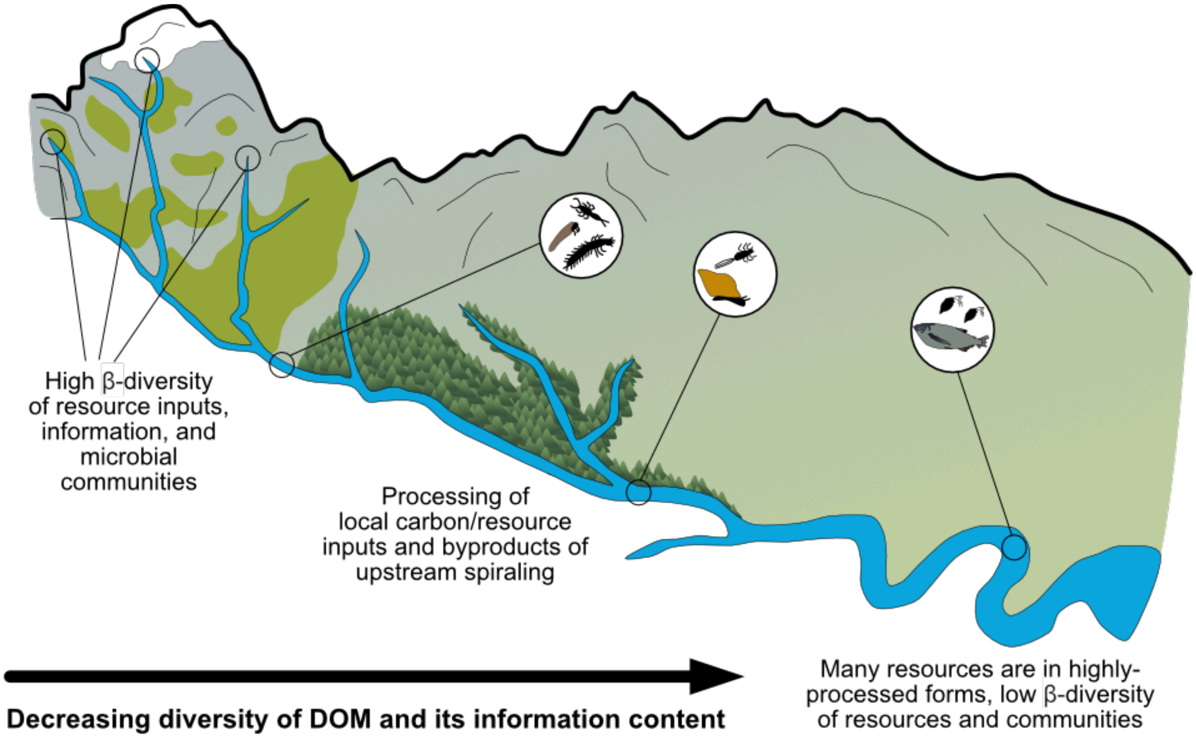


Figure 4. Information processing and movement along the river continuum (see Box 3). Chemical diversity of dissolved organic matter is high in headwaters, as is **β**-diversity of microbial and macroinvertebrate communities. Each of these types of diversity represent syntactic information. Moving downstream along the river continuum, species turnover results in changing community composition. Organisms consume both local resources and those borne by the current, taking advantage of any inefficiencies of resource processing by upstream communities. As a result, we predict that the diversity of carbon forms and the information contained therein decline in downstream reaches.

Box 3: Information in Hierarchical Meta-Ecosystems: A Case Study

Meta-ecosystems are arranged in a variety of ways, from continuous gradients to patches of one habitat type embedded in a matrix of another, distinct habitat (Gounand *et al.* 2018a). The spatial configuration of ecosystems in relation to each other can be important in determining the links between them. In particular, resources move passively along physical gradients of gravity, wind, or currents, unless they are actively moved by organisms counter to these gradients (Gounand *et al.* 2018b). Thus, information transferred among ecosystems, and the directionality of such information flows, could also be expected to follow general patterns if the ecosystems are hierarchically configured along physical gradients.

One particularly enigmatic meta-ecosystem is that of stream and river networks, which form hierarchical, dendritic branching structures connected by downstream flow (Fagan *et al.* 2009). For four decades, ecologists have characterized the spatial organization of habitats within river networks according to the River Continuum Concept, which posits that the community in each part of the river processes not only local resources, but those that are exported from upstream (Vannote *et al.* 1980) (**Figure 4**). As carbon and nutrients are transported downstream, they are transiently taken up by living organisms and then released, usually in other forms, to travel farther downstream — a concept called spiraling (Schmitz *et al.* 2010). They are therefore both resources for and products of organismal metabolism. Thus, downstream communities benefit from any inefficiencies in resource processing by upstream communities, and meta-ecosystem efficiency increases as it is measured over larger and larger sections of the network (Battin *et al.* 2008). These freshwater meta-ecosystems are embedded in a terrestrial matrix and connect to ponds, lakes, wetlands, and ultimately marine ecosystems, setting up a layered, multi-scale network of material, energy, and information flows.

In this hierarchically-structured meta-ecosystem, chemical diversity of dissolved organic matter (DOM) declines downstream. The DOM is "processed" from its original forms (primarily as soil organic carbon and terrestrial detritus) as organisms use it and transform it, and as physical processes degrade it. Thus, moving downstream through a river meta-ecosystem, an increasing amount of DOM is in a more completely processed, and thus less reactive, state (Mosher *et al.* 2015). The effect of this spatial pattern in DOM identity on the biological community has primarily been considered through a lens of DOM as a resource. For example, the diversity of the biofilm-associated microbial community can decline with downstream distance in some river networks as well, presumably due to both spatial metacommunity processes and resource diversity (Besemer *et al.* 2013). However, the molecules that comprise DOM also contain information. The chemical structure of DOM represents syntactic information, as does the diversity of chemical forms of organic matter present in a location. It is also likely that organisms respond to the information contained in DOM. In other settings, *Escherichia coli* exhibit differential chemotaxis for various glucose sources (Cremer *et al.* 2019), and marine bacteria use chemotaxis to congregate around lysing diatoms (Smriga *et al.* 2016). Bacterial consortia in lakes can use chemotaxis to navigate to a specific carbon source and take it up (Glaeser & Overmann 2003). Therefore, the information contained in organic matter and its metabolites may play a mechanistic role in some community assembly processes, which ultimately result in communities being sorted along the river continuum with changing resource types. From a thermodynamic perspective, more favorable compounds (those requiring less energy to process) are also associated with higher aerobic respiration rates (Stegen *et al.* 2018; Garayburu-Caruso *et al.* 2020; Song *et al.* 2020), suggesting microbes use information carried by organic molecules to preferentially target those that are more thermodynamically favorable (Graham *et al.* 2017).

Thus, DOM and metabolites represent material, energy, and information all in a single package, and organisms interact with these particles in all of those capacities in stream and river meta-ecosystems. Following the empirically-supported prediction of decreasing DOM diversity and complexity along the river continuum, we propose that the diversity of information contained in DOM in the water column should also decline in downstream reaches of stream and river meta-ecosystems (**Figure 4**). Given the organismal responses to information highlighted throughout this work, a difference in information quantity and complexity could in fact mediate some of the shifts in biodiversity and ecosystem function through river networks. Ecological metabolomics can be used to holistically describe chemical information and organismal responses to it through chemicals conveyed in soil (van Dam & Bouwmeester 2016), water (Sogin *et al.* 2019), or the air (Rivas-Ubach *et al.* 2019), and may help disentangle the potential roles of DOM and particulates as material, energy, and information.

An initial challenge is to define information from a quantitative perspective. That is, what makes up information, and by what units can we measure it, if any? Decisions about how to answer these questions may depend on the type of information being considered as well as the agents present in the system. A second challenge relates to the peculiar nature of information, compared with matter and energy: both syntactic and semiotic information need not be fixed quantities within a system, but can be created, conserved, modified, and even destroyed. Carefully considering the quantitative and temporal dynamics of information will be key to theoretical explorations of information in ecology. Third, and relatedly, information can travel and be stored within matter and energy, or independently from either (for example, in organic carbon, **Box 3**). How can we quantify and represent the different ways in which information can travel within and across ecosystems? Network analysis and machine learning algorithms provide potentially important tools for ecologists to trace the independent movement of information in biological systems (Meise *et al.* 2020; Valentini *et al.* 2020).

In addition to fundamental questions about information itself, there are further challenges in how to incorporate organismal responses to information into ecological frameworks — that is, once information is present and perceived, what is its effect? Information comes in many forms (e.g., light, sound, temperature, presence/absence, molecules). Research so far has focused on a single type of information at a time, but is there a way to incorporate multiple types of information in a single study/model (see also **Box 2**)? This is both a philosophical question, and a very practical one, as it may logistically limit empirical study designs and computationally limit theoretical work. Yet it is also an essential one, because organismal responses likely depend on the totality of different pieces of information they sense, which modify one another's effects or may act synergistically or antagonistically to determine responses (Ghazanfar & Schroeder 2006; Clobert *et al.* 2009; Gravem & Morgan 2016). Analogous to multi-stressor research, it is likely inaccurate to predict organismal responses to information as a simple additive sum of isolated responses to each type of information. Furthermore, statistical and theoretical models will need to choose a function to relate information to organismal responses. In some cases, organisms may exhibit a linear, dose-dependent response to information, but responses may also be non-linear based on some threshold required to elicit a response or may even be approximated by a binary presence/absence measure of information. Appropriately choosing how to model the effects of one or more types of information will substantially affect how the inclusion of information shapes predictions of meta-ecosystem dynamics.

Opportunities to Incorporate Information Into Ecological Predictions

What is the relative importance of energy, matter, and information flows in regulating meta-ecosystem dynamics? Disentangling the mechanisms and impacts of agent-mediated information transfer will be an essential step towards integrating information into the meta-ecosystem framework. Indeed, the current rising interest in developing meta-ecosystem models accounting for agent-based transfers of nutrients and energy across ecosystems (Gounand *et al.* 2018a; Subalusky & Post 2018; Guzman *et al.* 2019; McInturf *et al.* 2019) offers a unique opportunity to include information as a third currency in ecological interactions. Furthermore, these models could consider how the spatial arrangement of and relationships between ecosystems (**Box 3**), and reduced animal movement driven by habitat loss and fragmentation

(Tucker *et al.* 2018), affect the flow of information between ecosystems. Considering and confronting the challenges mentioned above will enable ecologists to account for information in new ways, which will undoubtedly reveal new aspects of ecology and alter our understanding and predictions of the world. We see several avenues for research that may be particularly fruitful once this process has begun (see **Box 3, Figure 4** for a case study). In particular, we can begin to examine how altering traditional assumptions about organismal information use (or lack thereof) could affect predictions. Here, we offer a few examples of hypotheses incorporating information, as fodder for what we hope is a flourishing of information-infused meta-ecosystem research.

The spatial scale of information use and movement

A majority of the effects of organism-mediated transfer of information on ecosystem dynamics mentioned above likely depend on the ability of organisms to use information and on the amount of information used in making movement decisions (Guzman *et al.* 2019). A large body of literature, ranging from population to movement ecology, investigates these dynamics under the assumption that individual agents base their actions on a complete and exhaustive knowledge of their surroundings — often referred to as the “perfect knowledge” assumption. Several influential frameworks in ecology rest on this assumption, from the Ideal Free Distribution to the Landscape of Fear/Opportunity (Gaynor *et al.* 2019) and the Green Wave Hypothesis (van der Graaf *et al.* 2006). However, this assumption poses significant problems due to the finite ability of agents to perceive and detect information from the environment in both space and time — i.e., the agent’s *perceptual range* (*sensu* Lima & Zollner 1996). Theoretical and empirical researchers alike have developed ways to, where possible, address the limitations of this assumption and, where not possible, to describe their findings as exceptions or deviations from this assumption. However, we posit that these challenges could be at least partially overcome by recognizing the implicit contributions of biological information to population, community, and ecosystem dynamics and their ‘meta’ extensions — and then reframing them using quantitative descriptions of the information exchanges that underlie them (O’Connor *et al.* 2019).

An agent’s perceptual range can vary greatly with its body size (Mech & Zollner 2002; McGill & Mittelbach 2006), its needs and goals (Powell & Mitchell 2012), the ecosystem’s structure (Pawar *et al.* 2012), and the presence or absence of other agents (Laundré *et al.* 2010; Northfield *et al.* 2017; Schmitz *et al.* 2017). Combining these approaches with seminal theoretical insights (e.g., Lima & Zollner 1996) and recent methodological advances (O’Connor *et al.* 2019; Riotte-Lambert & Matthiopoulos 2020) enables an investigation of how individual differences in perceptual abilities may be transmitted to populations, communities, and eventually ecosystems, and how these exchanges of information influence meta-community and meta-ecosystem dynamics (Guzman *et al.* 2019). For instance, while the overall ecological conditions experienced by agents in an ecosystem may be similar, differences in body size cause agents to perceive the ecosystem’s structure and features differently (Kiltie 2000; Haskell *et al.* 2002). In turn, these experiential differences in the way individuals interact with information modify the way they move over and use the landscape (i.e., spatial information processing; Guzman *et al.* 2019). Developing ways to empirically quantify and account for information production, processing, and transfer by agents could, then, allow for testing theoretical predictions such as those pertaining to the emergence of home ranges (Beecham & Farnsworth 1998; Farnsworth & Beecham 1999; Spencer 2012). Where an individual falls on the gradient from imperfect to perfect information use determines how efficiently it uses space. Resulting effects on home range size could affect the number of conspecifics an ecosystem can support and encounter rates between consumers and resources, influencing productivity and energy flux at the ecosystem and meta-ecosystem level. Likewise, accounting for information could help test predictions about movement and connectivity dynamics over heterogeneous landscapes (Pe'er & Kramer-Schadt 2008; Fagan *et al.* 2017), and ultimately what ecosystem boundaries agents cross and the patches they connect. These questions are particularly relevant as habitat loss and range shifts push agents into new contexts where they may be less able to extract meaning from signals. Moving away from the perfect knowledge assumption to embrace information-infused studies of how organisms assemble over and interact with the landscape could shed light on the role they play in ecosystem-wide processes, such as nutrient cycling, productivity, and stability, especially under global change.

Predicted effects on biodiversity and ecosystem function

While some fields of ecological theory have simplistically assumed that organisms have perfect knowledge of their environments, aspects of metacommunity theory have in fact assumed the opposite — that dispersal is uninformed by distance, environmental conditions, or community characteristics. This assumption has important consequences for predictions of meta-community and -ecosystem dynamics. For example, the spatial insurance hypothesis (Loreau *et al.* 2003a) posits that in spatially and temporally heterogeneous metacommunities, moderate levels of dispersal maintain local species richness (α-diversity), and thus regional ecosystem function and stability. As environmental conditions shift in each patch in the metacommunity, dispersal makes it more likely that a species suited to the new conditions is present, either because they had a small, transient population despite being an inferior competitor under prior conditions, or through new immigration. Without organismal dispersal, the dominant species in each patch could drive others to extinction under one set of environmental conditions, only to face population declines when they are poorly adapted to future conditions. On the other hand, very high levels of dispersal homogenize communities so that similar dynamics play out at the landscape scale. Spatial insurance, then, ensures that there are well-suited species present in many patches at most times through species turnover, thus maintaining ecosystem productivity and conferring the stability of metacommunity ecosystem function. Foundational work on the spatial insurance hypothesis assumed dispersal was equal between species and that connections were global (Loreau *et al.* 2003a), though more recent work has addressed some of these assumptions (Shanafelt *et al.* 2015; Thompson *et al.* 2020). Yet it is clear that organisms use information in dispersal and settlement decisions. This is not only true of animals and microbes, but also plants, whose dispersal can be informed by the animals that carry propagules (endozoochory), where release of propagules may be triggered by environmental or conspecific stimuli (e.g. masting), and where germination, analogous to settlement, depends on environmental conditions. Therefore, a logical next step is incorporating informed, context-dependent dispersal (**Table 1, Figure 2**) into models of meta-ecology, and the ecosystem function and energy flux which emerge from community composition (Bannar-Martin *et al.* 2018; Barnes *et al.* 2018).

Considering how information shapes feedbacks between organisms and their environments in a spatial context leads to some logical predictions and other more complex questions. Compared to uninformed dispersal, we hypothesize that organismal use of information should accelerate the speed at which species in a metacommunity re-sort themselves into local patches as environmental conditions fluctuate. In other words, relatively lower levels of dispersal should be able to provide spatial insurance when that dispersal is informed. Thinking at the ecosystem level, this spatial exchange of organisms should thus maintain higher levels of productivity and ecosystem function at both local and landscape scales. On the other hand, some mechanisms of spatial insurance could be diminished compared to what would happen under the same rate of uninformed dispersal, because fewer immigrants should settle in patches where they are ill-suited (but could later capitalize if conditions changed in their favor). We could thus hypothesize reduced α-diversity if patches are primarily composed of previously dominant species which were well-suited to past conditions and recently arrived species which are well-suited to current conditions but lack some other species that may be better adapted to future conditions. This hypothesis has implications for metacommunity stability as lower patch occupancy increases the stochastic risk of extinction and thus may lead to reduced regional species richness (γ-diversity). Furthermore, we can ask how resource subsidies between patches of a meta-ecosystem could affect these dynamics. Nutrient flows can destabilize meta-ecosystems when consumer movement is analogous to diffusion (Marleau *et al.* 2010). If organisms could direct their movement based on either the information contained in the nutrient flows themselves or on the patch conditions resulting from those flows — including patterns of diversity and community composition — would this mitigate their effects? Or would feedbacks between resource flows and context-dependent dispersal further destabilize meta-ecosystems? Finally, organisms within or across trophic compartments differ in their use of information, the scale at which they perceive information, and how close they come to perfect knowledge of their landscapes, with likely effects on meta-ecosystem dynamics.

Conclusions

The flow of information within and among ecosystems has vital consequences for ecosystem functioning and stability. Accounting for information in meta-ecosystem processes is thus key to understanding how dynamics such as fitness, organismal movement, and trophic interactions influence ecosystem function, as well as predicting how these processes will be affected by anthropogenic pressures and global change. There is an immediate need to employ empirical approaches to quantify information and its flow in ecological systems at multiple scales. While the strategies and techniques used to study information in ecosystems may differ from those used to study energy and matter, the need to do so is no less important. Integrating information into empirical and theoretical meta-ecosystems research poses significant challenges. However, by identifying open questions and methodological roadblocks and presenting new hypotheses for how information could impact meta-ecosystem dynamics, we aim to stimulate future work that will make significant strides towards addressing the role of information in ecological systems.

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