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CONCEPTS & THEORY

Could the lateral transfer of nutrients by outbreaking insects lead to consequential landscape-scale effects?

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Abstract. The processes that transfer nutrients laterally over large distances are limited within terrestrial ecosystems. Here, we present the hypothesis that outbreaking insects can sometimes transport consequential amounts of embodied nutrients over long distances, thereby connecting ecological dynamics across space and leading to potential emergent effects at the landscape scale that have not been specifically addressed heretofore. Based on previously published data on insect population density, individual body mass, and nutrient content, we present initial quantitative estimates of nitrogen and phosphorus fluxes for various outbreaking insect species in different ecosystems. The results suggest that during the phases of major population change within an outbreak cycle, this process may transfer, over a given area, amounts of nutrients that exceed annual input from contemporaneous levels of atmospheric deposition, particularly for phosphorus. In addition, the relative strength of the process was likely even higher in the preindustrial era, especially for nitrogen, due to a weaker anthropogenic influence on atmospheric deposition at that time. The values we have found are comparable to the results from previous studies on 2-D nutrient fluxes by other animals and that have been considered consequential for ecosystem processes. We further illustrate the implications of the process for the spatial distribution of nutrients and resulting ecological complexity and argue that the process is inherently scale dependent, contrary to vertical fluxes like atmospheric deposition. Moreover, we provide suggestions for future studies, both empirical and theoretical, that would better quantify the strength of the process and assess its implications. Given that the productivity of most natural terrestrial ecosystems depends primarily on locally recycled nutrients and that spatial source–sink nutrient dynamics has been shown to have important ecological consequences, the long-distance lateral transfer of nutrients by outbreaking insects appears like a relevant landscape-level process worthwhile of more specific attention.

Key words: cross-scale feedbacks; nutrient fluxes; nutrient limitation; outbreaking insects; scale dependence; source–sink dynamics; spatial heterogeneity.

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> *By morning the wind had brought the locusts; they invaded all Egypt and settled down in every area of the country in great numbers. […] Nothing green remained on tree or plant in all the land of Egypt.*
>
> —The Bible; Book of Exodus

Introduction

The bulk of nutrient cycling in terrestrial ecosystems happens among plants, soil, and microbes, resulting in very localized exchanges (Chapin et al. 2002). Terrestrial nutrient cycling diagrams therefore focus on the "vertical," or "1-D," fluxes consisting of atmospheric exchanges, hydrological exports, and the localized transfers among nutrient pools at a given location (Bormann et al. 1977, Johnson and Henderson 1989, Likens et al. 1994). The lateral transfers of nutrients over much larger distances within terrestrial ecosystems, for example through "biological vectors" (Likens et al. 1994), are sometimes acknowledged, but usually left unquantified. Yet these lateral, or "2-D," nutrient fluxes give rise to a spatial source–sink dynamics that has the capacity to modulate plants productivity through indirect interactions among patches (Gravel et al. 2010*a*), can affect regional-level plant succession and persistence (Gravel et al. 2010*b*), and may even influence the outcome of conservation efforts (Loreau et al. 2013). In addition to these cross-scale ecological feedbacks, the lateral transfer of nutrients can modify vegetation productivity across space because, at least for nitrogen (N) and particularly phosphorus (P), natural ecosystems mostly rely on locally recycled nutrients (Cleveland et al. 2013). And since nutrient availability could be the main control on net ecosystem production in forests at least (Fernández-Martínez et al. 2014), the lateral transfer of nutrients may also be consequential for carbon cycling.

The specific pathways for 2-D nutrient fluxes have been much less studied than their 1-D counterparts, especially for large-distance transfers. Within terrestrial ecosystems *per se*, the abiotic nutrient flows, e.g., through soil solution or litter dispersal (Gravel et al. 2010*a,b*), occur over short distances. Transfers by animals, on the other hand, can happen at the landscape scale. Most identified vectors in terrestrial ecosystems consist of large mammalian herbivores, for example, wildebeest and other large grazers in the Serengeti (McNaughton 1985), elk and bison in Yellowstone National Park (Frank et al. 1994), or deer in the European mosaic of agricultural fields and forest patches (Abbas et al. 2012). These animal-mediated 2-D fluxes could be responsible for anomalously low productivity in nutrient-exporting vegetation types (McNaughton 1985), as well as net nutrient movements from high to low elevations (Frank et al. 1994), fields to forests (Abbas et al. 2012), and across a P-rich basalt to P-poor granite geological boundary (Wolf et al. 2013). Moreover, now-extinct large animals may have played a dominant role in landscape-level nutrient cycling thousands of years ago, particularly for P in the Amazon (Doughty et al. 2013). Terrestrial biogeochemistry is also affected by 2-D allochthonous nutrient exchanges, as exemplified by the consequential fluxes of salmon-derived marine nutrients in coastal forests of western North America (Hilderbrand et al. 1999, Helfield and Naiman 2001, Gende et al. 2002, Field and Reynolds 2011).

At a completely different individual scale, insects have multiple and major impacts on 1-D nutrient cycling that are also well recognized. Insects directly alter the amount, quality, and timing of nutrients transferred from plants to soil in different environments (Hunter 2001, Chapman et al. 2003, Metcalfe et al. 2014) and indirectly affect vertical nutrient cycling by changing the physical environment (e.g., soil moisture) and, sometimes, vegetation composition (Belovsky and Slade 2000, Hunter 2001, Lovett et al. 2010). The consequences of insect activity on processes like primary productivity or nutrient leaching vary not only among ecosystems (Hunter 2001) but also in the same system for different levels of insect density (Belovsky and Slade 2000). Consequently, it is not surprising that insect outbreaks, which by definition imply sudden changes in total population, often cause particularly strong impacts. Since literally Biblical times (the 8th plague of Egypt), spectacular locust outbreaks (Fig. 1) in arid and semiarid environments have struck the imagination and often caused agricultural havoc

Fig. 1. Outbreak of desert locust (*Schistocerca gregaria*) in southwestern Morocco in November 2004. Photo credit: Magnus Ullman.

(Uvarov 1955, Lockwood 2004, FAO 2009). The numerous ecological consequences of insect outbreaks are increasingly being recognized (Yang 2012), and the resulting 1-D nutrient pulses have been quantified for different types of outbreaking insects: leaf-eating insects (Hunter 2001, Lovett et al. 2002, le Mellec et al. 2011), periodical cicadas (*Magicicada* spp.) that spend most of their life cycle underground and emerge for reproduction (Whiles et al. 2001, Yang 2004), and tree-killing bark beetles (see the Mikkelson et al. 2013 review).

In this article, we hypothesize that the lateral transfer of nutrients by outbreaking insects (LTNOI) is a relevant landscape-level (i.e., at scales ≥10 km) process, entailing various potential impacts on ecological complexity and biogeochemical cycles. Through the embodied nutrients they carry around, outbreaking insects can indeed give rise to "resource pulses" having temporary and persistent ecological effects (Yang et al. 2008). Insect outbreaks also involve large and rapid changes in population size that could allow them to mediate the carbon cycle (Schmitz et al. 2014). Furthermore, outbreaking insects are examples of the nutrient vectors involved in source–sink ecosystem dynamics (Gravel et al. 2010*a,b*, Loreau et al. 2013). While many previous studies have highlighted the relevance of the 2-D nutrient fluxes caused by terrestrial insects and other arthropods like spiders (Edwards and Banko 1976, Polis et al. 1997, Baxter et al. 2005, Nowlin et al. 2007, Schmitz et al. 2010), these studies have, however, not often addressed the distinctive characteristics of outbreaking insects and, above all, have only considered these 2-D fluxes as allochthonous inputs to isolated habitats like caves, new volcanic areas, and alpine snowfields, or between aquatic and terrestrial ecosystems. Here, we rather focus on the role of outbreaking insects in the lateral redistribution of nutrients within the terrestrial ecosystem where they normally occur (i.e., their range), a process that has apparently been overlooked heretofore.

In the following sections, we first provide some initial quantitative estimates of the amounts of nutrients that could potentially be redistributed as a result of insect outbreaks in different ecosystems (Section "The Case for the LTNOI Process"). Then, we discuss the potential role of the LTNOI process in the formation of spatial patterns for nutrient distribution, its inherent scale dependence, and its potential to foster additional ecological complexity through emergence and other nonlinear feedbacks (Section "Implications of the LTNOI Process"). We further recommend specific research avenues in order to better assess the LTNOI strength and consequences (Section "Further Assessing the LTNOI Process") and conclude that correctly appreciating this process might help us refine our understanding of spatial ecology and biogeochemistry (Section "Conclusions").

The Case for the LTNOI Process

Conceptual justification

The strength of the LTNOI process at the landscape scale rests upon the combination of three features: (1) the high proportion of nutrients in insect bodies; (2) the change in total population biomass of outbreaking insects; and (3) the long-distance movement of individual outbreaking insects.

The first condition is met by herbivorous insects in general. Despite substantial variability among species and even for different individuals of the same species, insects are usually much richer in nutrients than the plants they consume (Sterner and Elser 2002). Given that their dry weight is on average ~10% N and ~1% P (Elser et al. 2000), herbivorous insects can, in a sense, be conceived of as plant-derived nutrient concentrates.

Major changes in population are critical for the strength of LTNOI, because the potential for animals to substantially alter biogeochemistry through their own embodied nutrients resides in their *variation* in absolute biomass (Vanni et al. 2013). Outbreaking insects meet this second condition almost by definition. For example, the density of early-life stages (egg masses or second-instar larvae) of the eastern spruce budworm (*Choristoneura fumiferana*) varies by a factor of 10000 over an outbreak cycle, which lasts about 35 yr in the forests of eastern Canada (Royama et al. 2005). Locusts are so well adapted to outbreaking cycles that, for most species, the high-density individuals differ morphologically and physiologically from the low-density individuals (Simpson and Sword 2008). A single flying swarm of locusts can contain from a few million to many billion individuals (Simpson and Sword 2008, FAO 2009), representing a biomass (live weight) of the order of 1 tonne/ha. In the forests of eastern United States, the synchronous emergence from underground, at precise intervals of either 13 or 17 yr, of ~500 kg/ha (live weight) of periodical cicadas within a few weeks (Williams and Simon 1995) is an explosive ecological and biogeochemical event.

Periodical cicadas, however, fly a few hundred meters at most during an outbreak (Cook and Holt 2006), while the spatial synchrony of various "forest pest" outbreaks over large areas is probably often caused by regional stochasticity (e.g., weather) rather than by the emigration of individuals from eruptive centers (Peltonen et al. 2002, Liebhold et al. 2012). On the other hand, the desert locust (*Schistocerca gregaria*) can migrate over ~5000 km, one of the highest distance-to-body-length ratio of all animals (Alerstam et al. 2003). Although wingless, the Mormon cricket (*Anabrus simplex*) can travel 40–80 km per year during outbreaks (USDA 1994). Many individuals from major outbreaking forest insects also disperse, generally aided by wind, over distances >50 km, including the spruce budworm (Greenbank et al. 1980) and the mountain pine beetle (*Dendroctonus ponderosae*) (Jackson et al. 2008). In summary, various outbreaking insects meet the third condition in order for the LTNOI process to be relevant at the landscape scale.

Initial quantitative estimates

To further assess its relevance, the LTNOI process should be compared with other nutrient sources and sinks. Ideally, this comparison would involve mapping the 2-D fluxes associated with the lateral transfer of nutrients embodied in outbreaking insects over entire landscapes. Unfortunately, the data required to do so are not currently available. We nonetheless performed a simplified assessment, comparing the import or export of nutrients by outbreaking insects during the migrating stage of their life cycle to atmospheric deposition over the same area (see Appendix for complete details). Table 1 presents, for various outbreaking insects in different ecosystems and regions of the world, the results of this assessment.

For all insects, we performed "high-population density" estimates aiming to represent the highest

Table 1. Possible lateral transfer of nutrients by outbreaking insects during 1 yr for a given area, divided by the annual atmospheric deposition of nutrients (bioavailable fraction only) over the same area (unitless ratio). For each nutrient (N = nitrogen, P = phosphorus), the value reported is for our central estimate of atmospheric deposition over the entire region, whereas the numbers in parentheses reflect the ratios based on the highest and lowest atmospheric deposition values over the entire region. Note that the regions used to estimate atmospheric deposition do not encompass the full range of the insects. See Appendix for complete details.

Insect	Ecosystem type	Ratio, N	Ratio, P
High-population density estimates			
Desert locust	(Semi-)arid areas; Northern Africa and Arabian Peninsula	104.4 (31.3–313.3)	64.3 (4.5–450.0)
Spruce budworm	Forests; eastern Canada	0.9 (0.6–2.3)	4.6 (3.4–68.8)
Forest tent caterpillar, western domain	Forests, western Canada	4.5 (2.3–11.3)	52.0 (15.6–>156.1)
Forest tent caterpillar, eastern domain	Forests; eastern Canada	1.9 (1.1–5.6)	10.4 (7.8–156.1)
Bigheaded grasshopper	Grasslands; Wyoming (United States)	1.9 (1.2–4.2)	116.1 (23.2–>116.1)
Mountain pine beetle	Forests; British Columbia (Canada)	1.0 (0.4–1.7)	1.6 (1.2–2.4)
Total-outbreak area estimates			
Bigheaded grasshopper	Grasslands; Wyoming (United States)	0.5 (0.3–1.1)	31.0 (6.2–>31.0)
Mountain pine beetle	Forests; British Columbia (Canada)	0.3 (0.1–0.6)	0.5 (0.4–0.8)

Table 2. Values (in kg-N·ha^{-1}·yr^{-1} or kg-P·ha^{-1}·yr^{-1}) from previous studies on the lateral transfer of nutrients by animals.

Mechanism	Values, N	Values, P	References
Arthropod fallout on snowfields	0.04	0.003	Edwards and Banko (1976)
Ungulates annual migration	17†	…	Frank et al. (1994)
Salmon eaten by bears	0.05‡	…	Hilderbrand et al. (1999)
Sea turtle eggs on beach	30	3	Bouchard and Bjorndal (2000)
Carnivorous birds to freshwater	0.2§	0.05§	Hahn et al. (2007)
Periodical cicadas to ponds/streams	4.3¶	0.3¶	Nowlin et al. (2007)
Crows, urban to forest areas	23	2.3	Fujita and Koike (2009)
Deer, fields to forests	0.6#	0.09#	Abbas et al. (2012)

Notes: "…" means no data available.
† Net value (addition of 27, minus removal of 10).
‡ Value per bear, within 500 m from the stream.
§ Mean values for "external" inputs.
¶ Median values.
# Values for the average forest cover and "realistic scenario."

LTNOI fluxes during an outbreak, based on the values available in the literature. The results (Table 1) suggest that the flux of nutrients embodied in outbreaking insects can represent many years worth of atmospheric deposition of bioavailable nutrients, up to about a century for N in the case of the desert locust and for P in the case of the bigheaded grasshopper (*Aulocara elliotti*). These values represent a single lateral transfer by outbreaking insects over a given area and thus do not account for the frequency at which the process happens. For example, if desert locusts were to affect the same area every 20 yr, the resulting mean N flux would be roughly five times (central estimate) as substantial as continuous atmospheric deposition.

By design, these high-population density fluxes likely overestimate the average magnitude of the LTNOI process over the entire area affected by an outbreak. For two insects, we were able to further compute "total-outbreak area" estimates that were representative of the LTNOI over the whole landscape impacted, during the outbreak phase of population increase (mountain pine beetle) or decrease (bigheaded grasshopper). These total-outbreak area estimates were approximately three to four times smaller than the corresponding high-population density values (Table 1). For both types of estimate, the differences across species reflect not only the variations in total nutrient fluxes by the outbreaking insects but also the changes in atmospheric deposition over different regions. For example, the differences between the western and eastern domains for the forest tent caterpillar (*Malacosoma disstria*) come entirely from the higher N and P deposition in eastern than in central-western North America.

The previous assessment involved LTNOI magnitudes of 0.1–23.5 kg-N·ha^{-1}·yr^{-1} and 0.01–2.3 kg-P·ha^{-1}·yr^{-1}, based on the high-population density estimates, over the area directly impacted by an outbreak event (Table S1). These values are comparable to the results from previous studies on 2-D nutrient fluxes by animals (Table 2), which have often been judged as consequential for their ecological and biogeochemical impacts. Note that these other fluxes do not account either for the frequency at which the transfer happens. In some cases, for example the salmon-derived nutrient fluxes due to bears (Hilderbrand et al. 1999), the transfers likely happen each year over the area studied. In other cases, for example the fluxes of nutrients embodied in periodical cicadas to aquatic ecosystems (Nowlin et al. 2007), the transfers are, however, irregular, similar to the LTNOI process.

The previous comparisons with atmospheric deposition (Table 1) and other animal-mediated 2-D nutrient fluxes (Table 2) bring quantitative support to the LTNOI hypothesis. This support is enhanced by the fact that these LTNOI values came from independent estimates for different insect species. Nevertheless, one must remain cautious regarding this initial assessment due to the uncertainty inherent to such exercises. For example, the global CO_2 emissions by termites were initially estimated to reach 13 Pg-C/yr (Zimmerman et al. 1982), which is higher than

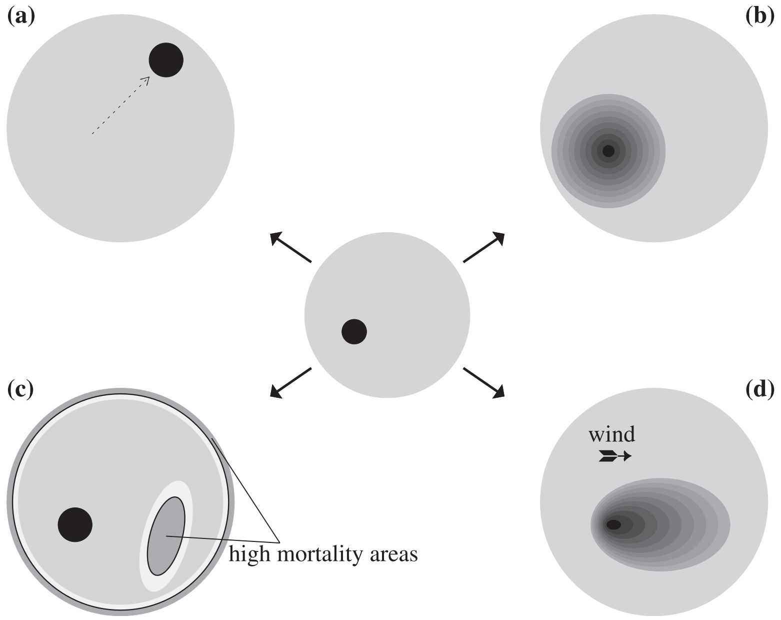

Fig. 2. Consequences of the lateral transfer of nutrients by outbreaking insects (LTNOI) process for the distribution of nutrients across the landscape, for a fixed insect range. The initial landscape state is pictured in the central part of the figure, where the shading intensity represents the concentration of a single nutrient. (a) The process simply moves the nutrient across the landscape, without changing the overall spatial heterogeneity. (b) The process diffuses the nutrient away from its original hotspot, decreasing the overall spatial heterogeneity. (c) The process concentrates the nutrient in sink areas, increasing the overall spatial heterogeneity. (d) Same as in (b), but illustrating the impact of prevailing winds during the dispersal phase.

current anthropogenic emissions, before being subsequently downscaled by a factor of almost 15 (Sanderson 1996). While more definitive estimates will, require dedicated studies (see Section "Further Assessing the LTNOI Process"), one must also be aware that the relative importance of the LTNOI process was almost certainly higher in the past, particularly for N, due to lower atmospheric nutrient deposition. Indeed, over the regions included in Table 1, the ratio of contemporaneous to preindustrial atmospheric deposition is about 1.5–15 for N (Galloway et al. 2004) and 1.1–2 for P (Mahowald et al. 2008).

Implications of the LTNOI Process

Spatial pattern of nutrient distribution

Insect outbreaks can recur in the same region for long periods of time, with documented examples of over 1000 yr for the larch bud moth (*Zeiraphera diniana*) in the Alp forests (Esper et al. 2007) and the Oriental migratory locust (*Locusta migratoria manilensis*) in eastern China (Tian et al. 2011). Over such long periods, outbreaking insects may thus contribute to spatial pattern formation in nutrient distribution.

Consider a hypothetical, purely terrestrial landscape with an initial heterogeneous distribution for a given nutrient (Fig. 2, central portion). A first possibility would be for the LTNOI process to simply move the nutrient across the landscape, without modifying the overall spatial heterogeneity (Fig. 2a). However, ongoing lateral transfers of the nutrient will more likely end up decreasing or increasing the preexisting spatial gradients (Power and Rainey 2000). Similarly to nutrient redistribution by large mammalian herbivores (Doughty et al. 2013, Wolf et al. 2013), the process could lead to a diffusive flow that would decrease the initial spatial heterogeneity (Fig. 2b). Two different mechanisms can give rise to a diffusive flow from outbreaking insects. First, the nutrient content of primary consumers is not perfectly homeostatic, but depends to some extent on the nutrient content of the plants they eat (Sterner and Elser 2002). Random outbreak dispersal alone can thus result in a net flux away from nutrient hotspots. Second, insects' growth rates increase with food nutrient content (Mattson 1980, Sterner and Elser 2002). Ceteris paribus, absolute increases in the biomass of an outbreaking insect, along with the associated nutrient export following emigration, should consequently tend to be higher in nutrient hotspots than over the rest of the landscape.

Conversely, the dispersal process could increase the initial spatial heterogeneity if stable population sink areas exist within the insect range. The nutrient concentration would increase in these high mortality areas, from which relatively few insects would emigrate, and decrease in other source areas of the range (Fig. 2c). Such source–sink population dynamics has been observed for various locust species—including the now-extinct Rocky Mountain locust (*Melanoplus spretus*) that devastated vast agricultural regions in North America up to the late 1800s (Lockwood and DeBrey 1990, Lockwood 2010)—and probably involves spatial variations in moisture regime and vegetation type (Uvarov 1955, White 1976, Veran et al. 2015). The African armyworm (*Spodoptera exempta*) agricultural pest also apparently does not return from the limits of its migratory range (Chapman et al. 2015). In forests of North America, temperature often confines outbreak areas to a portion only of the entire distribution of the tree hosts (Dukes et al. 2009, Bentz et al. 2010); hence, it seems likely that outbreaking insects often disperse into regions of high overwintering mortality at the edge of their range. Finally, the outbreaking insects performing migration circuits that are (approximately) closed (Deveson et al. 2005) can also create spatial heterogeneity in nutrient distribution, as long as the emigrating and immigrating population sizes differ.

Of course, all the previous implications of the process (simple translation, diffusion, or concentration of the nutrient, with the possible influence of stable dominant winds in some cases; Fig. 2d) can co-occur in a given landscape. Since the distribution of different nutrients can show distinct spatial patterns (Li et al. 2013, Liu et al. 2013) and spatial source–sink dynamics can evolve differently across nutrients (Loreau et al. 2013), the same outbreaking insect could, at least temporarily, diffuse one nutrient and concentrate another one concurrently. Moreover, the process is insect-specific because nutrient content can vary by an order of magnitude across insect species (Mattson and Scriber 1987, Sterner and Elser 2002). Note that although ecological stoichiometry has heretofore focused mostly on N, and to a lesser extent on P (Sterner and Elser 2002, Lind and Barbosa 2012), insects appear to be potassium-rich but calcium-poor compared with other potential biological vectors like birds and mammals (Mattson and Scriber 1987).

Inherent scale dependence

A fundamental characteristic of the LTNOI process is its inherent scale dependence, as suggested by our initial quantitative estimates (high-population density vs. total-outbreak area, Table 1). The import or export of nutrients caused by the process over a given area is necessarily the strongest for the spatial extent at which the difference in insect density between immigration and emigration reaches its maximum value. At the other extreme, the import or export of nutrients over the full insect range is necessarily zero, because the process simply transfers nutrients within the range boundaries. The potential strength of the process, therefore, has to decline as the spatial extent considered increases, whereas the 1-D fluxes, while varying spatially over the insect range, are not inherently scale dependent (Fig. 3).

As illustrated in Fig. 3, the import and export curves can have different shapes. The maximum export corresponds to the highest net population growth, over two consecutive generations, of the dispersing life stage of the insect. The main factors influencing this net population growth, for example host quality, may very well vary over relatively short distances. The maximum import, on the other hand, corresponds to very high mortality of the insect into the area where it has dispersed. The factors responsible for such population declines, for example weather-driven overwintering mortality, are likely correlated over longer distances. In such circumstances, the net import-to-export balance of the process could itself be scale dependent. In order to conserve nutrients, however, the integral of this net balance

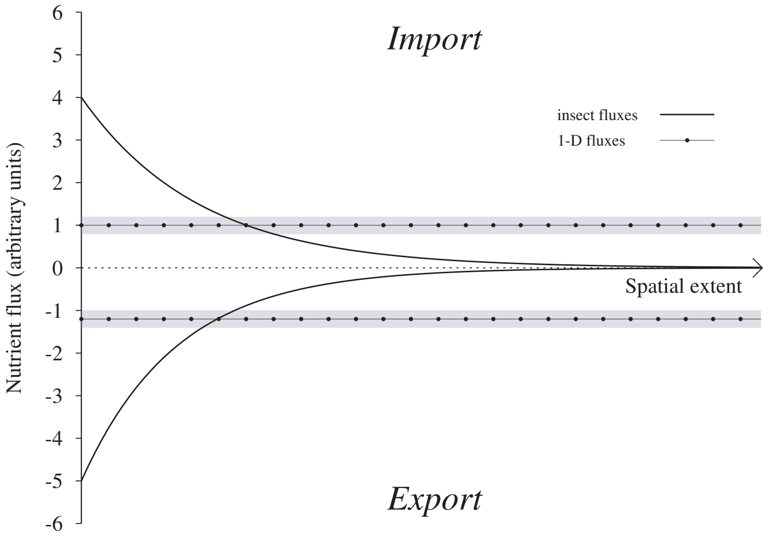

Fig. 3. Potential strength of fluxes over the insect range as a function of the spatial extent considered, for nutrient import and export from insect 2-D fluxes (solid curves) and from 1-D fluxes (lines with circles). As illustrated, the insect import and export curves do not need to be symmetrical, but the total area between each curve and the y-axis (dashed line) must be the same in order to conserve nutrients. The 1-D import and export fluxes do not need to be equal and can vary in space over the insect range, as represented by the gray bands, but do not show an inherent scale dependence. All values are hypothetical.

(or, equivalently, the difference between the "area under the curve" for the import and the export; Fig. 3) over the entire insect range needs to be zero. Note that the exact shape of the import and export curves depends on various factors related to both the insect (e.g., aggregating and dispersal behavior) and the landscape (e.g., presence and clumping of hosts), and almost certainly differs among, for example, locust swarms that can cover hundreds of km^2 (Sanchez-Arroyo 1997, FAO 2009) vs. the much less cohesive emigration flights of the spruce budworm (Greenbank et al. 1980).

Potential for ecological complexity

Spatiotemporal patterns much more complex and sophisticated than the ones illustrated in Fig. 2 occur in various natural systems (Solé and Bascompte 2006). The cause of the traveling waves observed in larch bud moth outbreak dynamics can be assigned to preexisting habitat heterogeneities, for example, quality (Bjørnstad et al. 2002) or connectivity (Johnson et al. 2004). However, complex spatiotemporal patterns can arise spontaneously in an initially homogeneous environment from the simple interaction of diffusion and nonlinear processes (Shinbrot and Muzzio 2001). For herbivores more specifically, complex spatiotemporal patterns can result from the aggregating behavior of insects combined with their response to the changes in plant quality that they induced themselves (Lewis 1994). Selective foraging on deciduous vs. evergreen tree species can also give rise to complex patterns (Pastor et al. 1999). None of these previous studies, however, explicitly considered the possibly multiplying effect from the 2-D nutrient fluxes associated with the herbivores movement. Given the tight nutrient constraints on plant productivity in most natural ecosystems (Cleveland et al. 2013) and the control imposed by appropriate food sources on outbreak dynamics, the LTNOI process might substantially enhance or alter the complex spatiotemporal patterns initiated by insects.

Simply comparing the magnitude of LTNOI with 1-D nutrient fluxes (Table 1) might underrate the process propensity for emergent features with cascading ecological consequences (Parrott and Meyer 2012). For example, an empirical study has shown that the local-scale availability of P can modulate atmospheric P deposition through a positive feedback loop involving vegetation growth (Runyan et al. 2013). Since small-scale lateral nutrient fluxes can lead to ecosystem-level emerging properties even under stable conditions (Gravel et al. 2010*a*), it seems reasonable to suppose that the large fluctuations underlying the LTNOI process could also give rise to cross-scale impacts resulting from emergent vegetation responses and other cascading effects. It is quite conceivable that subsidies from outbreaking insects have ecosystem-scale impacts similar to salmon-derived nutrient subsidies in coastal forests, which have been shown to be a good predictor of total bird density and diversity (Field and Reynolds 2011). Moreover, the sudden import or export of large amounts of nutrient constitutes an example of the "pulsed subsidies" that can, through different responses at the individual, population, and community levels, have ecological legacies that persist much longer than the resource pulse itself (Yang et al. 2008).

Additional considerations

Range shift.—As mentioned previously, outbreaks from the same insect species can recur for centuries, and probably millenniums, over the same range. Yet outbreaking insects can also be forced to shift their range over long periods of time, for example in response to glaciation cycles. The shift can also be relatively rapid, as with the ongoing climate warming that has already led to a poleward movement in many outbreaking forest insects (Klapwijk et al. 2012). The mountain pine beetle in western North America provides a spectacular example of range expansion, with the insect now present, and successfully reproducing on a new host, in a novel environment on the other side of the Canadian Rockies (Cullingham et al. 2011). Habitat destruction can also reduce the distribution of an outbreaking species, even if the borders of its range are not modified (Uvarov 1955).

Regardless of the cause, the possibility (or obligation) of range shift implies that LTNOI can itself be a mobile process within terrestrial ecosystems. The implications presented above remain overall applicable during a range shift, but can give rise to an additional transient spatial dynamics. For example, the concentration of nutrients by outbreaking species at the edge of their range (Fig. 2c) would keep track with the shifting range boundaries, although the strength of the newly created spatial gradients would be much lower if the shift happens quickly. Remnant spatial nutrient gradients left behind by the shifting outbreaking insects would likely decrease progressively due to abiotic and biotic diffusive flows, but might also be maintained through self-organizing processes involving invertebrates and plants (McKey et al. 2010).

Other insects and invertebrates.—Outbreaking insects draw a lot of attention due to their spectacular population dynamics, yet they represent only a small share of all insect species. The "eusocial insects" (mostly ants, termites, wasps, and bees) are actually much more dominant and successful across the world (Wilson 1990), with an estimated biomass of ~400 million tonnes (live weight) for termites only (Sanderson 1996). Ants and termites are already recognized as major biogeochemical actors (Jones 1990, Sagers et al. 2000, Frouz and Jilková 2008). As for noninsect invertebrates like earthworms, millipedes, and mites, their biomass has often been estimated to outweigh by an order of magnitude the biomass of large animals in the same ecosystem (Brockie and Moeed 1986).

Nonoutbreaking invertebrates should thus have the capacity to contribute to lateral transfer of nutrients when they move to new habitats, for example following natural or human disturbances (Eggleton et al. 1996, McCullough et al. 1998). In general, the total variation in population biomass and the dispersal distance are, however, much more limited for nonoutbreaking invertebrates, strongly constraining their role in landscape-level 2-D nutrient transfers. This possibly explains why, albeit substantial at scales smaller than 1 ha, the impacts of ants on landscape biogeochemistry seem to be indirect and rather limited (Cammeraat and Risch 2008). Similarly, the documented major impacts of invasive earthworms on nutrient cycling apparently result from their modification of 1-D fluxes (Watmough and Meadows 2014). Without disregarding the considerable effect that nonoutbreaking invertebrates can have on biogeochemistry, we therefore consider that LTNOI is a qualitatively different process, worthwhile of specific consideration.

Second-order factors.—During an insect outbreak, many individuals are consumed by parasitoids (i.e., parasites that end up killing their host) and predators. Compared with mortality induced by weather, disease, or lack of food, the nutrients embodied in consumed insects return much less directly to plants. Their exact fate within highly interconnected food webs (Williams et al. 2002) can vary considerably, but in the broadest sense, these consumed nutrients will eventually become available to plants unless a sustained increase in the food web total biomass creates an effective sink (Vanni et al. 2013). While acknowledging that consumptive losses can modulate the strength of the LTNOI process, we want to also underline the effectiveness of outbreak dynamics and the associated spatial aggregation in avoiding such losses, at least to predators (Williams and Simon 1995, Sword et al. 2005). The limited evidence available further suggests that forest insect outbreaks seldom result in stable population increases for their consumers (Yang 2012). Consumptive losses should also be minor for locusts, whose outbreak collapse seems to depend on weather (Uvarov 1955, White 1976).

Landscapes are not purely terrestrial, but rather include aquatic components like streams and lakes, and the range of an outbreaking insect can also border large fresh- or salt-water bodies. Despite their apparent capacity to avoid flying over water by detecting polarized light reflections (Shashar et al. 2005), desert locusts sometimes drown in the ocean (Uvarov 1955). Dead bodies of periodical cicadas also make substantial allochthonous subsidies to ponds and streams (Nowlin et al. 2007). Consequently, aquatic ecosystems can constitute sink areas that remove nutrients from the terrestrial component of the landscape. From a purely terrestrial point of view, the LTNOI process can thus lead to a net landscape-scale export, contrary to what we discussed for Fig. 3. Of course, emerging aquatic insects can in turn transfer nutrients back to the terrestrial component of the landscape, though this transfer is generally limited to riparian zones (Baxter et al. 2005, Gratton and Vander Zender 2009).

FURTHER ASSESSING THE LTNOI PROCESS

Better assessing the strength of the LTNOI process will require dedicated studies going beyond the initial quantitative estimates presented earlier (Table 1). More quantitative research should further complement the previous conceptual analyses (Figs. 2 and 3) in order to better explore the possible implications of the process. We present here a few initial suggestions about possible next steps.

Both enriched tracers and variations in the natural abundance of isotopes have been used successfully for different types of biogeochemical studies (Robinson 2001). Nonetheless, tracers appear inappropriate due to the cost and scales (multi-year, landscape-level studies) involved, while changes in the natural abundance of isotopes might not prove sensitive enough. We think that the best strategy consists of quantifying LTNOI through mass–movement studies. Radar has long been used to follow the flight of insects (Chapman et al. 2015), the number of individuals being estimated by radar also (Greenbank et al. 1980), from ground measurements (Deveson et al. 2005), or from aerial capture (Jackson et al. 2008). For large insects, radiotelemetry can serve to track individuals (Sword et al. 2005). Due to the high variability of biomass (McGhehey 1971, Lorimer 1979) and nutrient content (Sterner and Elser 2002) even among individuals of the same species, dispersing insects should be sampled and analyzed in the laboratory in order to get more precise numbers.

Theoretical approaches could also provide fruitful insights into the consequences from the LTNOI process, including its potential for cross-scale and cascading impacts. Building upon the many previous 2-D spatially explicit studies of outbreaking insects or other animals (Pastor et al. 1999, Bjørnstad et al. 2002, Johnson et al. 2004, Solé and Bascompte 2006) by including patch-level nutrient dynamics with inter-patch fluxes (Gravel et al. 2010*a*) would likely prove a straightforward and efficient strategy. Another avenue would consist of using process-based terrestrial ecosystem models that already represent the suite of interactions between plants and their abiotic environment, and modify them to include the LTNOI process. For example, dynamic global vegetation models, which simulate the competition among different vegetation types and compute the exchanges of carbon, water, and energy between the land surface and lower atmosphere, increasingly account for the biogeochemistry of N and P (Levis 2010). Representing LTNOI within such models would allow to test for possible consequences of the process on a wide array of ecological, biogeochemical, and climatic phenomena.

For both empirical and model-based studies, we suggest focusing on regions where the process is likely to have a stronger relative impact. As a first criterion, the atmospheric deposition of nutrients (Dentener et al. 2006, Mahowald et al. 2008) should be low or at least comparable to the 1-D losses. As a second criterion, the region should witness a small landscape-scale diffusion of nutrients by mammalian herbivores (Wolf et al. 2013). For practical reasons, we finally suggest to consider regions that are readily accessible, and where outbreaks are relatively easy to forecast or identify. Based on the previous set of criteria, we tentatively put forward two possible test cases: (1) the Australian plague locust (*Chortoicetes terminifera*) in eastern Australia and (2) the forest tent caterpillar in the central-western Canadian boreal forest. The desert locust across Africa and the Middle East also shows a very strong potential for LTNOI-related studies (i.e., vegetation-limited areas receiving low atmospheric N deposition, with huge swarms tracked by the FAO "Locust Watch" early warning system; FAO 2009), but also faces noticeable challenges (i.e., unpredictable outbreaks occurring within a large region that is not easily accessible everywhere).

Conclusions

Due to the high concentration of nutrients in insect bodies, the recurring changes in absolute population biomass, and the dispersal of individuals over long distances, we suggest that the lateral transfer of the nutrients embodied in outbreaking insects (LTNOI) has the potential to be a consequential landscape-level ecological process. Initial quantitative estimates comparing LTNOI to 1-D atmospheric deposition (Table 1) and to other animal-mediated 2-D nutrient fluxes (Table 2) brought support to this hypothesis. These estimates also highlighted the variation of LTNOI according to the insect species and location considered and suggested that overall, LTNOI seems currently more significant for P than for N (Table 1). Given the large changes in atmospheric N deposition since preindustrial times (Galloway et al. 2004), LTNOI almost certainly had a stronger relative impact on N in the past than it has today.

The LTNOI process comprises several features that have been recognized as necessary steps toward a more complete and sophisticated understanding of ecosystem processes at various scales, including spatially-explicit nutrient budgets and more specific knowledge of the organisms responsible for 2-D nutrient fluxes (Gravel et al. 2010*a*), the integration of energy, material, and organism fluxes over large spatial scales (Loreau et al. 2013), "fully animated" biogeochemical cycles recognizing the possible multiplier effects from animals (Schmitz et al. 2014), and complete population trajectories of migrating insects (Chapman et al. 2015). We further showed that the LTNOI process can both increase and decrease preexisting spatial gradients in the distribution of nutrients (Fig. 2), shows an inherent scale dependence that is absent from 1-D nutrient fluxes (Fig. 3), and may lead to complex spatiotemporal patterns, bottom-up cross-scale feedbacks, and ecological legacies.

Dedicated research is required to better appreciate the LTNOI process and assess its possible implications. There is no doubt that outbreaking insects carry embodied nutrients over landscapes, but the actual strength of the process, as well as the scales over which it plays an important role, remain to be determined. We suggest that the real question consists of identifying the circumstances under which the process actually matters. At one extreme, the landscape-scale effects of LTNOI are possibly negligible for outbreaks of the barely mobile gypsy moth (*Lymantria dispar*) in northeastern United States (Liebhold et al. 2012), where pollution has greatly increased the atmospheric deposition of nutrients (Galloway et al. 2004, Mahowald et al. 2008). At the other extreme, the nutrients moved by swarms of billions of locusts that quickly wax and wane in vegetation-poor areas (Uvarov 1955, White 1976, FAO 2009) less affected by anthropogenic nutrient inputs (Galloway et al. 2004, Mahowald et al. 2008) can hardly be trivial for these ecosystems (Fig. 1). Adding 2-D fluxes to the already recognized role of outbreaking insects in 1-D nutrient cycling may end up providing us with a more complete view of ecology and terrestrial biogeochemistry.

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