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Movement with meaning: integrating information into meta-ecology

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Fluxes of matter, energy and information over space and time contribute to ecosystems' functioning and stability. The meta-ecosystem framework addresses the dynamics of ecosystems linked by these fluxes but, to date, has focused solely on energy and matter. Here, we synthesize existing knowledge of information's effects on local and connected ecosystems and demonstrate how new hypotheses emerge from the integration of ecological information into meta-ecosystem theory. We begin by defining information and reviewing how it flows among ecosystems to affect connectivity, local ecosystem function and meta-ecosystem dynamics. We focus on the role of semiotic information: that which can reduce an individual's – or a group's – uncertainty about the state of the world. Semiotic information elicits behavioral, developmental and life history responses from organisms, potentially leading to fitness consequences. Organisms' responses to information can ripple through trophic interactions to influence ecosystem processes, their local and regional dynamics, and the spatiotemporal flows of energy and matter, therefore information should affect meta-ecosystem dynamics such as stability and productivity. While 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), many ecological models currently account for neither the spatio–temporal distribution of

Synthesis

Ecosystems exist in connection with each other, forming meta-ecosystems through flows of energy, matter, and information. Information plays a potentially key role in shaping local and meta-ecosystems dynamics, especially as the Anthropocene unfolds and information landscapes change. However, until recently, information has been absent from meta-ecosystem ecology. This paper offers a guide to different types of ecological information, synthesizes current knowledge on their local and meta-ecosystem effects, andidentifies challenges in incorporating information into meta-ecology. The paper offers new hypotheses for how an information-aware framework may shed light on key ecosystem processes.

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information nor its perception by organisms. We identify the empirical, theoretical and philosophical challenges in developing a robust information meta-ecology and offer ways to overcome them. Finally, we present new hypotheses for how accounting for realistic information perception and responses by organisms could impact processes such as home range formation and spatial insurance, and thus our understanding of ecological dynamics across spatial and temporal scales. Accounting for information will be essential to understanding how dynamics such as fitness, organismal movement and trophic interactions influence meta-ecosystem functioning, and predicting how ecosystem processes are affected by anthropogenic pressures.

Keywords: energy flux, life history, meta-community, organismal movement, social information, spatial processes

Introduction

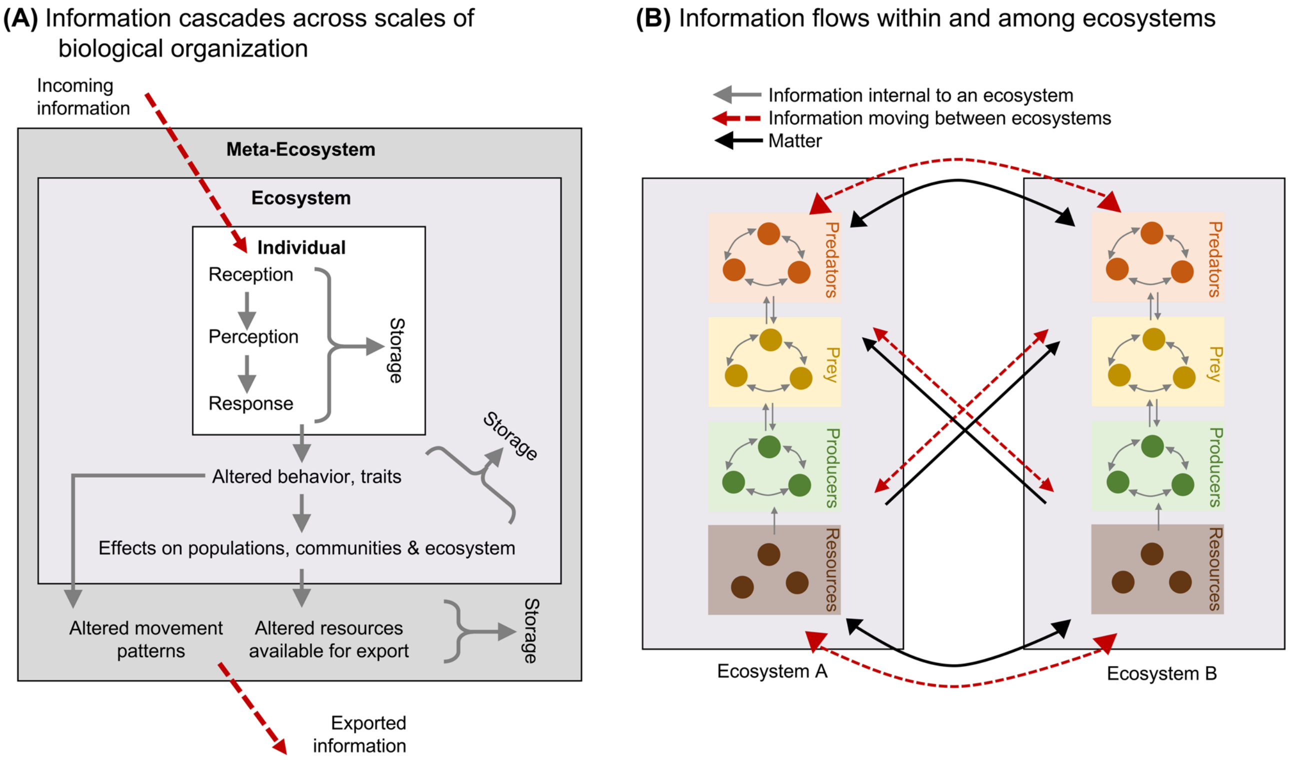
Interactions between organisms and the environment are structured in space (Lovett et al. 2005), and ecosystems are intrinsically open and connected. Meta-ecosystem theory (see the Table 1 for definitions of italicized terms) integrates the movement of organisms with a landscape ecology perspective on movement and cycling of matter and nutrients, and considers both flows among trophic compartments and within and among ecosystems (Loreau et al. 2003a). Conceptualizing the world as a network of meta-ecosystems has helped our understanding of the importance of cross-ecosystem fluxes to biodiversity, ecosystem functioning, stability and spatiotemporal dynamics, as well as how these dynamics regulate the fluxes themselves (Gounand et al. 2018b, Schiesari et al. 2019).

Meta-ecosystem theory thus provides a framework for addressing 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, 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 (O'Connor et al. 2019). Its interpretation reduces uncertainty about current and future states of a system. Although often transferred with energy or matter, information possesses unique properties that may require different methods of study than energy or matter: it can be transferred by energy or matter, but is not conserved in the same ways. Thus, information should be viewed as a critical but distinct currency that flows within and among ecosystems similarly to matter and energy (Fig. 1, Marleau et al. 2020), that can alter energy and matter transfer at all levels, from genes to ecosystems. Fundamental interactions between organisms and their environment(s) depend on stocks and flows of all three building blocks of life. These interactions bridge landscapes and ultimately establish biological pathways that span from local to global scales (Doughty et al. 2016, Gounand et al. 2018a).

As a field, ecology has not yet grappled explicitly with the dynamics of information in linked ecosystems. Yet, the movement of information necessarily accompanies the

Table 1. A glossary with definitions of key terms for an information-based meta-ecology.

Term	Definition
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 agents [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).
Ecosystem functioning	The combined effect of multiple ecosystem functions and properties (Gamfeldt et al. 2008).
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 agent, which has processed or interpreted it, to (an)other agent(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 and matter (Loreau et al. 2003a) – an arrangement that is ubiquitous in nature and also includes flows of information.
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. We argue that this definition should include information as well.
Perceptual range	The distance at which an agent can perceive or detect information (Lima and Zollner 1996).
Semiotic information	Something that decreases an agent'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.



(A) Information cascades across scales of biological organization

(B) Information flows within and among ecosystems

Figure 1. In a meta-ecosystem framework, information is exchanged within ecosystems and across ecosystem boundaries. (A) Information can impact every level of biological organization, and/or be stored to influence future dynamics. Individual organisms receive information, and their responses can influence population, community and ecosystem dynamics within their ecosystems as well as the connectivity of ecosystems across the landscape (that is, the meta-ecosystem). Note that the red dashed arrows showing the origin and export of information are intended to be general and unspecific – the information that organisms receive can originate inside or outside of their local ecosystems, and the information that they produce can likewise remain local, or be exported from the ecosystem. (B) Within ecosystems, organisms exchange information within and among species (gray arrows) and with the abiotic environment. Information can also enter from, or be exported to, another ecosystem (red dashed arrows). Meta-ecosystem studies often consider matter and energy exchanges among ecosystems (black arrows); however, there is also information exchanged between ecosystems (red dashed arrows). Matter also moves within ecosystems, and information use and production by organisms can influence resource quality and quantity. However these dynamics have been omitted from the figure for simplicity.

movement of energy and matter, and information transfer and information use by organisms both mediate and contribute to spatial feedbacks in ecological dynamics (Gil et al. 2018, O'Connor et al. 2019, Marleau et al. 2020). Failing to account for information results in key knowledge gaps 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 and the resulting feedback and feedforward processes (Bernhardt et al. 2020). Understanding the myriad ways that humans are altering the information landscape – by changing the meaning of information, or disrupting its transmission or detection (Szymkowiak and Schmidt 2022) – may also help predict the effects of anthropogenic actions on ecosystems both near and far from the activity itself (Box 1).

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 how it is studied in the ecological literature. We then review evidence of how information influences ecosystem dynamics through organismal behavior, development and life history, and 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 theory and make initial hypotheses (Table 2) about how its incorporation could alter assumptions and predictions about meta-ecosystem and other meta-ecological dynamics.

What is information, ecologically?

Information is something that decreases uncertainty about the state of a system or the outcome of an event (Anderson 2008, O'Connor et al. 2019). Within this broad definition of information lie other, precisely-defined concepts essential to an understanding of ecological information. Information can be treated in terms of its quantity and structure (syntactic information) or quality and interpretation (semiotic information) (Donaldson-Matasci et al. 2010, O'Connor et al. 2019). Syntactic information is the information generated

Box 1. Human alteration of information in meta-ecosystems

An increasingly relevant issue is how information generated by human activity affects not only the local ecosystems where it is produced, but also travels across ecosystem boundaries. 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 (henceforth, 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 individual organisms to time life-history events or determine behavior. For example, evidence suggests that ALAN can change the timing of flowering, budburst and leaf fall in trees (Bennie et al. 2016). As such, ALAN can elicit indirect, bottom–up effects altering ecosystem connectivity, for instance by reducing the resources available for herbivores (Bennie et al. 2015). 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). Within aquatic ecosystems, light also 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). Despite the many documented biological consequences of ALAN, its effects on ecosystem functions are not yet fully understood (Sanders et al. 2021). ALAN is far from the only impact that humans are having on information landscapes; as an additional example, noise pollution is pervasive even in terrestrial protected areas (Buxton et al. 2017b), raising the question of their efficacy for conserving ecological interactions and the processes that arise from them. Thus, recognizing sensory pollutants as information may allow a better understanding of their likely effects on species (based on traits) and ecosystems (based perhaps on size, trophic complexity or connectivity). This in turn could enable better predictions of (meta-)ecosystem dynamics under global change, and reduce the likelihood of ecological surprises that arise from the synergistic or antagonistic effects of information and other components of global change.

Another important way that humans are altering the way that information mediates ecosystem dynamics is by altering the meaning of cues (Szymkowiak and Schmidt 2022). Because organisms are attuned to predictable informational cues in their surroundings, 'ecological traps' can 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 and Gysel 1978).

by the arrangement of matter or energy (or 'objects' more generally) in space and time. By contrast, semiotic information is the meaning associated with syntactic information by an agent (Short 2007), and it may be measured as the fitness value of syntactic information (Donaldson-Matasci et al. 2010). Semiotic information is related to the concept of a cue in behavioral ecology (Wagner and Danchin 2010), but its broader definition enables it to encompass non-behavioral responses by organisms. For example, consider a sign warning of a specific danger. Two observers (agents) may receive the same syntactic components of information (the sign's contents) but assign different semiotic value to it based on how much that syntactic information is likely to influence fitness (e.g. one agent might not understand the sign) and may therefore respond in different ways or not at all. Furthermore, this warning sign could trigger not only a behavioral response, but a demographic or developmental pathway (e.g. changes in offspring production or sex ratios, investment in escape mechanisms over nutrition or growth). Thus, an understanding of semiotic information is crucial to describing and predicting ecological dynamics because individual responses depend not on the actual syntactic information (e.g. something we can measure in the environment, such as habitat suitability or the presence of a signal) but the agent's interpretation of it – that is, the perceived habitat suitability or the perceived meaning of the signal. We use the term 'agent' to refer to individual organisms (e.g. a plant, animal, fungus or microbe), but other entities are also information-processing agents. Cells, individual organisms, populations and ecosystems contain, transmit, respond to and copy information.

Some information is internal to an organism, including genetic material, body condition and traits. Internal information may be perceived by the organism (e.g. hunger, water stress, reproductive status) or hard-coded (e.g. genetic and trait information). Genetic information can influence (meta-)ecosystem dynamics through individuals' expressed phenotype (Des Roches et al. 2018). More specifically, genes interact with the environment to determine phenotypes, and these phenotypes can influence higher-level variables via effect traits (Violle et al. 2007) such as nutrient excretion rates (Palkovacs et al. 2009, Matthews et al. 2011). Genes can influence every level of biological organization including (meta-)populations, (meta-)communities and (meta-)ecosystems (Miner et al. 2005, Matthews et al. 2011, Toju et al. 2017,

Table 2. Examples of hypotheses arising from the integration of information into meta-ecosystem theory. For each hypothesis, we identify initial research questions and suggest empirical and theoretical ways to test them.

Hypothesis	Research questions	How to test
The spatial configuration of meta-ecosystems determines the magnitude and effects of information flows, and the composition of ecological information	How do ecosystems' similarity and proximity affect information flows among them? How does this shape biodiversity patterns? How does the structure of ecological information present in constituent ecosystems change through hierarchical meta-ecosystems?	Empirical (e.g. spatial microcosm experiments, new analyses of biogeochemical data) and theoretical (e.g. meta-ecosystem models) tests of the effects of information from donor ecosystems that differ in spatial configuration (e.g. distance, direction).
Information perceptual ability influences trophic interactions in meta-ecosystems.	How does information perceptual ability affect organismal density, encounter rates, trophic energy and matter flux in meta-ecosystems?	Additional data collection and synthesis of organism-driven material flows in meta-ecosystems; integration of empirical data into theoretical tests, e.g. by incorporating nutrient and energy transfer into individual-based models of organismal movement on landscapes
Information use determines space use efficiency	Does information and its use influence competition dynamics within and across ecosystems?	Develop field techniques to assess how the effectiveness of information use affects the intra- and interspecific strength of competition
Organismal information use alters spatial insurance mechanisms in meta-communities	Does informed dispersal stabilize or destabilize meta-ecosystem dynamics relative to random dispersal?	Theoretical (e.g. meta-community and meta-ecosystem models incorporating informed dispersal) and empirical (e.g. linked micro- or mesocosm/pond) tests of effects on meta-ecosystem dynamics

Des Roches et al. 2018), a phenomenon termed the 'extended phenotype' (Whitham et al. 2003). There is a literature on the 'genes-to-ecosystem' connection that we will not recreate here (Whitham et al. 2008, Bailey et al. 2009, Crutsinger 2016, Stange 2021), however, many of the dynamics we describe throughout this paper are underlain by the interaction between genotype, phenotype and the environment.

In addition to internal information, there is a wealth of external information such as environmental conditions or biotic interactions that by definition requires perception by an organism to elicit a response. While nature is full of potential (i.e. syntactic) 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 and Danchin 2010). There is an extensive literature about information, cues and public versus private information in the context of behavioral ecology (see Danchin et al. 2008 as one comprehensive treatment of this topic), however our goal here is not to rehash or review this field, but rather to consider broader responses to information across taxonomic groups, including animals, plants and microbes – for instance, by considering behavioral, life history, physiological, and/or developmental responses. While ecologists often view individual organisms as the agents that take in and process information, multiple agents in a population or community may respond to the same information. Idiosyncratic information transfer from one agent 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. For example, environmental information can generate idiosyncratic information transfer, where only a small proportion of a population receives the information, but their response generates new information that can influence the rest of the population, e.g. alarm calls (Meise et al. 2020). Alternatively, populations of organisms like migratory birds can undertake coordinated, aggregate responses to information such as photoperiod or temperature. Through behavioral modifications, individual-level responses can thus generate information that is transmitted to other organisms and ultimately has consequences for populations (e.g. demography), communities (e.g. trophic cascades) and ecosystems (e.g. alteration of the environment) (Fig. 1a, 2, Schmitz et al. 2010, Wilmers and Schmitz 2016). Understanding how individual organisms' responses to information affect higher levels of organization is thus a promising research avenue through which to understand ecosystem and meta-ecosystem dynamics.

Why focus on information in meta-ecology?

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). CESs do not allow for emigration and immigration of individuals, as compared to meta-ecosystems that allow for transfer of materials, organisms and information across ecosystem boundaries (Levins 1969). Material transfer across ecosystem boundaries is so common that meta-ecosystems are nearly ubiquitous and are often simply referred to as ecosystems (but see caveats in Guichard and Marleau 2021). Studies of CESs indicate that isolating ecosystems limits chemical cycling, contributing to the potential for ecosystem functional losses, most obviously through the loss of grazers (Taub and McLaskey 2014, Taub 2019). Thus, one emergent property of meta-ecosystems is that the fluxes across ecosystem boundaries can confer stability through a material version of the 'rescue effect' (sensu Stacey et al. 1997), which allows for maintained elemental cycling. However, as essential as these spatial fluxes are for sustaining ecosystems, they

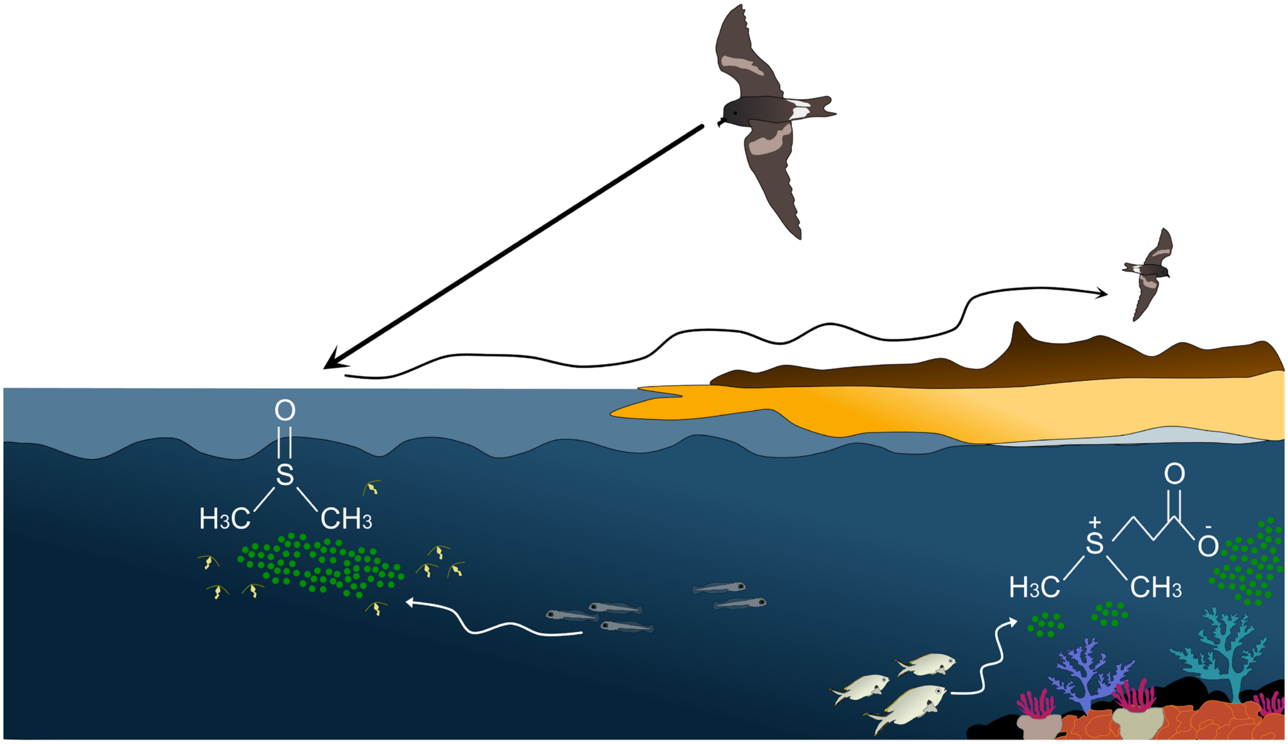


Figure 2. Dimethyl sulphide (DMS, left) and the other chemical compounds in its biochemical pathway (such as dimethylsulfoniopropionate, DMSP, right) are released by marine phytoplankton after senescence or consumption by grazers (Savoca et al. 2016, but see Dell'Ariccia et al. 2017 for additional considerations on DMS production at sea). 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 and 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 and 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 and eliciting foraging responses in sea turtles without providing the forage they seek (Savoca et al. 2016, Pfaller et al. 2020).

can also destabilize them. For example, theoretical work has shown that resource flows between ecosystems often destabilize meta-ecosystems (e.g. the paradox of enrichment), while exchanges of consumer biomass can stabilize them (Gounand et al. 2014, Marleau et al. 2014).

Information may contribute to meta-ecosystem dynamics because it is a distinct currency from matter and information. In this framework, one currency may be used as an investment of sorts in another. Energy and materials are required to store, transmit, interpret and reproduce information (O'Connor et al. 2019). Thus, the allochthonous materials that provide additional energy sources in almost all ecosystems (Gounand et al. 2018a), and separate them from CES's, also enhance information flow within and among ecosystems. This conversion between currencies underlies the functioning of ecosystems and defines their structure (Marleau et al. 2020). Why, then, is this third currency not accounted for in the meta-ecosystem framework? One reason may be that meta-ecosystems are typically depicted with flows of resources and/or biomass among trophic compartments within and among ecosystems (Gravel et al. 2010, Marleau et al. 2010, Gounand et al. 2014), with the dynamic of interest being the stocks and flows of these trophic compartments, rather than specific biological mechanisms linking them (but see Earl and Zollner 2017, Bampoh et al. 2019). As a result, 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. 2018b). Crucially, all of these mechanisms depend on information use by the organism(s). In the next section, we provide examples of the pathways through which these mechanisms affect meta-ecosystem dynamics.

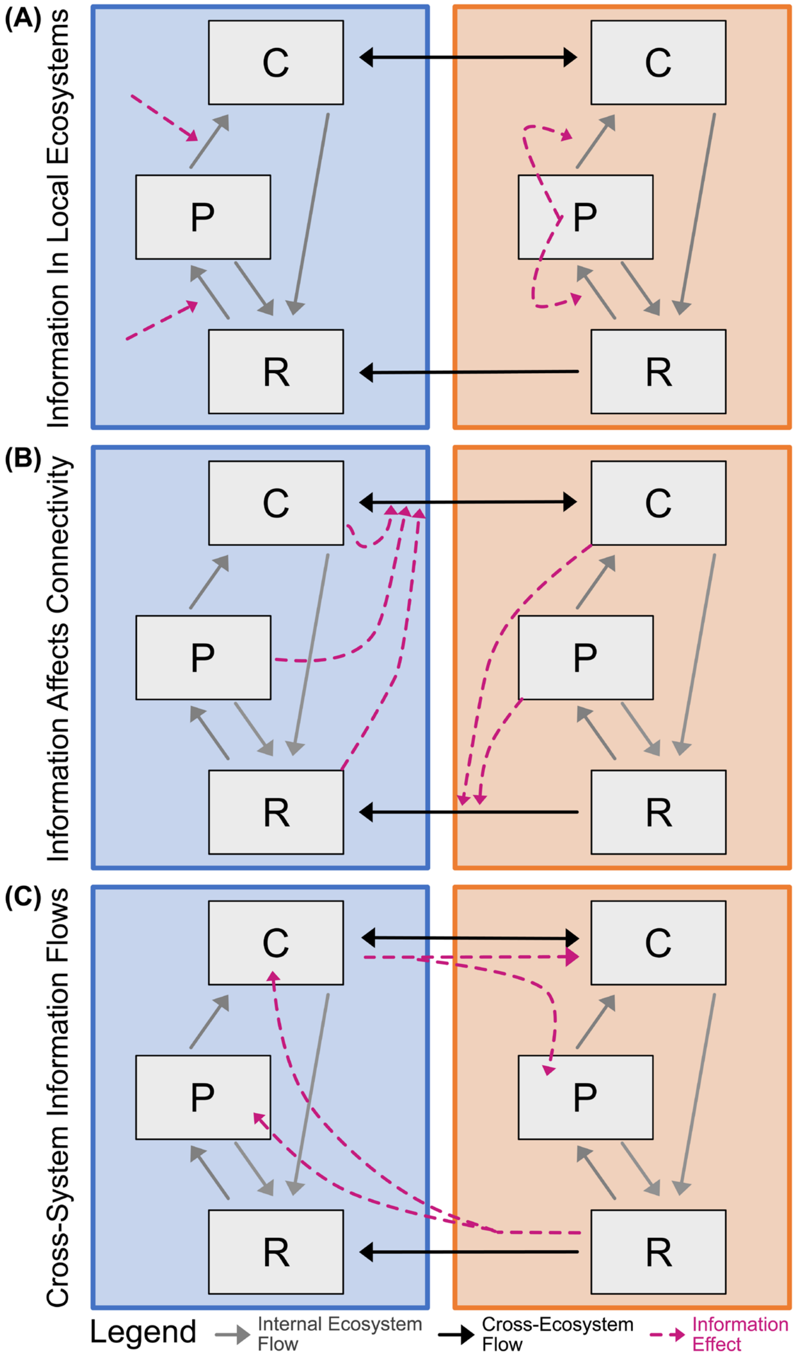


Figure 3. The effects of information on a conceptual two-patch meta-ecosystem model with bidirectional movement of consumers (C) and unidirectional movement of resources (R), both shown by black arrows and negligible dispersal by producers (P, not shown). Gray arrows show internal flows of matter and energy within local ecosystems, as in Gravel et al. (2010). We demonstrate six ways that ecological information can influence these within- and cross-ecosystem flows (red dashed lines). Each meta-ecosystem panel shows the mechanisms discussed in one subsection of the 'information in meta-ecosystems' section of the text. (A) Locally produced, abiotic information can influence producers and consumers and thus the flows of matter and energy connecting trophic compartments (shown in blue ecosystem). Biotic information can influence these same flows: in the orange ecosystem, information from producers affects how producers take up resources, and the trophic flux between producers and consumers. (B) Information about resources, producers and consumers can inform cross-ecosystem movement of consumers (shown originating in blue ecosystem). Likewise, it can affect the quality, quantity, timing and duration of cross-ecosystem resource flows (shown originating in orange ecosystem). (C) Information moves among ecosystems with movement of consumers (shown from the blue to the orange ecosystem) and resources (shown from the orange to the blue ecosystem), affecting organisms and thus ecological dynamics in the recipient systems. Note that we show red dashed arrows in either the blue or orange patch of each panel for visual clarity but, in reality, information effects occur in both patches – i.e. across the meta-ecosystem.

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 (Fig. 1). In this section, we first provide a short primer on how information affects ecosystem dynamics by eliciting changes in the behavior, life history, physiology and development of organisms. We then discuss how information can influence meta-ecosystem dynamics via the movement of organisms and materials. Finally, we highlight how the influence of information arriving in an ecosystem from an external source is a particularly understudied yet potentially powerful effect on local ecosystem dynamics (Fig. 3).

Information influences ecosystem dynamics

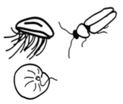
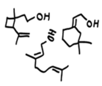
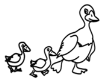
Before addressing information in spatially-linked ecosystems, it is important to review the effects of information on ecosystem dynamics more generally (Table 3). These effects arise because organisms respond to semiotic information to potentially increase their fitness via life history, behavioral and 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 (Fig. 3a). Therefore, information scales from individual-level effects to ecosystem-level consequences (Massol et al. 2017, Gounand et al. 2018b; Table 1), which manifest through one to few agents (e.g. individuals or a population within a species), or many agents (e.g. individuals from diverse taxa) (Schaefer et al. 2004, Gil and Hein 2017, Gil et al. 2020). The importance of organismal responses to information is general across taxonomic groups and ecosystems, as illustrated by the following examples focused on the three mechanisms of behavioral, life history and developmental responses. First, behavioral responses of animals can alter key elements of local ecosystem dynamics such as primary production, nutrient cycling and population density, as was recently reviewed by Wilson et al. (2020) in the context of behavioral responses to human activity. Plants also 'behave', for example inducing chemical defenses when exposed to herbivory, and these chemical changes can subsequently limit microbial-mediated decomposition and therefore resource and nutrient cycling (Burghardt et al. 2018). Secondly, life history responses to information can influence biomass production, such as when 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 and Baskin 1998, Karban 2008). Finally, 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 and 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 and dispersal from biofilms (Hall-Stoodley et al. 2004, McDougald et al. 2012, respectively), which affect how bacteria and other microorganisms contribute to carbon and nutrient cycling. The pattern that organismal responses to information determine rates of ecosystem processes is thus very general, although the magnitude and direction of effects are context-dependent.

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 (Fig. 3b). Examples of informed dispersal, migration and foraging movement between ecosystems abound (Table 4). For example, animals moving across heterogeneous landscapes in search of resources (e.g. food items, refugia from predators, or mating partners) move faster when they encounter low-quality habitat, increasing rates of range expansion (Crone et al. 2019). Organisms continuously integrate information collected from their surroundings and from their internal state to initiate, halt or alter their movement among ecosystems. Analogous to the components of the animal movement ecology paradigm stating that internal state, navigation capacity and movement capacity determine an animal's movement path (Nathan et al. 2008), similar dynamics have been well documented in plants. Information (the internal state as well as external information) influences plant flowering and fruiting, seed dormancy and germination (Rathcke and Lacey 1985, Baskin and Baskin 1998, Veits et al. 2019) – the steps of dispersal from gamete to new individual, several of which encompass movement capacity. Information therefore mediates not only animal-mediated, but also plant-mediated connectivity among ecosystems by influencing the transfer of materials and information among ecosystems (Fig. 2), which in turn may reinforce ecosystem heterogeneity (Monk and Schmitz 2022).

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. 2018a). The effects of such subsidies on recipient ecosystems depend on their quantity, quality, timing and duration (Marcarelli et al. 2011, Schindler and Smits 2017, Subalusky and 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. Genetic information is one determinant of development, leading to

Table 3. Different types of information have characteristic scales of exchange and may be more likely to connect similar versus dissimilar ecosystems or patches. These differences influence their effects on local ecosystem dynamics and organismal movement.

	Type of syntactic information	Proximity and scale of transmission	Source	Ecological effects
	Light	Local, possibly regional	Abiotic or anthropogenic origin	Light is a cue for development (Fankhauser and Chory 1997) and behavior (Karban 2008); visibility affects trophic interactions (Tabor et al. 2004) and perceived risk thereof (Palmer et al. 2017), thus altering behavior; navigational aid and indicator of spatial positioning (Ragni and Ribera D'Alcalà 2004) (Box 1)
	Light	Local, possibly regional	Biotic origin	Bioluminescence can function as a cue in enabling or preventing trophic interactions (De Cock and Matthysen 2003, Haddock et al. 2010)
	Sound/sonic signaling	Local and possibly regional	Abiotic or anthropogenic origin	Sonic information about climate, weather and fire influence behavior and animal navigation (Paterson et al. 2013) (Box 1)
	Sound	Local and possibly regional	Biotic origin	Alarm calls, mating calls and other vocalizations inform behavior (Seyfarth et al. 2010); used for navigation (Farina 2014)
	Chemicals	Local and possibly regional	Abiotic or anthropogenic origin	Chemicals produced via abiotic processes, including those synthesized by humans, are used as indications of habitat quality or as navigational cues (Dittman and Quinn 1996, Hinojosa et al. 2018)
	Info-chemicals	Local and possibly regional	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 and Nevitt 2008) (Fig. 2)
	Magnetic fields	Local to global	Abiotic or anthropogenic origin	Used to navigate at multiple scales (Wiltschko and Wiltschko 1988, Hays 2013)
	Genetic information	Local to global	Biotic origin, including anthropogenic actions	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 are introduced (Weeks et al. 2017, Kyriazis et al. 2021)
	Cultural information	Local to regional	Biotic origin, including anthropogenic	Organismal behavior transmitted to new individuals via observation or learning alters behavior, life history, movement patterns and trophic interactions (Helfman and Schultz 1984, Gil et al. 2018, Jesmer et al. 2018)

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; Gounand et al. 2018a, McInturf et al. 2019), organismal use of information affects the quantity and timing of these resource subsidies to any particular location.

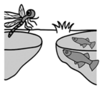
Information simultaneously and continuously influences meta-ecosystem connectivity in all of these ways, across levels of biological organization and spatial scales. For example, a suite of chemical cues can influence fine-scale microbial dynamics in the ocean, as well as drawing macro-organisms with enormous foraging ranges to new patches before they return ocean-derived resources to land (Fig. 2). The multi-layered, multi-scale connections in networks of ecosystems are thus underlain by information processing by organisms, which plays a fundamental role in shaping the structure and functioning of meta-ecosystems.

Information from donor ecosystems impacts the dynamics of recipient ecosystems

Information influences population, community and ecosystem properties, yet existing knowledge on these effects arises mostly from information produced and acted upon within a single ecosystem (Schmidt et al. 2010, Gil et al. 2018). However, information arriving from outside an ecosystem's boundaries (i.e. from a 'donor' ecosystem) can also have strong effects on organisms and ecosystem dynamics in the 'recipient' ecosystem (Fig. 3c). Information can arrive in the form of mobile, dispersing or migrating organisms with a myriad of indirect and direct effects (Table 1, 2). For example, in an experiment with lizards, whether immigrants arrived from a high-density or a low-density patch influenced the dispersal rates of lizards from the arrival patch in some contexts (Cote and Clobert 2007). Two-patch experiments with ciliates found that when immigrants arrived from patches with higher resource availability, this sometimes altered dispersal rates by the residents in their arrival patch – but interestingly, whether this increased or decreased departures depended on the genetic identity of the resident ciliates, that is, on internal information (Jacob et al. 2015).

Resources or detritus exported by one ecosystem, a typical flow considered in meta-ecosystems (Loreau et al. 2003a), also contain information (Marleau et al. 2020; Box 2), as do vocalizations or infochemicals (e.g. pheromones, kairomones) that cross ecosystem boundaries. For example, female

Table 4. Organismal movement is influenced by the reception and processing of information, with various ecological effects. Note: the organisms moving transmit some types of information outlined in Table 3; here, we primarily describe the organisms' information use.

	Type of organismal movement	Movement scale	Similarity of patches connected	Types of information informing movement	Ecological effects of organismal movement
	Movement of mobile consumers foraging in many similar patches	Local to regional	High	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 and 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) (Fig. 3b)
	Condition-dependent dispersal	Local to regional	High: organism must be able to live in both source and target patch	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 and 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	Internal and external information	As above, but based on an individual's perception of external biotic and abiotic conditions rather than its own condition/phenotype.
	Life history movement	Local	Typically low (life stages live in different ecosystem types)	External and possibly internal information	Amphibians use information to navigate and select breeding pools (Buxton et al. 2017a); conspecific density and predator cues alter timing of metamorphosis and emergence to a new ecosystem (Relyea and Rosenberger 2018)
	Migration settlement decisions	Continent/global	High to low	External and internal information	Animals use a variety of information sources to decide where to settle after migration, e.g. infochemicals (Dittman and Quinn 1996) or social information (Doligez 2002)

frog pond visitation depends on vocalizations that reach far beyond the habitat where they are produced and draw females to new breeding habitat (Buxton et al. 2015). This movement thus depends on information about male body size, condition and overall attractiveness inferred from distant male frogs' songs (Bernal et al. 2006, Akre et al. 2011). The frogs' movement subsequently impacts ecosystem dynamics by adding gametes which either grow into additional consumers, or are consumed as resources, contributing to trophic energy flux. Conversely, the information landscape deprives ecosystems with less attractive vocalizations from receiving these inputs. 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.

The challenge of accounting for information

Organismal life history, developmental and behavioral responses to information require at least two things: the information itself and its perception. There is a large body of research regarding the latter – how detection or perception of information affects fitness, life history, behavior, and/or development (DeBose and Nevitt 2008, Schmidt et al. 2010, Wagner and Danchin 2010) – which could, for instance, be built into individual-based meta-ecosystem models. The distribution and movement of information itself, however, is much less addressed and lacks an obvious starting point for inclusion in meta-ecology research. While accounting for ecosystem exchanges of information may very well improve our predictions and understanding of these systems (O'Connor et al. 2019, Marleau et al. 2020), underlying theoretical and empirical challenges first need to be resolved. In this section, we identify several of these challenges, ranging from practical to philosophical.

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. This is true both of empirical research, and theoretical approaches, and we can look at three different modeling studies as examples. Marleau et al. (2020) model information as an ecosystem property affecting consumer density, and this property can change over time as a function of consumer and/or resource density. In contrast, O'Connor et al. (2019) model the fitness of individuals in a population which have traits for information acquisition, storage, communication and use. Meanwhile, Gil et al. (2017) model information as affecting individual organisms' probability of finding food and avoiding predation. Incorporating these approaches into models of spatially-linked ecosystems could yield insights into meta-ecosystem dynamics.

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

Box 2. 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. 2018b). 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. 2018a). 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.

River networks are hierarchically structured meta-ecosystems that form dendritic branching structures connected by downstream flow. These meta-ecosystems are embedded in a terrestrial matrix and connect to ponds, lakes, wetlands and ultimately coastal and marine ecosystems, setting up a layered, multi-scale network of material, energy and information flows. For four decades, ecologists have characterized the spatial organization of habitats within river networks according to the River Continuum Concept, which predicted 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) (Fig. 4). As carbon (i.e. particulate and dissolved organic matter, 'DOM') and nutrients are transported downstream, they are transiently taken up by living organisms and then released, usually in other forms, to travel farther downstream. 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). Experimental work in hierarchical meta-ecosystems has already shown that materials exported from upstream communities with varying biotic compositions have different impacts on downstream communities and ecosystems (Harvey et al. 2017), however this work did not disentangle the resource versus information effect of the transferred organic material.

In hierarchical riverine meta-ecosystems, DOM is 'processed' from its original forms by biotic and abiotic processes. Moving downstream from the headwaters (where more organic matter enters the waterway per unit area or volume) to the coastal delta, an increasing amount of DOM is in a more completely processed 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

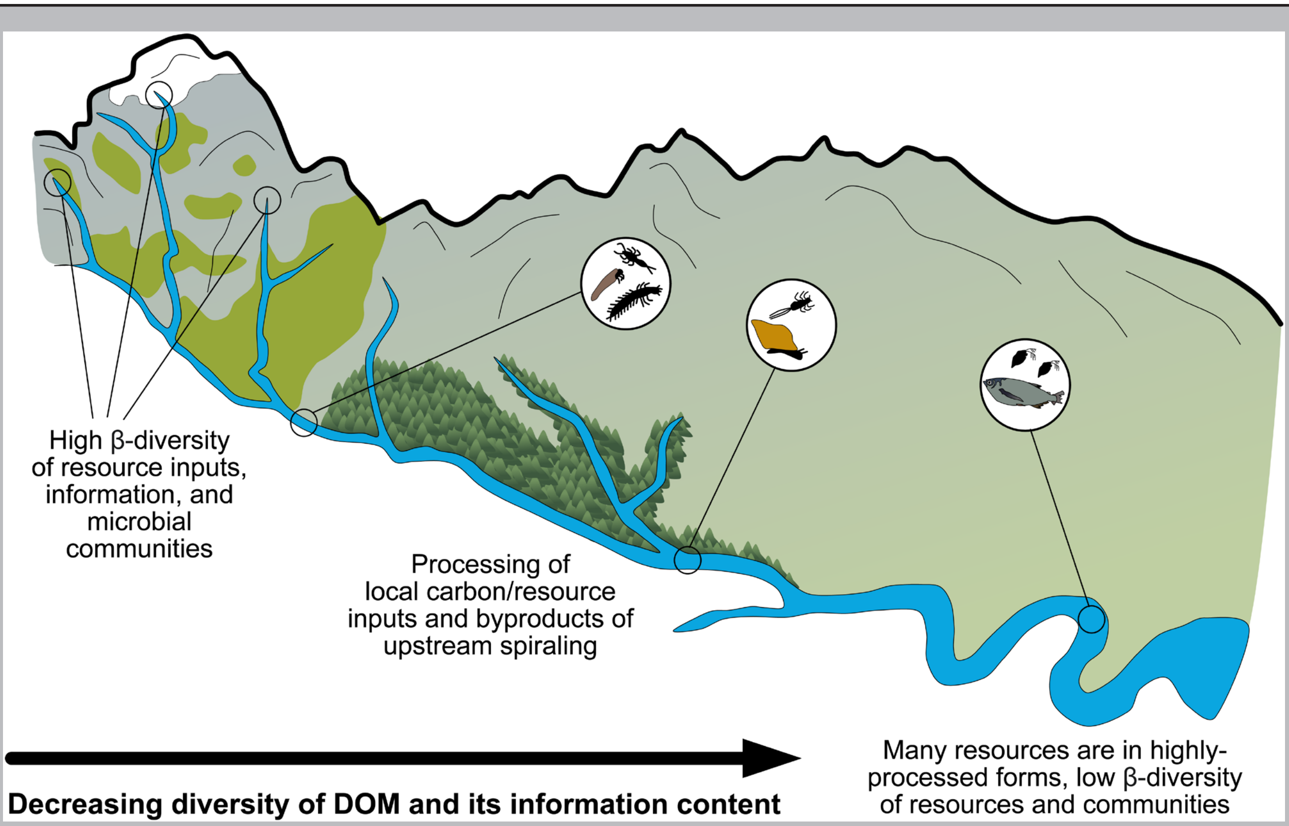


Figure 4. Information processing and movement along the river continuum. Chemical diversity of dissolved organic matter is high in headwaters, as is β-diversity of microbial and macroinvertebrate communities. Each of these types of diversity represent syntactic information. Moving downstream along the 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. There are opportunities to leverage new thermodynamic theory to quantify information within DOM and its spatiotemporal variation.

DOM as a resource. For example, resource diversity has been presumed to contribute to patterns of higher diversity of the biofilm-associated microbial community in headwaters compared to further downstream in some river networks (Besemer et al. 2013). However, the molecules that comprise DOM also contain information. The elemental stoichiometry and molecular structure of DOM represents syntactic information, as does the diversity of chemical forms of organic matter present in a location – in fact, the assemblage of organic molecules that make up DOM pools in different habitats can be viewed as analogous to local ecological communities (Danczak et al. 2020). An outstanding question is whether the DOM resource pool contributes to the assembly and functioning of ecosystems' biotic components, which could respond to the information contained in DOM: that is, does this syntactic information become semiotic information? There are hints this may be true at fine scales: marine bacteria use chemotaxis to congregate around lysing diatoms (Smriga et al. 2016), while bacterial consortia in lakes can use chemotaxis to navigate to a specific carbon source and take it up (Glaeser and Overmann 2003). In stream meta-ecosystems, more thermodynamically favorable compounds (those providing more energy from oxidation) are associated with higher aerobic respiration rates (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). In fact, DOM chemistry can be a better predictor of respiration rates, a key ecosystem function, than potential and expressed metabolic pathways in microbial communities (Graham et al. 2018).

Molecules that comprise DOM thus represent material, energy and information all in a single package (Marleau et al. 2020), 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 (Fig. 4). The new insights discussed above have been revealed by ultra-high-resolution characterization of DOM, and suggest spatial organization of information processing and content. Given the organismal responses to information highlighted throughout this work, hierarchically-structured patterns in information quantity and complexity could mediate shifts in biodiversity and ecosystem function throughout river networks.

An important challenge in testing the hypothesis of hierarchically-structured information is finding ways to describe and quantify the information content within DOM, and how that content changes as the biological lens changes across species and communities. One possibility is leveraging new thermodynamic theory developed in Song et al. (2020), which provides quantitative insight into among-molecule variation in the efficiency with which organic molecules can be turned into microbial biomass; we refer to this as 'thermodynamic efficiency.' Most immediately, existing data (e.g. those from Mosher et al. 2015) could be re-analyzed to evaluate gradients in the diversity of thermodynamic efficiency across stream networks. The theory can additionally be extended to apply across specific biogeochemical gradients. We specifically hypothesize that the information carried as 'thermodynamic efficiency' of organic molecules is more valuable when oxygen is less available to support microbial metabolism. This is due to an increasingly strong influence of thermodynamics on biogeochemical rates as oxygen becomes less available (i.e. under more reducing conditions). If valid, this proposed link among oxygen concentrations, thermodynamic efficiency and information value could be used to include the information content of DOM into dynamic mechanistic models, such as reactive transport models (Steefel 2019) often used to simulate and study the hydro-biogeochemistry of river corridors

destroyed. Carefully considering the quantitative and temporal dynamics of information will be key to theoretical explorations of information in ecology (see Gil et al. 2020 for an example of how theoretical work can incorporate these considerations). Third, and relatedly, information can travel and be stored within matter and energy in a variety of ways (for example, in organic carbon, Box 2, Fig. 4, Marleau et al. 2020). This complicates choices for how to quantify and represent the different ways in which information can travel within and across ecosystems.

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), and 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 (van Bergen et al. 2004, Ghazanfar and Schroeder 2006, Clobert et al. 2009, Gravem and 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 (Hein et al. 2018, Marleau et al. 2020). 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? We see several avenues for information-centric meta-ecological research that may be particularly fruitful for answering this question. In particular, we can begin to examine how altering traditional assumptions about organismal information use (or lack thereof) could affect predictions. In this section, we offer a few examples of hypotheses incorporating information, as fodder for what we hope is a flourishing of information-infused meta-ecosystem research.

Within animal ecology, a widespread assumption is that individual agents base their actions on a complete knowledge of their surroundings (i.e. 'perfect' knowledge). Frameworks such as 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) rest on this assumption. While foundational work began to test and expand the family of ideal distribution models to account for how information and imperfect knowledge shape agents' interactions with and within heterogeneous landscapes (Abrahams 1989, Nocera et al. 2009), the 'perfect knowledge' assumption remains widespread. This poses significant problems due to the finite ability of real-world agents to perceive and detect information from the environment in both space and time (Lima and Zollner 1996). An agent's information gathering and use abilities vary with its body size (Mech and Zollner 2002) and physiology (Abrahams 1989), its needs and goals (Powell and Mitchell 2012), the ecosystem's structure (Pawar et al. 2012) and the presence or absence of other agents (Nocera et al. 2009). In turn, these experiential differences in the way agents interact with information modify the way they move over and use resources across the landscape (Stephens and Krebs 1987, Guzman et al. 2019, Hein and Martin 2019).

We predict that where an individual falls on the gradient from imperfect to perfect information use determines how efficiently it uses space and other resources. Resulting effects on home range size and selection of optimal resources could subsequently affect the number of conspecifics an ecosystem can support and encounter rates between consumers and resources, influencing productivity, nutrient recycling and energy flux at the ecosystem and meta-ecosystem level. Likewise, incorporating an individual's position on this perfect–imperfect knowledge axis could improve predictions about movement and connectivity dynamics over heterogeneous landscapes (Abrahams 1989, Pe'er and Kramer-Schadt 2008, Nocera et al. 2009, Fagan et al. 2017), ultimately enhancing our understanding of what ecosystems are connected by such movement. These questions are particularly relevant as habitat loss, range shifts and harvest of organisms cause reactions in the density of information-producing organisms and push agents into new contexts where they may be less able to extract meaning from environmental and biotic signals.

While some fields of ecological theory have simplistically assumed that organisms have perfect knowledge of their environments, aspects of metacommunity theory have assumed no knowledge – that is, that dispersal is uninformed by distance, environmental conditions or community characteristics. This assumption has important consequences for predictions of meta-community and meta-ecosystem dynamics. For example, the spatial insurance hypothesis (Loreau et al. 2003b) posits that in spatially and temporally heterogeneous metacommunities, moderate levels of dispersal maintain local species richness (α-diversity) and ecosystem productivity, and confer regional stability of ecosystem function (i.e. meta-ecosystem dynamics). Foundational work on the spatial insurance hypothesis assumed dispersal was equal between species and that connections were global (Loreau et al. 2003b). Although more recent work has addressed some of these assumptions (Shanafelt et al. 2015, Thompson et al. 2020), it is clear that organisms use information in dispersal and settlement decisions to a much greater extent than has been explored so far (for example, through chemotaxis; reviewed by Painter 2019). This is not only true of animals and microbes (e.g. when to emerge from a sporulated state), but also of 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 or sporulation, depends on environmental conditions. 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, and should thus maintain higher levels of productivity and ecosystem functions at both local and landscape scales (i.e. in the meta-ecosystem). 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. 2014). 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 (Abrams 2007), would this mitigate the effects of such nutrient flows? Or would feedbacks between resource flows and context-dependent dispersal, in combination with nutrient recycling by the organisms themselves, further destabilize meta-ecosystems?

The current rising interest in developing meta-ecosystem models accounting for agent-based transfers of nutrients and energy across ecosystems (Earl and Zollner 2017, Gounand et al. 2018b, Subalusky and Post 2018, McInturf et al. 2019) offers a unique opportunity to include information as a third currency in meta-ecosystem theory. A practical next objective with these modeling approaches could be to consider how the spatial arrangement of ecosystems affect the flow of information among them. The successful transmission of information depends on the ability of information to flow between disparate ecosystems and thus, analogous to resource flows, may be more likely among ecosystems that are in close proximity (Gounand et al. 2018b). However, unlike energy or matter flows, flows of information also depend on the ability of organisms in receiving ecosystems to detect and process new information, which may partly depend on ecosystem similarity (which has interesting implications for meta-ecosystems that include novel, human-altered and human-engineered ecosystems). For example, more similar ecosystems (e.g. two ponds, versus a pond and a forest) are more likely to harbor communities of functionally similar taxa that may have comparable information sensing and processing abilities. While adjacent but dissimilar ecosystems are likely connected by resource and energy flows, similar ecosystems may be connected by a dispersal-based exchange of individuals that decays with distance or other physical controls (e.g. zooplankton dispersal among ponds, seed dispersal among plant patches) (Gounand et al. 2018b, McLeod and Leroux 2021). Because resources and individuals carry different types of information, we predict that reduction and fragmentation of these flows will have unequal impacts on meta-ecosystem dynamics.

Conclusions

As we have shown, the flow of information within and among ecosystems has vital consequences for ecosystem functioning and stability. Accounting for information in meta-ecosystem processes is key to understanding how dynamics such as fitness, organismal movement and trophic interactions influence ecosystem functions, as well as predicting how these processes will be affected by anthropogenic pressures and global change. Furthermore, the peculiar nature of information opens up entirely new avenues of research. For instance, can ecosystems and meta-ecosystems as a whole receive and respond to information flux? And, if so, is this information flux sufficient to establish a connection between these organizational units, in the same way as inorganic nutrient transfer or organismal movement does? There is an immediate need to employ empirical approaches to quantify information and its flow in ecological systems at multiple scales to begin building a quantitative and qualitative knowledge base on the characteristics, dynamics and influence of this currency. Integrating information into empirical and theoretical meta-ecosystems research poses significant challenges. However, by identifying open questions and methodological roadblocks and presenting new hypotheses (Table 2) 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 meta-ecological systems.

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Data availability statement

This paper contain no additional data.

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