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Unifying sources and sinks in ecology and Earth sciences

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ABSTRACT

The paired source and sink concepts are used increasingly in ecology and Earth sciences, but they have evolved in divergent directions, hampering communication across disciplines. We propose a conceptual framework that unifies existing definitions, and review their most significant consequences for the various disciplines. A general definition of the source and sink concepts that transcends disciplines is based on net flows between the components of a system: a source is a subsystem that is a net exporter of some living or non-living entities of interest, and a sink is a net importer of these entities. Sources and sinks can further be classified as conditional and unconditional, depending on the intrinsic propensity of subsystems to either produce (source) or absorb (sink) a surplus of these entities under some (conditional) or all (unconditional) conditions. The distinction between conditional and unconditional sources and sinks, however, is strongly context dependent. Sources can turn into sinks, and *vice versa*, when the context is changed, when systems are subject to temporal fluctuations or evolution, or when they are considered at different spatial and temporal scales. The conservation of ecosystem services requires careful consideration of the source–sink dynamics of multiple ecosystem components. Our synthesis shows that source–sink dynamics has profound consequences for our ability to understand, predict, and manage species and ecosystems in heterogeneous landscapes.

Key words: source, sink, ecology, evolution, earth sciences, conservation, ecosystems.

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I. INTRODUCTION

In a period when human domination of the Earth's ecosystems is altering the ecology of the entire planet (Vitousek *et al*., 1997), understanding the interactions between the various components of the Earth system is becoming increasingly vital. Predicting the fate of available energy, limiting nutrients, toxic pollutants, or living organisms and its global consequences requires thorough knowledge of the multiple pathways through which living and non-living entities transform into each other and move in space. Increasingly the paired concepts of sources and sinks are used in the environmental sciences to describe both the chemical transformations and the spatial displacement of living and non-living entities. These concepts are so commonly used that their meaning is often taken for granted. For example, scientists, policy makers, and even the general public are now familiar with carbon sources and sinks, which have been popularized by the reports of the Intergovernmental Panel on Climate Change (http://www.ipcc.ch/publications_and_data/publications_and_data_reports.shtml). In the Earth sciences, sources and sinks are used rather loosely to denote any subsystem or process that contributes to adding (source) or removing (sink) a substance (e.g. carbon) to or from the system being considered (e.g. the atmosphere). The terms are descriptive, and they seem so intuitive and uncontroversial that we have been unable to find any formal definition in the Earth science literature.

In ecology, however, the source and sink concepts evolved in different directions, which mirror the historical divergence between the conceptual, theoretical and methodological frameworks of the two main subdisciplines of ecology, i.e. ecosystem ecology and population/community ecology (Loreau, 2010). Ecosystem ecology has followed the lead of the Earth sciences, adopting their relatively neutral, descriptive usage of the terms (Loreau, Mouquet & Holt, 2003; Chapin *et al*., 2006). By contrast, population ecology has gradually shifted focus to the demographic causes and consequences of spatial flows of individuals across populations (Pulliam, 1988; Dias, 1996). In population ecology, the source and sink concepts are no longer meant merely to describe where individuals originate from and where they move to, but also seek to capture the intrinsic demographic characteristics of local populations (i.e. the balance between births and deaths) that generate spatial flows of individuals across heterogeneous landscapes. As a result, they have had important applications in conservation biology (Liu *et al*., 2011), evolutionary ecology and population genetics (Kawecki, 2004), and metacommunity ecology (Mouquet & Loreau, 2003; Leibold *et al*., 2004).

But linking patterns and processes is notoriously difficult. Population biologists soon realized that the interpretation of the sink concept in terms of underlying demographic processes was ambiguous. This generated a proliferation of new terminology to distinguish between stronger and weaker versions of this concept. Perhaps the best known of these distinctions is that between 'true sinks' and 'pseudo-sinks', depending on whether local recruitment fails to balance local mortality in a population because of intrinsic habitat quality or simply because of the increased competitive pressure resulting from immigration of conspecific individuals (Watkinson & Sutherland, 1995). Other distinctions have been proposed between 'hard' and 'soft' sinks (Schmidt *et al*., 2000), between 'absolute' and 'relative' sinks (Kawecki, 2004), and between 'fundamental' and 'realized' sources and sinks (Gravel *et al*., 2010*a*), depending on the factors that cause the imbalance between local mortality and local recruitment. Some concepts also describe specific situations, such as 'Allee' and 'black-hole' sinks (Holt, 2011).

This terminological profusion suggests that we have reached a point where the source and sink concepts need to be re-examined, so that greater clarity and greater consistency is attained across disciplines. Failure to do so might lead to conceptual confusion, fragmentation of research agendas, lack of communication among disciplines, and ultimately reduced ability to meet the scientific challenges of our time. Our main objectives herein are to propose a conceptual framework that unifies the various definitions of the source and sink concepts, and to review some of their most significant consequences for ecology, evolution and Earth sciences.

II. CLARIFYING THE CONCEPTS

(1) Core definitions based on net flows

The original content of the source and sink concepts was fairly consistent across scientific disciplines. Sources and sinks have been used in the Earth sciences from at least the early 1970s to describe the components of the Earth system where a chemical substance originates from and where it is absorbed or destroyed (Pressman & Warneck, 1970). Again, think of the use of carbon sources and sinks in

Table 1. Terms used to define different source and sink concepts in this review (in bold), and related terms from the ecological and Earth science literature

Term	Definition	References
(Net) source/sink	Subsystem that is a net exporter/importer of specific living or non-living entities within a broader ecological system	This paper
Source/sink	Compartment or process that contributes to adding/removing energy or materials to/from a system	Earth sciences, ecosystem ecology
Source/sink	Habitat that is a net exporter/importer of individuals	Pulliam (1988)
Conditional source/sink	Subsystem that produces/absorbs a surplus of specific living or non-living entities under some conditions	This paper
Pseudo-sink	Population in which recruitment does not balance mortality because of immigration of conspecific competitors	Watkinson & Sutherland (1995)
Soft sink	Habitat in which a species' recruitment does not balance mortality because of abundant conspecific or heterospecific competitors	Schmidt *et al*. (2000)
Relative sink	Habitat in which a species' recruitment does not balance mortality because of immigration of conspecific competitors	Kawecki (2004)
Allee sink	Habitat in which a population can persist in the absence of immigration at high density but not at low density	Holt (2011)
Realized source/sink	Habitat in which a species' density-independent growth rate is positive/negative in the presence of spatial flows	Gravel *et al*. (2010*a*)
Unconditional source/sink	Subsystem that produces/absorbs a surplus of specific living or non-living entities under all conditions	This paper
True sink	Population that would not be viable in the absence of immigration	Watkinson & Sutherland (1995)
Hard sink	Habitat unable to sustain a population	Schmidt *et al*. (2000)
Absolute sink	Habitat unable to sustain a population	Kawecki (2004)
Black-hole sink	Habitat unable to sustain a population and in which there is immigration but no emigration	Holt (2011)
Fundamental source/sink	Habitat in which a species' density-independent growth rate is positive/negative in the absence of spatial flows	Gravel *et al*. (2010*a*)

climate-change research and policy. The concepts were introduced in population and community ecology with a more distinct spatial connotation for local populations or habitats in which population persistence is due to immigration of individuals (sinks) and those from which these immigrants originate (sources) (Holt, 1984, 1985; Shmida & Ellner, 1984). The demographic implications of the spatial dynamics between sources and sinks were made clear in an influential paper by Pulliam (1988), who noted that at equilibrium births should exceed deaths in sources while the reverse should be true in sinks. Despite his focus on demographic rates Pulliam (1988, p. 654) clearly noted that his 'definitions apply strictly for equilibrium populations only', and that 'a more general definition of a source is a compartment that, over a large period of time (. . .) is a net exporter of individuals. Similarly, a sink is a net importer of individuals'. Thus, historically sources and sinks were first introduced to describe net flows from the former to the latter.

Here we keep this original emphasis on net flows, and define more generally a *source* as a subsystem that is a net exporter of specific living or non-living entities (energy, materials, or organisms) within any broader ecological system, and a *sink* as a net importer of these entities (Table 1). We suggest that the terms *net source* and *net sink* be kept where necessary to indicate that the observed flows are the result of an undefined number of smaller scale processes with potentially different effects on the direction of the flows. It must be clear, however, that all sources and sinks are defined first and foremost by net flows within a certain context determined by the system, the time scale and the spatial scale under consideration.

(2) The quest for intrinsic sinks in population biology

These descriptive flow-based concepts no longer suffice to capture the subtleties of the process-based demographic approach that population biology has largely taken in recent years following Pulliam (1988). The emphasis in this approach has been on the causes and consequences of the net spatial flows of individuals between patches, and more specifically on whether these flows reveal intrinsic differences in habitat quality or merely result from varying demographic processes. Assume, for instance, that one persistent local population of a species is a sink, i.e. the number of individuals that immigrate into this population is on average larger than the number of individuals that emigrate from the population. A classical example is the bay checkerspot butterfly (*Euphydryas editha bayensis*) in patches of serpentine grassland in southern Santa Clara County, California: small patches with a southern slope receive a net flow of immigrants coming from larger neighbouring patches with northern slopes (Harrison, Murphy & Ehrlich, 1988). There are at least two reasons why this population may be a sink: (*i*) habitat quality is too low for a viable population to establish itself in the absence of immigration; and (*ii*) habitat quality is high enough to sustain a viable population, but is lower than in neighbouring patches, so that immigration tips the balance from source to sink. In both cases, deaths will outweigh births on average because the influx of immigrants will be compensated by increased deaths if the population is to remain bounded. In the first case, however, deaths will outweigh births even in the absence of immigration, while in the second, immigration itself causes the local demographic deficit. In the case of the bay checkerspot butterfly, the habitat quality of small patches with a southern slope is too low to support local populations in the absence of immigration (Harrison *et al*., 1988). This scenario is the basis for the distinctions between 'true sinks' (first case) and 'pseudo-sinks' (second case) (Watkinson & Sutherland, 1995), or between 'absolute sinks' (first case) and 'relative sinks' (second case) (Kawecki, 2004).

Two important points need to be made about this classical scenario. First, the role of local demographic rates has been somewhat overemphasized since, when averaged over a long enough time period, local demographic rates necessarily mirror net flows between habitats. The critical difference between the two cases is whether habitat quality is low absolutely (a population cannot be sustained in the absence of immigration) or only relatively (relative to neighbouring sources). The only ways to tell the difference are either to study habitat quality directly, or to suppress immigration experimentally (Runge *et al*., 2006). Second, 'habitat quality' is an ambiguous concept because a species' environment is determined by a large number of biotic and abiotic factors. Both conspecifics and heterospecifics can dramatically alter habitat quality as perceived by an individual, either positively through niche construction or negatively through niche destruction (Kylafis & Loreau, 2011). In particular, the presence of heterospecific competitors can turn a good habitat into a bad one, and hence a source into a sink. To account for this possibility, Schmidt *et al*. (2000) proposed the distinction between 'hard sinks', in which abiotic factors prevent population persistence, and 'soft sinks', in which intra- and interspecific competition causes local mortality to exceed local recruitment. This distinction is a straightforward extension of the above distinctions between 'true' or 'absolute' sinks and 'pseudo-' or 'relative' sinks; it amounts to removing the demographic effects of heterospecific competitors, in addition to those of conspecific competitors, from the definition of 'habitat quality'. Virtually all recent studies on competitive coexistence in source–sink metacommunities and other spatially extended systems have defined sources and sinks in terms of competitive outcomes in the presence of heterospecific competitors (Loreau & Mouquet, 1999; Codeço & Grover, 2001; Yu & Wilson, 2001; Amarasekare, 2003; Mouquet & Loreau, 2003; Snyder & Chesson, 2004; Mouquet *et al*., 2006); consequently, all sinks in this literature would be 'soft' by Schmidt *et al*.'s (2000) definition.

But this distinction does not bring us any closer to a final resolution of the problem. Not only do many other types of species interactions come into play (e.g. predation and mutualism), but these interactions, and even the abiotic habitat template that seems the ultimate determinant of a species' persistence in one locality, can also be affected by spatial flows of biotic and abiotic ecosystem components from neighbouring localities (Loreau & Holt, 2004; Gravel *et al*., 2010*a*, *b*). For example, seabirds translocate large quantities of nutrients from the ocean to islands *via* their guano, such that islands that support seabird colonies have high plant production relative to islands without seabirds (Anderson & Polis, 1999). Islands too infertile to support a local population of some plant species in the absence of seabirds would traditionally be interpreted as 'true', 'absolute', or 'hard' sinks for those plant species, but, once occupied by seabird colonies, the same islands would be interpreted as sources. Furthermore, the same habitat that acts as a source for one ecosystem compartment is likely to act as a sink for other ecosystem compartments because of mass-balance constraints at the meta-ecosystem level (Loreau *et al*., 2003). The reciprocal fluxes between streams and riparian forests represent a clear example of such complex meta-ecosystem dynamics (Nakano & Murakami, 2001). Specifically, streams are sources for emergent aquatic insects but sinks for inorganic nutrients like N and P (Baxter, Fausch & Saunders, 2005). To account for the indirect effects of all sorts of spatial flows on a given species, Gravel *et al*. (2010*a*) suggested the distinction between 'fundamental' and 'realized' sources and sinks, depending on whether the species is able to sustain a local population in the absence of spatial flows, or only in their presence.

(3) Conditional *versus* unconditional sources and sinks

Given the broad array of ecological factors that potentially affect the persistence of species and their ability to produce emigrants or absorb immigrants, a single process-based criterion will generally not be able to distinguish unambiguously between habitats that act as sinks because of their low intrinsic quality ('true', 'absolute', 'hard', or 'fundamental' sinks) and those acting as sinks conditionally ('pseudo-', 'relative', 'soft', or 'realized' sinks). The same also holds for sources. But it may nevertheless be desirable to keep the contrast between a stronger and a weaker version of the source and sink concepts as utilized in population and community ecology. Therefore we propose to adopt a more general distinction between *conditional* and *unconditional* sources and sinks that is not tied to any specific process: a subsystem is a *conditional source (sink)* if it produces (absorbs) a surplus of some living or non-living entities of interest under some but not all conditions; it is an *unconditional source (sink)* if it does so under all conditions (Table 1). Conditions include variations in spatial flows of the entities of interest, but they may also include any of the conditions discussed above – i.e. varying abundance of conspecific competitors, presence or absence of heterospecific competitors, presence or absence of spatial flows from other ecosystem components –, as well as others, such as variations in abiotic conditions, presence or absence of resources (Holt, 1984, 1985), consumers (Loreau

& DeAngelis, 1997), or mutualists, and human impacts. Thus defined, conditional and unconditional sources and sinks encompass all previous distinctions as special cases (Table 1).

The distinction between conditional and unconditional sources and sinks, however, makes sense only within a well-defined context that determines the range of conditions under which sources and sinks are being studied. This context includes the system under consideration, the factors that affect the source–sink status of its components, and the specific spatial and temporal scales at which it is studied. Generally speaking, the broader the context, the less sources and sinks are likely to be unconditional. For instance, if the time window considered is extended to arbitrarily long times while keeping a focus on short-term dynamics, all sources and sinks are likely to be conditional because of long-term physical, chemical, geological and biological changes at the Earth's surface. In this limiting case, the unconditional source and sink concepts lose their meaning and usefulness. But over shorter ecological time scales, the source–sink status of natural systems can greatly depend on the time window considered (Johnson, 2004) (Fig. 1), and the distinction between conditional and unconditional sources and sinks becomes relevant once a time window has been defined. We explore the scale dependency of sources and sinks further in Section V.

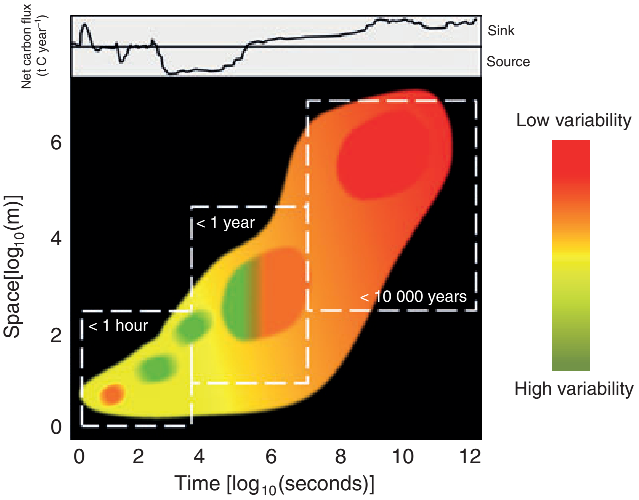

Fig. 1. Hypothetical Stommel diagram illustrating the scale dependency of sources and sinks. The diagram may be applicable, for instance, to the status of a typical boreal forest as a net source or sink of atmospheric carbon (Kurz *et al.*, 2008). The top panel (black line) shows the net carbon flux as it could be measured in one particular location at different time scales. The main panel shows the variability of the net carbon flux at different spatial and temporal scales. The forest acts as carbon sink with little variability (red) over long time scales and large spatial scales, but its net carbon flux is highly variable at some scales (green) due to episodic disturbances that cause large tree mortality, such as fires and pest outbreaks. During these episodes, the forest turns into a carbon source. The black zone indicates scales for which no data are available.

(4) Strength of sources and sinks

The *conditionality* of sources and sinks should be distinguished from their *strength*. The *strength* of a source (sink) can be defined as the strength of its propensity to produce (absorb) a surplus of the entities of interest under given conditions as a result of its local dynamics. Although we might expect weak sources and sinks to be conditional more frequently than strong ones because small changes in conditions may easily lead them to switch from source to sink status and *vice versa*, in principle conditionality and strength are distinct dimensions. For instance, a habitat may be a strong sink for a vulnerable prey species when a voracious predator sustained by some alternative prey is present, i.e. the vulnerable prey has a strongly negative local population growth rate because of predation and persists only by virtue of strong immigration from elsewhere. The same habitat, however, may be a weak, or even a strong, conditional source for the same species in the absence of either the predator or of its alternative prey, i.e. the vulnerable prey has a weakly, or even strongly, positive local population growth rate and sends out emigrants to other patches (R. D. Holt, personal communication). Thus, in the presence of the predator and its alternative prey, the habitat is a strong, yet conditional, sink for the vulnerable prey.

Since the source–sink status of a subsystem can change depending on its conditions, its strength as a source or a sink is also likely to vary with conditions; therefore there is little prospect of devising a simple measure of the intrinsic strength of sources and sinks. In the simple scenario (which has often been used in the literature) where a single source is connected to a single sink, the ratio of net spatial flow to standing stock could be used as a straightforward measure of the strength of each subsystem as source or sink. But as soon as three or more subsystems are connected, the net spatial flow between any two subsystems is constrained by spatial flows that take place between other parts of the system, such that it becomes partly uncoupled from their local dynamics. A case in point is the debate initiated by some evolutionary biologists about the relationship between reproductive value and the source–sink status of a habitat (Rousset, 1999; Kawecki, 2004). Because evolutionary biology is interested in long-term fitness, not instantaneous growth rate, population geneticists tend to use the concept of reproductive value (i.e. the asymptotic probability that a future individual sampled randomly from all populations has a current ancestor in the focal population) when examining the evolutionary consequences of environmental heterogeneity. When three or more populations are connected, an unconditional source can have a low reproductive value if it is connected to another unconditional source that does not receive immigrants because in the absence of local adaptation all genes will eventually originate from the latter (Rousset, 1999; Kawecki, 2004). The source and sink concepts were not designed to address this particular issue, and therefore we feel that they should be kept separate from quantification of reproductive values. A more general conclusion from this debate, however, is that net flows cannot be used to measure the intrinsic strength of a subsystem as source or sink in systems with multiple subsystems. Any measure based on net flows will reflect the balance between the various forces at work in the system as a whole.

III. THEORY

The concepts presented above can be formalized using a simple general model describing the deterministic dynamics of the stock of some specific living or non-living entities in a local ecosystem, X_{i}. These entities potentially interact with a set of local environmental (biotic and abiotic) factors, denoted by a vector $\mathbf{E_i}$, as well as with a set of environmental factors beyond the boundaries of the focal ecosystem (which may include the same entities elsewhere), denoted by a vector $\mathbf{E_e}$, that determine the strength of spatial flows. Assume, for the sake of simplicity, that net spatial flow, captured in function F_{i}, and local growth, described by function G_{i}, do not strongly interact, such that their contributions to the rate of change of the stock considered are additive (Loreau *et al.*, 2003). The latter can then be written as

$$\frac{dX_{\mathrm{i}}}{dt} = G_{\mathrm{i}}\left(X_{\mathrm{i}}, \mathbf{E_i}\right) + F_{\mathrm{i}}\left(X_{\mathrm{i}}, \mathbf{E_i}, \mathbf{E_e}\right) \tag{1}$$

Defining sources and sinks formally with this model is straightforward. The local ecosystem is a source of the entities of interest over some period of time Δt if the time-averaged net spatial flow, $\overline{F} = \frac{1}{\Delta t}\int_{\Delta t} F_{\mathrm{i}}\,(t)\,dt$, is negative, and a sink if it is positive. Defining conditional and unconditional sources and sinks is less straightforward as these concepts seek to capture the intrinsic propensity of the local ecosystem to produce or absorb spatial flows of the entities of interest under a range of conditions. At equilibrium, local growth and net spatial flow cancel out (Pulliam, 1988). Therefore, both local growth and net spatial flow could in principle be used to define conditional and unconditional sources and sinks. Here we choose a definition based on local growth for the simple reason that population biology has traditionally focused on local demographic rates, which are generally easier to measure.

The local ecosystem can then be defined as a conditional source of the entities of interest if $G_{\mathrm{i}} > 0$, and a conditional sink if $G_{\mathrm{i}} < 0$, for at least some values of X_{i}, $\mathbf{E_i}$ and $\mathbf{E_e}$. It is an unconditional source if $G_{\mathrm{i}} > 0$, and an unconditional sink if $G_{\mathrm{i}} < 0$, for all values of X_{i}, $\mathbf{E_i}$ and $\mathbf{E_e}$ within the context considered. In the latter case, the entities of interest cannot persist in the absence of spatial flows, in agreement with previous criteria for unconditional sinks (Runge *et al.*, 2006). Clearly, conditional sources and sinks are expected to be more common than unconditional sources and sinks because the conditions that define them are less stringent. They also form the most flexible category of sources and sinks since they can be conditional for many different reasons, as discussed in the previous section.

A more specific model can further illustrate these concepts theoretically. Assume a minimal model of a local ecosystem (Loreau, 2010) in a patch *i*, in which there is a plant population, with nutrient stock per unit area P_{i}, and a limiting inorganic nutrient, with stock per unit area N_{i}. The inorganic nutrient pool is supplied with a constant input I_{i} of nutrient, and loses nutrient at a rate q_{i} per unit time. The plant population takes up inorganic nutrient at a rate $f_{\mathrm{i}}\,(N_{\mathrm{i}})$, and releases it at a rate m_{i} per unit time. A fraction λ_{i} of nutrient is lost from the ecosystem once released, the rest being recycled locally. In addition, the local ecosystem is connected to the surrounding ecosystems by diffusive flows of plants and nutrient, at rates d_{P} and d_{N}, respectively. Let P_{e} and N_{e} denote the plant and inorganic nutrient stocks, respectively, per unit area in the neighbouring external world. The model then reads (Loreau, 2010):

$$\frac{dN_{\mathrm{i}}}{dt} = I_{\mathrm{i}} - q_{\mathrm{i}}N_{\mathrm{i}} - f_{\mathrm{i}}\left(N_{\mathrm{i}}\right)P_{\mathrm{i}} + (1-\lambda)\,m_{\mathrm{i}}P_{\mathrm{i}} + d_{\mathrm{N}}\left(N_{\mathrm{e}} - N_{\mathrm{i}}\right) \tag{2}$$

$$\frac{dP_{\mathrm{i}}}{dt} = f_{\mathrm{i}}\left(N_{\mathrm{i}}\right)P_{\mathrm{i}} - m_{\mathrm{i}}P_{\mathrm{i}} + d_{\mathrm{P}}\left(P_{\mathrm{e}} - P_{\mathrm{i}}\right) \tag{3}$$

Let us focus on the role of this ecosystem as a source or as a sink for plants and assume for the time being that there are no spatial flows of inorganic nutrient ($d_{\mathrm{N}} = 0$). Equations (2) and (3) then map onto Equation (1) above with the following transformations: $X_{\mathrm{i}} = P_{\mathrm{i}}$, $\mathbf{E_i} = (N_{\mathrm{i}})$, $\mathbf{E_e} = (d_{\mathrm{P}}, P_{\mathrm{e}}, N_{\mathrm{e}})$, $G_{\mathrm{i}}(X_{\mathrm{i}},\mathbf{E_i}) = f_{\mathrm{i}}(N_{\mathrm{i}})P_{\mathrm{i}} - m_{\mathrm{i}}P$, and $F_{\mathrm{i}}(X_{\mathrm{i}},\mathbf{E_i},\mathbf{E_e}) = d_{\mathrm{P}}(P_{\mathrm{e}} - P_{\mathrm{i}})$. The ecosystem is a source of plants when $P_{\mathrm{e}} < P_{\mathrm{i}}$, and a sink when $P_{\mathrm{e}} > P_{\mathrm{i}}$. Assume now that patches differ only in their nutrient input, I_{i}, which governs their fertility. Since a higher fertility results in a larger plant nutrient stock, the source–sink status of the local ecosystem hinges on its relative fertility, i.e. its fertility compared with that of the surrounding ecosystems. Assume that $P_{\mathrm{e}} > P_{\mathrm{i}}$, i.e. the local ecosystem is a sink. At equilibrium, this would imply that local growth, $f_{\mathrm{i}}(N_{\mathrm{i}})P_{\mathrm{i}} - m_{\mathrm{i}}P$, is negative. This negative local growth, however, can have two causes: either (*i*) the local ecosystem is too unfertile to support a plant population in the absence of spatial flows, in which case it is an unconditional sink, or (*ii*) it is fertile enough to support a plant population but the spatial flow coming from more fertile neighbouring sites depresses local growth, in which case it is a conditional sink. Thus, the conditional or unconditional sink status of the ecosystem now depends on its absolute fertility, which here determines habitat quality. More precisely, it is easy to show that the equilibrium local inorganic nutrient stock, $N_{\mathrm{i}}{*}$, is $I_{\mathrm{i}}/q_{\mathrm{i}}$ in the absence of plants and $f_{\mathrm{i}}^{-1}(m_{\mathrm{i}})$ in their presence but in the absence of spatial flows. If $I_{\mathrm{i}}/q_{\mathrm{i}} > f_{\mathrm{i}}^{-1}(m_{\mathrm{i}})$, local fertility is high enough to support a plant population, and the ecosystem is a conditional sink; if $I_{\mathrm{i}}/q_{\mathrm{i}} < f_{\mathrm{i}}^{-1}(m_{\mathrm{i}})$, local fertility is too low to support a plant population, and the ecosystem is an unconditional sink.

The latter conclusion, however, depends strongly on the context considered. To see this, assume now that spatial flows of inorganic nutrient are present ($d_{\mathrm{N}} > 0$). The equilibrium

Table 2. Empirical examples of conditional and unconditional sources and sinks in ecology

Entity	Condition	Source	Sink	References
Conditional sources/sinks				
Beaver (*Castor Canadensis*)	Resource abundance	Lake with abundant, high-quality riparian vegetation	Lake with scarce or low-quality riparian vegetation	Fryxell (2001)
Snowshoe hare (*Lepus americanus*)	Tree density	Closed forest	Open forest	Griffin & Mills (2009)
Juvenile amphibians	Pond persistence	Perennial ponds	Short-term ponds	Semlitsch (2000)
Baird's tapir (*Tapirusbairdii*)	Hunting	Slightly hunted forests	Persistently hunted forests	Naranjo & Bodmer (2007)
Fish	Fishing	Marine reserve	Surrounding ocean	Russ & Alcala (2011)
Unconditional sources/sinks				
N, P, water		Headwater streams	Low-order streams	Vannote *et al*. (1980)
N, P, pesticides		Farmland	Streams	Burcher *et al*. (2007)
Marine detritus		Ocean	Island	Polis & Hurd (1995)
Adult salmon (*Salmo salar*)		Ocean	Fresh water	Verspoor *et al*. (2007)
Bay checkerspot butterfly (*Euphydryas editha bayensis*)		Large grassland patches with northern slope	Small grassland patches with southern slope	Harrison *et al*. (1988)

For the conditional sources and sinks we list the specific condition that determines their source–sink status.

local inorganic nutrient stock then becomes $(I_{\mathrm{i}} + d_{\mathrm{N}}N_{\mathrm{e}}^{*})/(q_{\mathrm{i}} + d_{\mathrm{N}})$ in the absence of plants. If $N_{\mathrm{e}}^{*} > I_{\mathrm{i}}/q_{\mathrm{i}}$, the spatial inflow of inorganic nutrient boosts local fertility, which in turn facilitates the establishment of a local plant population. As N_{e}^{*} gradually increases, the resulting increase in fertility can turn the local ecosystem from an unconditional sink into a conditional sink, and then even into a conditional source (Gravel *et al*., 2010*a*).

As another example of context dependence of the source–sink status of an ecosystem, assume that the ecosystem is initially an unconditional source for the resident plant species (i.e. $P_{\mathrm{i}} > P_{\mathrm{e}}$ and $f_{\mathrm{i}}(N_{\mathrm{i}}) > m_{\mathrm{i}}$ under all the conditions considered) but that another plant species that consumes the same limiting nutrient more efficiently is added. Competitive exclusion of the resident would then ensue in the absence of spatial flows, but immigration from neighbouring ecosystems can sustain a local resident population (Loreau & Mouquet, 1999). In this case, adding a heterospecific competitor has turned an unconditional source into a conditional sink for the resident. These two simple examples show clearly how broadening the context can dramatically alter the source–sink status of an ecosystem. Therefore, it is critical to keep the ecological context in mind when making inferences about sources and sinks.

IV. PATTERNS OF SOURCES AND SINKS IN NATURE

The source and sink concepts developed in the previous sections apply to all kinds of living (individuals, propagules) and non-living (energy, materials, dead organic matter) entities. But different entities are likely to vary in the type of spatial dynamics they exhibit in nature; therefore their status as conditional or unconditional sources and sinks is also likely to vary. Table 2 provides a few empirical examples from the literature.

Unconditional sources and sinks are expected to be comparatively common for non-living entities because of their passive movements, especially when these movements are unidirectional and driven by physical factors. For instance, at relatively small temporal scale but large spatial scale, physical constraints on fluxes of matter and energy lead to a predictable source–sink pattern: land is an unconditional source of minerals and organic matter, through rock weathering and nutrient and organic matter leaching from soils. The matter drained out from land feeds fresh waters, and in time, the ocean that represents an unconditional sink. This large-scale pattern driven by water flows is the basis of the river continuum concept (Vannote *et al*., 1980). At finer spatial scales these trends are more nuanced. For instance, fresh water can locally be a conditional source of matter and associated energy for the surrounding land through episodic flooding (Aalto *et al*., 2003). Biological transport mechanisms, however, greatly complexify the picture. Locally, living organisms can export or import matter and energy, thereby generating a wide range of conditional sources and sinks. For instance, nitrogen fixers can represent the main source of inorganic nitrogen to plants in terrestrial ecosystems (Vitousek & Howarth, 1991). Similarly, because of nitrogen fixers, the euphotic zone in the ocean represents a conditional source of available nitrogen, which is exported to deeper anoxic layers that represent a conditional sink, because of denitrifiers (Tyrrell, 1999). In terrestrial ecosystems, large herbivores may massively transfer matter between ecosystems, creating conditional sources and sinks over large scales (Augustine & Frank, 2001). Some biological transfers of nutrients are so predictable that they can be regarded as unconditional at fairly large spatial and temporal scales. For example, adult salmon (*Salmo salar*) migrations bring large quantities of marine-derived nutrients to freshwater and terrestrial ecosystems (Verspoor, Stradmeyer & Nielsen, 2007). These patterns, however, are always susceptible to small-scale disruptions due to a wide range of biological factors. For example, biotic disturbance during spawning and juvenile emigration of salmon may return large quantities of freshwater nutrients to the ocean (Moore *et al*., 2007). Similarly, the invasion of predators on islands colonized by seabirds may disrupt nutrient flows to islands and influence primary production (Maron *et al*., 2006). These examples again emphasize the context dependence of the conditionality of sources and sinks.

Conditional rather than unconditional sources should often be expected for living entities because interspecific competition is likely to reduce population growth rates below zero at high heterospecific densities. Organisms are also strongly susceptible to the impacts of human activities such as hunting, fishing and management of biological resources (Table 2). Unconditional sources, however, may occur within some contexts when competition is weak and population dynamics is mainly driven by local physical factors. Thus, large serpentine grassland patches with a northern slope act as unconditional sources for the bay checkerspot butterfly in California – at least during the time period they were studied – because quality of the abiotic habitat is the main factor that determines population growth and dispersal in this species (Harrison *et al*., 1988). Here again, however, it is not difficult to conceive of broader contexts that could turn these unconditional sources into conditional ones; for instance, over longer time scales, climate change and other anthropogenic impacts might affect the quality of these patches as habitats for the butterfly.

In heterogeneous landscapes mixing patches of good and bad quality, one may expect different patterns to emerge for organisms that are not individually capable of choosing the location where they live and for those that are capable of such a choice (Diffendorfer, 1998). In species with low mobility or where dispersal is controlled by abiotic factors, such as wind and water currents, source–sink dynamics should be relatively common. Consider for instance a plant species that lives in a landscape mixing fertile and unfertile patches. Fertile patches should support healthy populations that represent conditional sources of individuals or seeds to unfertile patches. In such a case, the heterogeneity of the landscape controls the source–sink dynamics in the metapopulation (Brachet *et al*., 1999; Mouquet *et al*., 2006).

By contrast, species with high mobility and the ability to assess habitat quality may tend towards balanced dispersal. Consider for instance a species of bird living in a heterogeneous landscape. If each individual bird is capable of choosing the location of its home range based on fitness assessment, in an 'ideal free distribution' fashion (Fretwell & Lucas, 1970), good patches will support populations with high densities and strong density dependence, bad patches will support populations with low density and low density dependence, and the individual fitness will be even across the landscape. The evenness will be maintained over time by the capacity of each individual to assess the landscape and move to the habitat that provides the highest fitness, thus balancing dispersal among patches of different quality (McPeek & Holt, 1992; Lemel *et al*., 1997). In such a case, the heterogeneity of density dependence will buffer landscape heterogeneity and prevent the emergence of source–sink dynamics. Note, however, that this is an ideal scenario that ignores many real-world complexities (e.g. imperfect information about habitat quality). Any mechanism that prevents ideal free distribution should result in the emergence of source–sink dynamics, and such mechanisms are widespread in nature (Fretwell & Lucas, 1970; Pulliam & Danielson, 1991; Jones, Pilkington & Crawley, 2006).

V. TEMPORAL DYNAMICS OF SOURCES AND SINKS

We have shown earlier that a source can turn into a sink, and *vice versa*, if the context is changed. This context includes not only the system considered and the various factors that affect the fluxes of entities among its components, but also the spatial or temporal scales at which the system is considered. Switching from source to sink, or from sink to source, occurs much more commonly than current theory and empirical data based on an equilibrium worldview might suggest, as a result of temporal fluctuations in the local system under study due either to external environmental forces or to the system's own internal dynamics (Table 3). Given the prevalence of temporal fluctuations of all kinds in nature, it is surprising that their consequences for sources and sinks have received so little attention so far.

If the period of time over which the system is observed is long compared with the characteristic time of its fluctuations and there is no long-term trend in its properties, the concepts and theory developed above for equilibrium sources and sinks can be generalized straightforwardly to non-equilibrium systems. This is because the average rate of change of the stock X_i in Equation (1) approaches zero over a long enough time period for any bounded system (Puccia & Levins, 1985). As a consequence, the long-term time-averages of local growth, $\overline{G_i}$, and of net spatial flow, $\overline{F_i}$, must cancel each other out just as in equilibrium systems, such that in principle sources and sinks can be defined in the same way as before, but using long-term average values instead of equilibrium values.

For most systems studied in ecology and in the Earth sciences, however, observation time is often relatively short compared with relevant fluctuations. Therefore, limiting the application of the source and sink concepts to very long periods of time (Pulliam, 1988) is often impractical or counterproductive. Short-term changes in systems that make them switch from source to sink, or from sink to source, can be as interesting to study as their long-term source or sink status. Many ecosystems undergo regular or episodic changes in their source–sink status, driven by a wide range of physical and biological factors (Table 3).

Table 3. Examples of mechanisms that may turn a source into a sink or *vice versa*, for both living and non-living entities

Mechanism	Entity	Example
Physical		
Fire	Insects	High-severity riparian wildfires stimulate the transfer of aquatic insects from the river to riverbanks (Malison & Baxter, 2010). With low-severity fires, however, riverbanks may switch from sinks to sources of insects.
Seasonal change in temperature	Nitrogen	Denitrification in river sediment varies seasonally with water temperature (McCutchan & Lewis, 2008). This may create nitrogen accumulation locally in sediment during winter (source), and nitrogen loss during summer (sink).
Global warming	Amphibians	Global warming increases seasonal drought in Yellowstone National Park, locally affecting ponds that were previously good habitat for amphibians (McMenamin *et al*., 2008), thus potentially turning conditional sources into conditional sinks for amphibians.
Drought	Carbon	Drought may be turning the Amazon rainforest from a long-term global conditional sink of atmospheric carbon into a global conditional source through reduced net primary production and increased tree mortality (Phillips *et al*., 2009; Zhao & Running, 2010).
Biological		
Intraspecific competition and facilitation	Plants	In semi-arid environments, a mix of intraspecific competition for water and facilitation in shrubs can create regular stripes of vegetated and bare soil (the so-called 'tiger bush'). This pattern moves in space and time (Klausmeier, 1999), creating a moving landscape of conditional sources and sinks of bushes.
Interspecific competition	Plants, nitrogen	Competition between legumes and grasses in pasture generates population cycles, which in turn generate a moving landscape of conditional sources and sinks of legumes, grasses, and soil nitrogen (Schwinning & Parsons, 1996).
Host–parasite interactions	Tussock moth	Interaction between tussock moth and its parasitoid generates moth outbreaks that move in time and space, creating a moving landscape of conditional sources and sinks (Maron & Harrison, 1997).
Predator–prey interactions	Mites	Predator–prey oscillations between predatory and herbivorous mites can create conditional sources and sinks of mites that move in time and space (Ellner *et al*., 2001).
Multitrophic interactions	Nitrogen	In oak savanna, deer may locally consume legumes, leading to decreased nitrogen fixation (Ritchie, Tilman & Knops, 1998), which may turn conditional sources of soil nitrogen into conditional sinks.
Human disturbances	Carbon	Human activities such as forestry, mining, and oil and gas exploration are disturbing boreal peatlands and permafrost soils, which has the potential to transform the latter from long-term carbon sinks into carbon sources (Schuur *et al*., 2009).

Recent changes in the pelagic food web of the Baltic Sea provide a good example of switching from source to sink and of its far-reaching ecosystem-level consequences (Casini *et al*., 2012). During the 1970s, the Baltic cod (*Gadus morhua*) population increased rapidly owing to favourable abiotic conditions and low fishing pressure, and consequently expanded to neighbouring areas, such as the Gulf of Riga, where cod is unable to sustain viable populations because low salinity prevents local reproduction but where adults can forage for prey and survive. Thus, during that period, the Baltic Sea was a conditional source of cod, and neighbouring areas in which cod populations were sustained by immigration from the Baltic Sea were unconditional sinks. The Baltic Sea cod population, however, suffered increased fishing pressure and altered environmental conditions during the 1980s, which turned it into a conditional sink. As a result, all cod populations collapsed, with considerable indirect effects on food-web structure and other organisms such as herring (*Clupea harengus*), zooplankton and phytoplankton in both initial source and sink locations.

Changes in the source–sink status of a system component are likely to be strongly scale dependent because the factors that drive these changes themselves are scale dependent (Fig. 1). For example, pine forests in western North America have acted as sinks of atmospheric carbon during much of the past century, but they turn episodically into sources following forest fires or outbreaks of mountain pine beetles (*Dendroctonus ponderosae*). Mountain pine beetles kill a large fraction of trees during outbreaks, thereby releasing significant amounts of carbon to the atmosphere for several years (Kurz *et al*., 2008). Switching of pine forests from carbon sink to carbon source occurs at specific spatio-temporal scales with no signature of these changes at other scales, very much like the situation portrayed in Fig. 1.

Source–sink dynamics at those scales can lead to patterns opposite to those expected intuitively from equilibrium properties. Since the long-term averages of local growth and of net spatial flow cancel each other out in each local system, one would expect negative covariance between average local growth and average net spatial flow in comparisons across different patches in the long run. Yet positive temporal covariance can occur in the short term in spatially coupled ecosystems provided that local growth and stock are temporarily correlated and fluctuations in stocks are asynchronous among ecosystems. These conditions can arise from either autocorrelated environmental fluctuations or density-dependent local growth.

Autocorrelated fluctuations in the local growth rate G can lead to transient inflation of abundance in sink populations because positive temporal autocorrelation in local *per capita* population growth rates tends to generate a positive covariance between *per capita* growth rate and abundance (Gonzalez & Holt, 2002; Roy, Holt & Barfield, 2005. For example, consider the simplest discrete-time stochastic sink population model:

$$N(t+1) = R(t)N(t) + I(t) \tag{4}$$

where $N(t)$ is abundance, $R(t)$ is *per capita* growth rate, and $I(t)$ is immigration in a local patch at time t. The patch is a long-term conditional sink if the temporal geometric mean of the *per capita* growth rate is smaller than 1 (Roy *et al.*, 2005). The time-averaged abundance is then

$$\overline{N} = \frac{Cov(R, N) + \overline{I}}{1 - \overline{R}} \tag{5}$$

where $\overline{R}$ and $\overline{I}$ are the time-averaged *per capita* growth rate and immigration, respectively, and Cov(R, N) is the temporal covariance between *per capita* growth rate and abundance (Roy *et al.*, 2005). When this covariance is positive, the abundance of the sink population is greater than its constant equivalent with the same average growth rate and immigration. A laboratory experiment with protozoans showed that environmental variability can indeed greatly inflate the mean abundance of sink populations, generate outbreak dynamics, and increase persistence time (Gonzalez & Holt, 2002).

Assume now a metapopulation in which each patch is a long-term sink as defined above but immigration results from passive emigration from all other patches across the metapopulation. Since emigration from each patch is likely to increase with local abundance, the inflationary effect of autocorrelated environmental fluctuations on local abundance translates into a positive covariance between local growth, G, and net spatial flow, F. For each sink patch, all other patches collectively act as a large regional source providing a steady stream of immigrants as long as dispersal is sufficiently weak and patches are not synchronized (Roy *et al.*, 2005). Thus, counter intuitively, a large ensemble of weakly coupled long-term sinks can behave as a collective source and persist indefinitely provided they fluctuate asynchronously. This mechanism, which has received some experimental support (Matthews & Gonzalez, 2007), is in essence the mechanism that underlies metapopulation persistence despite local population turnover (Jansen & Yoshimura, 1998).

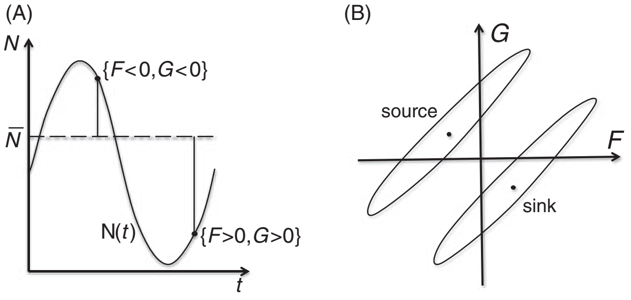

Fig. 2. (A) Emergence of positive temporal covariance between local growth, G, and net spatial flow, F, for a population that experiences self-sustained fluctuations in a patch. The graph plots population size, N, as a function of time, t, with periods where F and G have the same sign. $\overline{N}$ is average population size. (B) When two such patches are coupled, one can behave as a long-term conditional source and the other as a long-term conditional sink on average (dots), but self-sustained fluctuations around the average (ellipses) make each patch alternate between source and sink status in the short term. There is positive temporal covariance between F and G in each patch, but negative spatial covariance between F and G on average across patches.

Density dependence of local growth can have an effect similar to autocorrelated environmental fluctuations. Assume that local growth, G, of some biotic compartment involves density dependence with overcompensation and that net spatial flow, F, is driven by passive movement such as diffusion. High abundance of that compartment then generates overcompensation, and hence negative local growth, G, as well as movement of individuals to low-abundance sites, and hence negative F, provided fluctuations in abundance are not fully synchronized across sites (Marleau *et al.*, 2010) (Fig. 2A). The opposite situation is expected when abundance is low. A positive temporal covariance between net spatial flow and local growth then emerges within each site, despite the predicted negative spatial covariance between their long-term averages across sites (Fig. 2B). Microcosm experiments showed how such a fluctuating source–sink dynamics can lead to persistence of predator–prey systems (Amezcua & Holyoak, 2000). The presence of unconditional sinks, however, can also stabilize predator–prey fluctuations and increase persistence of the system (Schreiber *et al.*, 2006).

VI. EVOLUTION IN SOURCES AND SINKS

Evolution is another factor that can affect the source–sink dynamics of living entities. The effects of evolution depend on three main components: local selection in sources, local selection in sinks, and gene flow that connects the various parts of the landscape. Local selection is usually different in sources and sinks as the latter often differ in their abiotic conditions and population densities. Gene flow depends on the asymmetry in population densities between sources and sinks as well as on the evolution of dispersal. Although these various components may not be additive, for the sake of simplicity we consider them separately and we focus on evolution in a single species.

To understand the effect of local selection in sources, it is critical to know how local population density is affected by evolutionary dynamics. Because local selection is driven by differences in individual fitness, it is not straightforward to link selection and population density. A large body of theory shows that local selection can enhance population density, at least during part of evolutionary dynamics (e.g. Boudsocq, Barot & Loeuille, 2011). Such increases in population density may then fuel emigration from the patch, thus strengthening the source status of the patch. But local selection may also decrease population density. An extreme case of this outcome is evolutionary suicide (Webb, 2003; Parvinen, 2005), in which individual selection promotes population extinction. When local selection decreases population density, emigration is likely to decrease, thus potentially turning a source into a sink.

Local selection may also change population density in sinks, with important consequences for the migration balance of these patches, and therefore for the source–sink structure of the landscape. When environmental conditions deteriorate in a patch such that it becomes an unconditional sink, evolution may help the population to adapt and survive, a phenomenon known as evolutionary rescue (Gomulkiewicz & Holt, 1995; Bell & Gonzalez, 2009). In such situations, evolution has a positive effect on local population density and may turn the sink into a source, or at least turn an unconditional sink into a conditional one. At a larger scale, expansion of species ranges also results from turning former sinks into sources (Kirkpatrick & Barton, 1997; Case & Taper, 2000).

Many models have pointed out the importance of gene flow in constraining the source–sink structure of spatially structured populations (Hanski & Gaggiotti, 2004). Gene flow in turn is affected by the evolution of dispersal, which determines the number of migrants in and out of each patch (Ronce, 2007). As this affects the net flow of individuals between patches, the evolution of dispersal is an important constraint on source–sink dynamics in heterogeneous landscapes. Spatial variability in habitat quality influences the evolution of dispersal, and their combined effects govern which site will be a source or a sink (Mathias, Kisdi & Olivieri, 2001; Parvinen, 2002). When the source–sink status of local populations is generated by differences in carrying capacity and the strength of density dependence, carrying capacities with a high mean and variance may trigger selection for lower dispersal. Lower dispersal is then favoured because dispersers are most often migrating from large patches to small ones, where density dependence is fiercer, provided that the distribution of carrying capacities is not too skewed (Massol *et al*., 2011). By contrast, when the landscape contains many small populations and a few very large ones (skewed distribution of carrying capacities), disruptive selection is expected to drive dispersal rates. In this case, small populations become conditional sources for high-dispersal types while large populations serve as conditional sources for low-dispersal types (Massol *et al*., 2011).

Dispersal can also greatly affect the evolution of local adaptation, and hence the source–sink structure of the landscape (Bell & Gonzalez, 2011). Some models predict that intermediate dispersal rates should favour the evolution of habitat specialists, thereby turning some habitats into unconditional sources and others into unconditional sinks, whereas either low or high dispersal should favour the evolution of habitat generalists, thereby turning all patches into conditional sources (Ronce & Kirkpatrick, 2001). Habitats that have become unconditional sinks for one species can then act as vacant ecological niches, and hence become sources, for new specialist species provided that dispersal distance is sufficiently small and reproduction occurs between closely located individuals (Kawata, 2002).

Although we still have rudimentary understanding of the evolution of food webs in space, evolution in one species may also be expected to affect, or be affected by, the source–sink dynamics of its resources and consumers in a number of different ways (Fig. 3). First, if dispersal of consumers or resources is high enough (arrows 1 and 2 in Fig. 3), the selective pressures they exert on the target species are likely to homogenize across the landscape, which tends to decrease genetic or phenotypic diversity at the landscape scale (Loeuille & Leibold, 2008; Venail *et al*., 2008). Second, prey are generally maladapted to local conditions in sink habitats because a substantial proportion of them come from immigration. This maladaptation has important consequences for the maintenance and evolution of their predators (either the target species when resources are the prey or consumers when the target species is the prey: arrows 2 and 3 in Fig. 3). For instance, maladapted prey may have traits or behaviours that make them more vulnerable to predators in sources (Urban *et al*., 2008). Alternatively, sink habitats may provide selective pressures toward lower defence in prey (Hochberg & van Baalen, 1998). When these palatable prey migrate to more productive areas, they act as subsidies for local consumers. Third, the source–sink structure of inorganic resources (arrow 2 in Fig. 3) tends to create a fertility mosaic across the landscape that may promote spatial diversity in phenotypic traits, especially those incurring energetic costs (Hochberg & van Baalen, 1998; Loeuille & Leibold, 2008). Fourth, evolution of the target species may alter the spatial distribution of nutrient recycling (Loeuille & Leibold, 2008), which may in turn alter the source–sink status and spatial flows of nutrient across the landscape (arrow 4 in Fig. 3).

VII. CONSERVATION PLANNING FOR MULTIPLE SOURCES AND SINKS

Consideration of sources and sinks in population ecology has led to a call for large-scale, landscape-level conservation planning for species in order to account for their source–sink

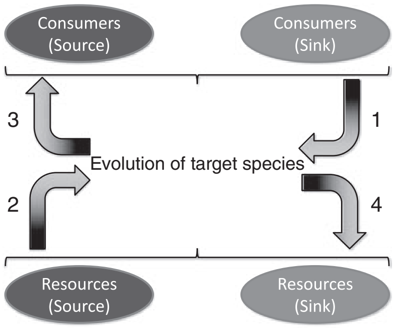

Fig. 3. Evolution and source–sink dynamics in a multitrophic context: evolution of a target species may be affected by the source–sink status of its consumers (arrow 1) or resources (arrow 2); it may also modify the source–sink status of its adjacent trophic levels (arrows 3 and 4).

dynamics (Pulliam & Danielson, 1991; Semlitsch, 2000; Runge *et al*., 2006; Vandermeer, Perfecto & Schellhorn, 2010). Our pervasive human footprint has led to habitat loss and fragmentation of natural ecosystems, two leading causes of biodiversity loss (Fahrig, 2003). Connectivity of local fragments must be ensured in order to sustain species persistence in sinks and to allow connections between sources. The majority of the conservation applications of source–sink theory have been for individual species (e.g. Donovan *et al*., 1995; Semlitsch, 2000). However, other entities (e.g. nutrients, water) have source–sink dynamics, and these dynamics are interdependent. As conservation planning for ecosystem services is receiving increasing attention (Chan *et al*., 2006), explicit consideration of source–sink dynamics for multiple entities becomes critical.

Our refinement of the source and sink concepts adds two components to conservation planning for entities with conservation value and for ecosystem services. First, a sink for one entity may be a source for another entity and *vice versa* – this is especially likely when different entities belong to different trophic levels or ecosystem compartments (Loreau *et al*., 2003). A number of physical and biological mechanisms may also lead to switches between sources and sinks (Table 3). Consequently, conservation planners should consider both the diversity of sources and sinks for different entities and fluctuations in sources and sinks in time and space (Fig. 4). Second, there is a need to think large for conservation planning of source–sink systems. Species and substances flow across habitat boundaries; therefore, management of specific patches must consider the surrounding landscape in order to be effective (McIntyre & Hobbs, 1999). By considering sources and sinks for multiple entities at large spatial extents, managers are led to consider landscapes as continuous source and sink surfaces as opposed to binary landscapes of sources and sinks. We argue that this is a more useful conceptualization of landscapes for conservation planning.

A landscape perspective on source–sink dynamics allows conservation planners to look at the complementarity of local source and sink compartments. For instance, by overlaying maps of unconditional sources for various species and substances, one could identify source hotspot regions (Fig. 4). Sources, however, may not always be desirable for all entities; for instance, nutrient flows may generate water pollution or eutrophication, and the spread of pathogens, parasites and invasive species is generally regarded as undesirable. Thus conservation planning for multiple ecosystem services will require careful definition of objectives and their implications for multiple ecosystem components. Changes in the conservation status of targeted areas are also likely to alter the source–sink dynamics of a wide range of ecosystem components with neighbouring areas through cascades of indirect effects mediated by both local interactions and non-local interactions arising from metaecosystem dynamics (Loreau *et al*., 2003). Successful conservation planning will require careful consideration of these indirect effects on other ecosystem components and other areas.

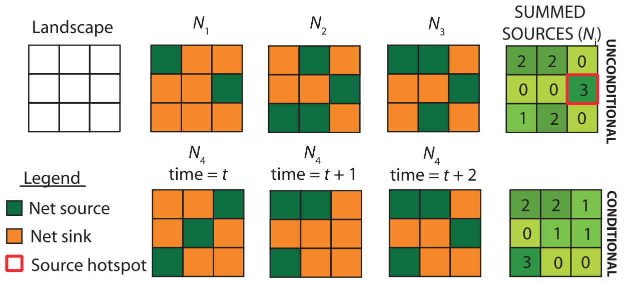

Fig. 4. Conservation planning based on identification of multiple unconditional (top) or conditional (bottom) source and sinks. Top: different entities, N_i, may have different unconditional source and sink patches. A landscape may be viewed as a continuum of source and sink sites for a suite of substances and organisms of conservation interest as opposed to a binary source–sink landscape. Resource managers may then use the distribution of unconditional sources and sinks to identify areas of high conservation priority, such as source hotspots in the example shown in the top row here. Bottom: conservation prioritization for conditional sources and sinks may depend on their spatial and temporal dynamics. For example, a single entity, N_4, may show temporal dynamics in the distribution of source and sinks. Consequently, resource managers may use the probability that a site is a conditional source or sink over a given time frame to identify areas of high conservation priority. In these simple examples, we assume all N_i sources are independent and have equal value.

VIII. CARBON SOURCES AND SINKS: MERGING BIOGEOCHEMICAL AND ECOLOGICAL PERSPECTIVES

We have argued above that the definition of sources and sinks is strongly context dependent. Since scale is a key component of context, we should expect different source–sink relationships to emerge at different scales. Scale differences can largely explain the different perspectives adopted by the Earth sciences, with their focus on global biogeochemical processes, and the bulk of ecology, with its focus on smaller-scale processes such as population dynamics. Ultimately, however, these different perspectives should merge into a comprehensive ecology of the biosphere that accounts for both small- and large-scale processes, and for both biogeochemical and demographic processes (Levin, 1992; Loreau, 2010). To illustrate how sources and sinks may differ strongly and yet be interconnected at different scales, let us consider carbon sources and sinks, which have attracted a great deal of attention recently because of their implications for climate change.

Fossil fuel emissions by humans are contributing to a steady increase in atmospheric carbon dioxide concentrations. Some 43% of anthropogenic carbon dioxide emissions, on average, remain in the atmosphere; the rest is absorbed by 'carbon sinks' on land and in the oceans (Le Quéré *et al.*, 2009). These 'carbon sinks', in effect, describe the global average net effects of terrestrial and marine ecosystems, which collectively act as net sinks of atmospheric carbon by taking up carbon through photosynthesis and storing it temporarily in the form of biological structures, soils, sediments, and dissolved inorganic carbon (Falkowski *et al.*, 2000). These global average net effects, however, result from the operation of a myriad of ecological processes that vary considerably in space and time. Even globally, the strength of the terrestrial carbon sink, which is largely driven by the world's forests (Pan *et al.*, 2011), shows wide year-to-year fluctuations (Le Quéré *et al.*, 2009). Drought induced by climate change might even be turning the Amazon rainforest, which alone accounts for 66% of global variations in terrestrial net primary production, from carbon sink into carbon source through reduced tree productivity and increased tree mortality (Phillips *et al.*, 2009; Zhao & Running, 2010). Similarly, human activities such as forestry, mining, and oil and gas exploration are disturbing, removing or burning boreal peatlands and permafrost soils, which has the potential to transform this global carbon storehouse from carbon sink (Schuur *et al.*, 2009) to carbon source, resulting in positive climate-change feedbacks.

Zooming in from the global to the landscape scale, a forest ecosystem that acts as a sink of atmospheric carbon is often also a source of organic carbon for nearby streams and lakes through litter fall (Vannote *et al.*, 1980; Caraco & Cole, 2004). This organic carbon is then decomposed in water bodies where it contributes to support a diverse food web. Some aquatic invertebrates subsequently move to the forest where they feed terrestrial predators, which in turn become prey to larger aquatic predators (Nakano & Murakami, 2001; Baxter *et al.*, 2005). These multiple reciprocal interactions generate a complex dynamic set of source–sink relationships at the interface between forests and fresh waters (Leroux & Loreau, 2012). The same forest may simultaneously be a sink of atmospheric inorganic carbon, a source of dead organic carbon, a sink of carbon in the form of adult aquatic invertebrates, and a source of carbon in the form of terrestrial invertebrate consumers. Which of these source–sink relationships is most relevant is but a matter of scale and context.

Making scale and context explicit will become increasingly important in studies of carbon sources and sinks as different perspectives might lead to communication problems, such as when some Earth scientists use a negative sign for net carbon flows to terrestrial sinks because they implicitly take the atmosphere as their reference system (Gurney & Eckels, 2011) whereas ecologists use a positive sign (Pan *et al.*, 2011). Only the latter usage, however, is consistent with our formal definitions (Section III).

IX. CONCLUSIONS

(1) The source and sink concepts are used frequently in ecology, evolution, and Earth sciences, but they have evolved in divergent directions, hampering communication across, and sometimes even within, disciplines. We have proposed a unifying conceptual framework to improve clarity as well as consistency across disciplines.

(2) A general definition of the source and sink concepts that transcends disciplines is based on net flows between the components of a system: a *source* is a subsystem that is a net exporter of some living or non-living entities of interest, and a *sink* is a net importer of these entities.

(3) Sources and sinks can further be classified as *conditional* and *unconditional*, depending on the intrinsic propensity of subsystems to either produce (source) or absorb (sink) a surplus of these entities under some (conditional) or all (unconditional) conditions.

(4) The distinction between conditional and unconditional sources and sinks, however, is strongly context dependent. Sources can turn into sinks, and *vice versa*, when the context is changed, when systems are subject to temporal fluctuations or evolution, or when they are considered at different spatial and temporal scales.

(5) The dynamics between sources and sinks has profound consequences for our ability to understand, predict, and manage species and ecosystems in heterogeneous landscapes, and yet it is still relatively poorly understood, particularly in fluctuating or changing environments. The conservation of ecosystem services requires careful consideration of the source–sink dynamics of multiple ecosystem components.

(6) One of the main future challenges will be to integrate the large-scale fluxes of energy, materials and living organisms in a coherent worldview that allows us to anticipate and respond to multiple changes in ecological systems, from local to global scales. We hope that our unifying framework will contribute to meeting this important challenge.

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XI. REFERENCES

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