Title

Vectors with autonomy: what distinguishes animal-mediated nutrient transport from abiotic vectors?

Permalink

https://escholarship.org/uc/item/3x63w60w

Journal

Biological Reviews, 94(5)

ISSN

1464-7931

Authors

McInturf, Alexandra G
Pollack, Lea
Yang, Louie H
et al.

Publication Date

2019-10-01

DOI

10.1111/brv.12525

Vectors with autonomy: what distinguishes animal-mediated nutrient transport from abiotic vectors?

Alexandra G. McInturf[1,*,†], Lea Pollack[2,†], Louie H. Yang[3] and Orr Spiegel[4]

[1]*Department of Wildlife, Fish, and Conservation Biology, University of California, One Shields Avenue, Davis, CA, 95616, USA*

[2] *Department of Environmental Science and Policy, University of California, One Shields Avenue, Davis, CA, 95616, USA*

[3]*Department of Entomology and Nematology, University of California, Davis, One Shields Avenue, Davis, CA, 95616, USA*

[4]*Sherman Building, School of Zoology, Faculty of Life Sciences, Tel Aviv University, Tel Aviv, 69978, Israel*

[*]Author for correspondence (E-mail: amcinturf@ucdavis.edu; Tel.: 513-504-8939).

[†]Equal first authors.

ABSTRACT

Animal movements are important drivers of nutrient redistribution that can affect primary productivity and biodiversity across various spatial scales.

Recent work indicates that incorporating these movements into ecosystem models can enhance our ability to predict the spatio-temporal distribution of nutrients. However, the role of animal behaviour in animal-mediated nutrient transport (i.e. active subsidies) remains under-explored. Here we review the current literature on active subsidies to show how the behaviour of active subsidy agents makes them both ecologically important and qualitatively distinct from abiotic processes (i.e. passive subsidies). We first propose that animal movement patterns can create similar ecological effects (i.e. press and pulse disturbances) in recipient ecosystems, which can be equal in magnitude to or greater than those of passive subsidies. We then highlight three key behavioural features distinguishing active subsidies. First, organisms can transport nutrients counter-directionally to abiotic forces and potential energy gradients (e.g. upstream). Second, unlike passive subsidies, organisms respond to the patterns of nutrients that they generate. Third, animal agents interact with each other. The latter two features can form positive- or negative-feedback loops, creating patterns in space or time that can reinforce nutrient hotspots in places of mass aggregations and/or create lasting impacts within ecosystems. Because human-driven changes can affect both the space-use of active subsidy species and their composition at both population (i.e. individual variation) and community levels (i.e. species interactions), predicting patterns in nutrient flows under future modified environmental conditions depends on understanding the behavioural mechanisms that underlie active subsidies and variation among agents' contributions. We conclude by advocating for the integration of animal behaviour, animal movement data, and individual variation into future conservation efforts in order to provide more accurate and realistic assessments of changing ecosystem function.

Key words: animal behaviour, behavioural ecology, energy flow, mobile links, movement ecology, nutrient cycling, spatial subsidies.

CONTENTS

I. INTRODUCTION: ANIMALS AS IMPORTANT VECTORS OF NUTRIENT TRANSPORT

The concentration of nutrients across multiple spatio-temporal scales establishes the foundation of ecosystem productivity and subsequent diversity within and across habitats. Geological processes such as tectonic movement and sedimentation determine the underlying distribution of essential resources (e.g. nitrogen, phosphorous, and carbon) that influence primary productivity and biomass (Cook & McElhinny, 1979; Vitousek, 2004; Elser *et al*., 2007; LeBauer & Treseder, 2008; Vitousek *et al*., 2013). This initial distribution is modified by environmental and physical factors ('passive subsidies'; Earl & Zollner, 2014), including wind, current, gravity and erosion (Zhao & Running, 2010; Cleveland *et al.*, 2013; Houlton & Morford, 2015; Morford, Houlten & Dahlgren, 2016). In addition to these abiotic processes, biotic vectors further redistribute nutrients through various mechanisms, mostly *via* animal movement (Fig. 1). Specifically, animals can displace resources, or serve as 'mobile links' (Jeltsch *et al*., 2013), within and among ecosystems, generating nutrient inputs that are referred to as 'active subsidies' (Earl & Zollner, 2014). Active subsidies often differ in their physical form (nutrient composition, lability, etc.), which can influence the pathways by which these nutrient influxes enter ecosystems (Marcarelli *et al*., 2011). Furthermore, animal vectors exhibit diverse behaviours that influence movement patterns and how nutrients are distributed. Ultimately, these behaviours allow active subsidies to be quantitatively important in ecosystem dynamics, but qualitatively different from passive subsidies in their nutrient deposition patterns.

There is an extensive body of research demonstrating that animals across taxa transport nutrients within and among ecosystems (e.g. Polis, Anderson & Holt, 1997; Helfield & Naiman, 2001; Bauer & Hoye, 2014; Adame *et al*., 2015). This literature shows that animals can redistribute large masses of nutrients in the environment by (1) consuming and transporting biomass (e.g. the deposition of waste products by migrating grazers such as wildebeest (*Connochaetes taurinus*; Holdo *et al*., 2007) and (2) serving as the supply of biomass themselves (e.g. *via* predator consumption or decomposition of wildebeest carcasses; Subalusky *et al*., 2017). Yet, while the impact of active subsidies in nutrient transportation has been convincingly demonstrated in many studies, empirical work has historically focused on the patterns of nutrient accumulation created by organism movement, neglecting the processes by which animal vectors (directly or indirectly) shape the ecosystem.

To address this limitation, recent work has explored how animal movement decisions influence the distribution of resources in space and time (e.g. Bauer & Hoye, 2014; Earl & Zollner, 2017). This requires consideration of the factors that drive an organism’s behaviour, such as characteristics of the external environment (e.g. initial nutrient distribution or presence of other agents). A recent framework argues that exogenous (external) factors such as mortality and competition risk, thermal conservation, and prey activity affect an animal’s behaviour at multiple hierarchical levels, from instantaneous decision-making to annual activity patterns such as migration (McCann, Zollner & Gilbert, 2017). Collectively, such factors interact with other drivers and constraints (such as the organism’s internal state, cognitive navigational capacity, and biomechanical motion capacity) to shape each movement path (Nathan *et al*., 2008). For instance, wildebeest respond to external factors such as drying vegetation through mass migration, and their collective movement ultimately results in a relatively large nutrient influx into local river systems (Subalusky *et al*., 2017). Predictions regarding future influx into rivers depend on the size of the expected wildebeest population, the future environmental conditions affecting their migration, and their consequent movement decisions. Thus, a more mechanistic understanding of active subsidy transport is critical for projecting alterations in nutrient patterns on the landscape, especially in light of ongoing environmental change, which can alter community composition (Barnosky *et al*., 2012; Dirzo *et al*., 2014), reduce population sizes (Both *et al*., 2006; Worm *et al*., 2006) and affect the movements of various species (Tucker *et al*., 2018). Consequently, an increasing body of literature now advocates modelling methods that consider animal movement when predicting the ecological impact of active subsidies (e.g. individual-based models, state-space models, hidden Markov models) (Earl & Zollner, 2017; Subalusky & Post, 2018).

Here, we review the quantitative importance of active subsidies and their ability to generate substantial ecological effects (i.e. press and pulse disturbances). We then offer a complementary behavioural perspective that identifies three fundamental features that separate active subsidies from passive subsidies. (1) First, active subsidies can move counter-directionally to environmental gradients, transporting nutrients in directions that oppose major abiotic forces like gravity, prominent wind flows, and prevailing currents (e.g. salmon swimming upstream). (2) Second, active subsidy agents can respond to the patterns of nutrients in their environment, creating positive or negative feedbacks with the distribution of abiotic resources. (3) Third, active subsidy agents respond to the presence and behaviour of other organisms, creating positive or negative feedbacks with aspects of the biotic environment, including other active subsidy agents. Finally, we call attention to an area for future study by discussing the potential impact of individual behavioural variation on active subsidy distribution. With the support of several examples from the existing literature that highlight these concepts, we conclude that understanding the behavioural context of animal movement is essential for predicting and conserving resource patterns formed by active subsidies in rapidly changing environments.

II. THE QUANTITATIVE IMPORTANCE OF ACTIVE SUBSIDIES

Recent work argues that the nutrient contributions from active subsidies can be of similar magnitude to those of passive subsidies, and are essential for many ecological systems (Earl & Zollner, 2017; Subalusky & Post, 2018). Even small organisms can show behaviours (e.g. emergence along the aquatic–terrestrial interface) that result in nutrient movements that are substantially greater than those generated by abiotic forces (Yang & Gratton, 2014). Similar evidence has been found in other systems with varying vector species (see Fig. 2). These impacts are highly dependent on the spatial and temporal scales of the subsidy's movement behaviour and its interaction with prevailing passive nutrient-movement processes. For example, populations of flying insects selectively follow prevailing winds, effectively redistributing large amounts of biomass on a regional scale in combination with abiotic processes (Hu *et al*., 2017).

In addition to sheer magnitude, active subsidy inputs can act like critical press or pulse perturbations within an ecosystem (defined below), depending largely on the temporal heterogeneity of animal movements (Bender, Case & Gilpin, 1984; Bauer & Hoye, 2014; Allgeier, Burkepile & Layman, 2017). Press disturbances are created by continuous movements that lead to a sustained nutrient influx; these can occur when active subsidy nutrient transport is relatively consistent in time, driven by repeated patterns of activity (Wagner, Jones & Gordon, 2004; Fagan, Lutscher & Schneider, 2007) (Fig. 3A). For example, Brazilian cave-dwelling bats (*Hipposideros* and *Eonycteris* spp.) sustain entire cave ecosystems through their nightly roosting behaviour, since their guano provides nutrients to an otherwise energy-poor system (Ferreira & Martins, 1999; Poulson & Lavoie, 2000; Fenolio *et al*., 2006; Bird *et al*., 2007; Kunz *et al*., 2011). Parallel examples also exist in marine environments (Williams *et al*., 2018). By contrast, pulse perturbations can occur when a less-common behaviour results in the instantaneous alteration of active subsidy behaviour or population density, and thus creates a flux of nutrients of large magnitude and short duration (Fig. 3B, C). For example, the mass migration of anadromous fishes can generate profound ecosystem impacts as they move nutrients from the marine environment to aquatic and terrestrial systems (Helfield & Naiman, 2001; Gende *et al*., 2002; Varpe, Fiksen & Slotte, 2005; Childress & McIntyre, 2015). Similar effects can result from the population dynamics and movements of many other animals, including insects (Yang, 2004; Yang & Gratton, 2014; Hu *et al*., 2017) and mammals (Roman & McCarthy, 2010; Subalusky *et al*., 2017). Depending on their frequency, pulses can be cyclic (within a regular interval) or irregular. Although the former is likely more predictable from the perspective of a consumer, irregular pulses (such as locust outbreaks) can produce greater shifts from baseline nutrient levels than mere seasonal changes (Fig. 3C). Thus, although it can be easy to ignore nutrient fluxes driven by animal behaviour as inconsistent or inconsequential when modelling community-level dynamics, it is important to note that presses and pulses generated by active subsidy input can be equally, if not more, instrumental to ecological processes as those of passive subsidies.

III. FEATURES THAT DISTINGUISH ACTIVE FROM PASSIVE SUBSIDIES

(1) Counter-gradient and cross-habitat transport

Passive subsidies (e.g. erosion, water flow) often follow a gradient of potential energy, such as downstream water flow. While there are exceptional examples where passively transported nutrients move against a gradient of potential energy (e.g. wildfire, volcanic eruptions and upwelling), these are generally localized events. Organisms, on the other hand, can widely and selectively redistribute resources by moving them in directions and/or to distances unachievable by most passive agents (‘counter-gradient transport’; Table 1). For instance, animals frequently exhibit behaviours (e.g. foraging, migration, refuging, nesting, breeding) that drive them to move against the topographic slope of mountains and hills. Notably, multiple behaviours can simultaneously shape animal movements and are rarely mutually exclusive; for instance, foraging and mating often both drive migration patterns. In a classic example, spawning salmon (*Oncorhynchus* spp.) annually swim hundreds of kilometers upstream from the ocean, leading to doubling or tripling of the amount of nitrogen and phosphorous in certain spawning habitats (Helfield & Naiman, 2001; Holtgrieve & Schindler, 2011; Deacy *et al*., 2016). Although juveniles eventually migrate (disperse) back to the ocean, an estimated 85% of marine-derived nutrients from carcasses or eggs remain in the food web upstream, supporting both aquatic and terrestrial food webs (Moore & Schindler, 2004). Similarly, insects that exhibit hill-topping behaviour (i.e. aggregating on hills or cliffs to mate; Capinera & Skevington, 2008) could also serve as a subsidy to the regions in which they gather, although this potential nutrient influx has yet to be explicitly quantified.

Counter-gradient movement by animal vectors likely occurs in systems where food resources and critical habitat (e.g. for breeding or nesting) are separated by an energy gradient (e.g. uphill) or ecosystem boundary. A prominent example is the vertical movement of deep-diving whales (e.g. *Physeter macrocephalus* and *Balaenoptera physalus*) throughout the water column as they feed in deep ocean layers and then rise to the surface to breathe (known as the ‘whale pump’; Fig. 4; Roman & McCarthy, 2010). In doing so, they move counter-directionally to the downward flux of key nutrients from the surface through the gravitational pull on aggregates and faeces (Roman & McCarthy, 2010). Through this process, cetaceans may transport up to 2.3×10^4 metric tons of nitrogen to the surface per year in areas such as the Gulf of Maine – more than all coastal point sources in that region (Roman & McCarthy, 2010). This movement may be particularly important in the open ocean because biological production here depends largely on nutrient dynamics within the photic zone (Longhurst & Harrison, 1989). Nutrients from whale waste (i.e. nitrogen) are utilized in this area for growth and photosynthesis by phytoplankton, which are then consumed by zooplankton and fish to fuel the biological pump. Without animal movement, these limiting nutrients would be entirely dependent on seasonal upwelling, which is restricted in time and space. Thus, the counter-directional redistribution of nutrients as a result of whale feeding behaviour during migration serves to expand the otherwise seasonal nutrient influx temporally and the locations covered by passive subsidies spatially.

Counter-gradient movement of nutrients by active subsidy agents has important implications for ecosystem function over time. This is particularly true when organisms traverse ecosystem boundaries in ways that passive subsidies cannot, enhancing connectivity among systems. For instance, birds can serve as an important conduit of carbon across the marine–terrestrial ecosystem boundary (Anderson & Polis, 1999; Adame *et al*., 2015; McFadden, Kauffman & Bhomia, 2016; Otero *et al*., 2018). Classic examples are avian species that forage at sea and nest on islands relatively uninhabited by other organisms (Anderson & Polis, 1999). Unlike the passive exchange by ocean waves of nutrients between marine and terrestrial ecosystems at the island boundary, seabirds consistently forage beyond this boundary, moving ocean nutrients further onto land. On nutrient-limited islands (e.g. desert or mangrove; Fig. 5), this supply of guano to terrestrial plants can also significantly change the nutrient cycles within an island by relieving nutrient limitation (Adame *et al*., 2015), and the increase in soil nitrogen and phosphorous concentrations has been shown to enhance plant growth and primary productivity (Anderson & Polis, 1999). On desert islands in particular, the effect of seabird roosting behaviour can lead to a 3- to 24-fold increase in populations of detritivores, herbivores, and predators, driving productivity and ecosystem-wide dynamics (Anderson & Polis, 1999). In these cases, daily foraging movements create an essential press-like disturbance for these ecosystems.

Furthermore, when animal vectors move along specific paths, they have the potential to transport nutrients more rapidly and over larger spatial scales than passive vectors. For example, the migration of sea turtles between foraging (i.e. marine habitat) and nesting grounds (i.e. coastal habitat) represents the long-distance movement of nutrients derived from the feeding grounds to selected coastal ecosystems (Bouchard & Bjørndal, 2000), creating a nutrient hotspot *via* both egg content and hatchlings (Bouchard & Bjørndal, 2000). Some species of migrating turtles can transport nutrients over significantly greater distances, at a higher consistency, and over a much shorter time scale than any form of passive subsidy transport (e.g. currents). For example, leatherback turtles (*Dermochelys coriacea*) that feed on jellyfish in the Arctic Circle annually return thousands of kilometers to tropical beaches to nest (Bjørndal, 1997). This nutrient movement supports food webs in the recipient ecosystems, including detrital consumers as well as larger terrestrial predators such as ants, crabs, foxes, and raccoons (Fowler, 1979; Stancyk, 1995). Notably, the spatial distribution of this influx depends on nest-site-selection behaviour. For example, loggerhead turtles (*Caretta caretta*) nest further from dunes than other species, and thus the nutrients they transport may contribute less to dune vegetation than to other components of the ecosystem (Witherington, 1986; Bouchard & Bjørndal, 2000). Such targeted transport emphasizes the unique role of behaviour (in this case, habitat selection) in ecosystem subsidies (Subalusky & Post, 2018). Seasonal migrations, like those performed by sea turtles, can create pulsed or cyclic perturbations of nutrient availability within a habitat. Consequently, such counter-gradient movements have the potential to generate important ecosystem impacts that reflect those of passive subsidies (i.e. can be consistent or cyclical in nature), but differ in terms of their pathway.

(2) Agents respond to the nutrient distribution patterns that they generate

Animal-mediated transport can also be reactive, driven by an organism’s behavioural response to its physical environment (e.g. environmental structure, climate, existing resource distribution). Specifically, resource distribution both influences and is influenced by organism movement, and this can lead to positive- or negative-feedback loops in nutrient accumulation (Earl & Zollner, 2017; Subalusky & Post, 2018). This feature of active subsidies is likely most prominent when nutrient influxes affect the resources that agents directly use. Specifically, if a nutrient influx by an animal vector directly affects its own food source (e.g. for a herbivore) or habitat structure (e.g. for a tree-nesting species), this may generate a stronger feedback loop compared to situations in which habitat selection is not heavily influenced by nutrient input. However, the direction of the feedback loop (positive or negative) and magnitude of the subsidy input depend on the strength of drivers that influence the behaviour of the active subsidy (see Table 1 for examples).

Positive-feedback loops are generated when organisms aggregate in an area of high resource availability and continue to contribute to its productivity through fertilization. One of the best-studied outcomes of this feature is the formation of resource hotspots, in which organisms preferentially revisit areas where they have already deposited nutrients (reviewed in Earl & Zollner, 2017). In these cases, the active subsidy agents can create and/or respond to an influx of resources. This process has been observed when seabird preference for nesting on certain islands has resulted in significantly elevated levels of plant-available nitrogen surrounding areas of concentrated guano deposits (McCauley *et al*., 2012; Adame *et al*., 2015; Graham *et al*., 2018). On nutrient-depleted mangrove islands, for example, seabirds improve the quality of their own habitat through the net influx of nutrient enrichment, rendering the islands more attractive to roosting seabirds and continuing to support – or even increasing suitability for – populations of these active subsidy agents (Adame *et al*., 2015; Fig. 5). Feedback loops like this increase primary productivity and strengthen autotroph communities (e.g. plants), which not only attracts agent conspecifics, but also heterospecifics. For example, in the African savannah–

woodland system, the grassy remnants of former livestock corrals (once fertilized by livestock dung) often form high-resource glade regions, which in turn attract ungulate grazers (Augustine, 2003; Muchiru, Western & Reid, 2008). As they forage within this habitat, ungulates fertilize the area with dung and urine, helping to maintain the productivity of the glade and attract other species to the area even long after the initial active subsidy agents have dispersed (Augustine, 2003; Muchiru *et al.*, 2008). These include superb starlings (*Lamprotornis superbus*), which nest on acacia trees around the outskirts of glades, taking advantage of the predictable insect abundance found within glades to provision hatchlings, and thus emphasizing how active subsidy movement influences both conspecific and heterospecific habitat use (Rubenstein, 2007, 2016).

Conversely, negative-feedback loops occur when organisms actively avoid certain locations and consequently limit nutrient influx from potential active subsidies. Most simply, this can occur due to resource depletion, such as when organisms spread nutrients from hotspots across a broader area and consequently avoid the initial hotspot locations once the nutrients have been depleted. On a small spatial scale, this takes place when frugivores disperse seeds from a tree (a local hotspot), reducing the hotspot and contributing to a more uniform distribution of resources as seeds from the fruit are spread from their source (Côrtes & Uriarte, 2013). Negative-feedback loops may also be more complex, driven by biotic interactions as well as behavioural responses to the environment across wider scales. For example, on tropical islets in the Central Pacific, invasive coconut trees (*Cocos nucifera*) tend to grow where they benefit from bird-transported nutrients (Young *et al*., 2010). However, seabirds (e.g. *Sula* spp.) prefer to roost in native trees (*Pisonia grandis* and *Tournefortia argentea*) over these invasive plants (Young *et al*., 2010). Thus, bird behavioural responses to coconut trees (i.e. repulsion) reduce the initial hotspot by reducing marine-derived subsidies in these locations and triggering nutrient-depletion patterns within the communities on these islands (Young *et al*., 2010). Negative-feedback loops can also form in existing hotspots when these areas become saturated with nutrients to the point of toxicity (‘subsidy overload’; Dutton *et al*., 2018), as in the case of eutrophication. For example, excessive amounts of nutrient deposition on seabird islands can lead to changes in species composition by killing certain plant species (Hogg & Morton, 1983; Ellis, Fariña & Witman, 2006). In general, since predicting when and how a feedback loop will form depends heavily on the system, considering the net impact of behavioural responses to existing nutrient distribution will require empirical work that is tailored to specific systems.

(3) Interactions among agents affect deposition patterns

Animal movement is not only affected by abiotic factors, like the physical environment or existing resource distribution, but also by the distribution and movement of other agents (i.e. direct interactions between organisms). These may be conspecific or heterospecific, representing competitors, mates, pathogens, prey or predators. Variation in behaviours as a result of other agents, like social attraction or anti-predator responses, thus affects the movement patterns and ecological implications of active subsidies. Furthermore, perturbations of the community composition (e.g. through the introduction of an invasive species or local extinctions) can also affect movement and the derived nutrient deposition patterns, again highlighting how predictions from phenomenological models alone may become inaccurate under changing environmental conditions.

Perhaps best studied is how predators influence subsidies through their effect on prey population size and behaviour (Schmitz, Hawlena & Trussell, 2010; Strickland *et al*., 2013). Most obviously, predation can directly affect nutrient deposition within an ecosystem *via* consumptive effects. For example, subsidies from wolf-killed carcasses in Yellowstone National Park have been shown to create temporary hotspots by attracting scavenging species such as ravens (*Corvus corax*), bald eagles (*Haliaeetus leucocephalus*), and smaller carnivores (Ripple *et al*., 2011). But independently of consumptive effects, the ‘landscape of fear’ generated by predator presence also shapes prey habitat preference, food choice, space use and distribution (Laundré, Hernández & Ripple, 2010, Schmitz *et al*., 2010). In turn, evasive behavioural responses to predator activity can affect the distribution of nutrients across a landscape. For instance, after the eradication of Yellowstone wolves (*Canis lupus*) in the early 20th century, relatively uninhibited populations of ungulates nearly doubled the rate of net nitrogen availability among grasslands through waste products (Frank, 2008). Several years following the reintroduction of grey wolves to the park, there was a notable decrease in net nitrogen availability in these grasslands. This change was likely driven by a shift in ungulate habitat-use patterns, rather than direct removal of these grazers by the reintroduced wolves (Frank, 2008). Thus, in situations where heterospecific interactions play a major role in agent movement, identifying the response (e.g. limited movement or altered patch use) will be critical for predicting how nutrient deposition will change in both space and time.

In addition to trophic-level interactions, conspecific interactions can aid in the formation of nutrient hotspots, particularly for species that utilize social information to make decisions about movement within and among habitats (i.e. ‘ecology of information’; Clobert *et al*., 2009; Schmidt, Dall & Van Gils, 2010). Specifically, social information generates correlations in behaviour and space use of multiple individuals (Gil *et al*., 2018), thus affecting both the nature and magnitude of active subsidy nutrient distribution across a landscape. For instance, breeding-site selection by many social agents is often based on conspecifics, such as when the presence of nesting marine birds provides cues about local breeding conditions (‘information barrier hypothesis’; Forbes & Kaiser, 1994; Schmidt *et al*., 2010), deterring individuals from dispersal to a new habitat. In this case, we would hypothesize that the subsequent social aggregation likely drives hotspot formation *via* the accumulation of nutrients in these areas

(Fig. 1). Central-place foraging behaviour by highly social animals can similarly cause the formation of nutrient hotspots *via* aggregation, especially if these central places remain stable over long periods (Clay *et al*., 2013). For example, colonial canopy ants (*Azteca trigona*) that continually return to a collective home base following foraging bouts can alter nutrient composition of the leaf litter below their nests *via* a steady stream of nutrient-rich excreta falling on the forest floor (Clay *et al*., 2013). In these cases, understanding how large, dense and spatially stable conspecific aggregations form is key for predicting the effect of social behaviour on nutrient influxes. Whether aggregating behaviour occurs on a daily (e.g. foraging or anti-predator response) or seasonal (e.g. breeding) basis would then determine the corresponding ecosystem effect (press or pulse), depending on whether the subsidy influx from this movement is consistent or cyclical.

IV. INDIVIDUAL DIFFERENCES AS A SOURCE OF VARIATION

Although almost entirely overlooked by the ecological subsidy literature, individual variation of within-population space use likely plays a role in generating nutrient-deposition patterns. This variation can arise from a combination of external and internal factors (Nathan *et al*., 2008). First, individuals might move differently simply because they occupy different habitats with differences in structure and composition. For example, individuals in resource-scarce areas might be forced to move more in search of these resources, resulting in longer transportation distances. Second, differences in movement patterns can arise from variation in individual life stage, sex, and morphology (Fraser *et al*., 2001). For instance, winged-morph insects readily disperse across distances and barriers that de-winged morphs are physically unable to overcome (Roff, 1986). Furthermore, such intraspecific differences can occur at multiple scales, reflecting variation among populations (e.g. along a latitudinal gradient), or differences within a population. Lastly, a growing body of literature is also linking differential space-use patterns with variation in life-history traits or behavioural strategies (Réale *et al*., 2010; Sih *et al*., 2012). Personality traits (defined as within-individual consistency in behavioural responses across time or contexts) may interact with environmental heterogeneity, resulting in personality-dependent dispersal and space use that can affect various ecological processes at the population and community levels (Cote *et al.* 2010*a*; Spiegel *et al*., 2017; Villegas-Ríos *et al*., 2017).

Evidence of consistent (phenotype-related) intra-population differences in dispersal distance, home-range size, habitat selection and other space-use axes is becoming more common in a wide range of taxa (Duckworth & Badyaev, 2007; Cote *et al*., 2010*b*; Harrison *et al*., 2014; Spiegel *et al*., 2015*b*; Patrick, Pinaud & Weimerskirch, 2017). Understanding these aspects of behavioural phenotype can provide greater insight into an organism’s role in nutrient distribution, as they can potentially affect the distance, rate, and amount of nutrients transported. For example, individual wandering albatross (*Diomedea exulans*) vary in the ratio of their exploration–

exploitation foraging behaviour (Patrick *et al*., 2017). Thus, different individuals likely move nutrients between patches at different rates. In this case, one might expect exploiters (i.e. those that spend more time in restricted-area search) to contribute more to local transport and hotspot formation than explorers (i.e. those that spend more time in long-distance travel), while the latter could contribute more to long-range transport and ecosystem connectivity. Similarly, individual brown bears (*Ursus arctos*) vary in the time spent foraging at salmon (*Oncorhynchus* spp.) spawning sites (Deacy *et al*., 2016). As previously mentioned, salmon are an important source of nutrients in upstream spawning habitats, and their consumers serve as the final link in transporting salmon-derived nutrients from marine and aquatic ecosystems to the terrestrial environment. Variation in salmon consumption by brown bears, as well as in post-consumption space use among individual bears (Leclerc *et al*., 2016; Hertel *et al*., 2019), would thus influence the extent to which cross-boundary active subsidy transport occurs.

Furthermore, variation in space use can lead to spatial structuring of phenotypes within a population (e.g. Duckworth & Badyaev, 2007; Cote *et al*., 2010*a*; Spiegel *et al*., 2017), which could then affect the spatial structuring of nutrient inputs. Examples of such spatial structuring are exemplified by non-native introductions, where individuals found on the invasion front have both morphological and behavioural differences compared to individuals in established areas (e.g. Gruber *et al.* 2017). In these cases, larger and bolder individuals commonly found at the dispersal front would be expected to deposit greater amounts of subsidies at further distances. Scenarios like this suggest that incorporating intraspecific differences in space use can help provide a better understanding of how the same population of animal vectors may simultaneously generate differing patterns of nutrient deposition within and among habitats.

V. CONSERVATION IMPLICATIONS

There is increasing recognition that the materials exchanged *via* animal vector links should be incorporated into management decisions to maintain resilience and ensure future ecosystem function (Lundberg & Moberg, 2003). Previous work has highlighted some of the major implications of removing active subsidy agents in altered ecosystems (Subalusky & Post, 2018). Among these, human-induced rapid environmental change (HIREC; Sih, Ferrari & Harris, 2011) can cause population reductions or even local extinctions, resulting in fewer active subsidy agents (Barnosky *et al*., 2011; Dirzo *et al*., 2014; Earl & Zollner, 2017; Subalusky & Post, 2018). For example, the movement of nutrients from sea to land *via* seabirds and anadromous fish has been reduced by 96% due to the loss of these species (Doughty *et al*., 2016). The reduction of animal vector populations and subsequent active subsidy influxes also has a variety of indirect ecological effects. For instance, moth migration altered by changes in large-scale weather patterns affects the movement of Brazilian free-tailed bats

(*Tadarida brasiliensis*), since these bats rely heavily on this seasonal resource to gain fat for their own autumn migrations (Krauel *et al*., 2018).

Although the number of applied models incorporating organism movement is increasing (Holyoak *et al*., 2008; Grüss *et al*., 2011), understanding how behavioural responses change in altered environments can lend greater predictive power to changes in active subsidy nutrient distribution than considering movement patterns alone (Fraser *et al*., 2018). For example, HIREC could reduce the extent of active subsidy agent movement by increasing fragmentation (i.e. creating physical barriers to movement) or by generating a plastic change in behavioural response (e.g. alterations in habitat use or home-range size). In addition, because many large species tend to travel further, they may exhibit higher sensitivity in behavioural responses to anthropogenic change, altering their movement more significantly and thus inhibiting their ability to act as active subsidies (Tucker *et al*., 2018). Moreover, HIREC can affect the phenotypic composition within populations, through selection of certain life-history traits, behavioural types or morphologies (e.g. Cooke *et al*., 2007; Biro & Post, 2008; Parsons, Morrison & Slater, 2010). For example, human harvesting selects against phenotypes with large size, fast growth rates, and high activity and boldness (Biro & Post, 2008; Huntingford, Mesquita & Kadri, 2013). At both local and broader scales, removal of more mobile phenotypes within certain species would limit nutrient distribution by active subsidy agents. Conversely, for recently introduced species, selection may favour bolder individuals that might achieve greater dispersal distances (e.g. Duckworth & Badyaev, 2007) and therefore transport nutrients further into novel environments. A third scenario is also possible, by which more behaviourally plastic species or individuals are best able to adapt to HIREC by calibrating their behaviour to the current circumstances (e.g. Crowley *et al*., 2019). For example, recent modelling of Burmese python (*Python molurus bivittatus)* behaviour suggests that species able to exhibit adaptively flexible dispersal behaviour are most successful in population expansion (Mutascio *et al.,* 2017).

In general, one critical step for managers and policy-makers will be to recognize the limitations of spatially restricted forms of management to enact more proactive conservation measures for mobile animal vectors. For such animals in the pelagic environment, including sharks and whales, alternative options could include dynamic (i.e. mobile) or seasonal marine protected areas to cover key locations in a given species' range (Game *et al*., 2009). In terrestrial habitats, movement corridors could protect large migratory or far-ranging species (Silveira *et al*., 2014; Spiegel *et al*., 2015*a*; Belote *et al*., 2016) such as raptors and insects. Regardless of management form, given the alarming evidence of reduction in biomass and movement ranges of various species exposed to increasing levels of anthropogenic change, we suggest prioritizing conservation approaches that facilitate the maintenance of active subsidy behaviour across taxa.

VI. CONCLUSIONS

(1) The role of animal behaviour in the flow of resources has been underappreciated. Here we suggest that consideration of the behaviours that drive animal movement patterns can provide a better understanding of ecological processes.

(2) Animal behaviours operate at various spatial and temporal scales, and can generate effects that are quantitatively similar to passive subsidies in nature (i.e. press and pulse perturbation) and, in some cases, can be equal or greater in magnitude.

(3) Active subsidy transport processes differ qualitatively from those of passive subsidies in that they are behaviourally driven. Three features of animal behaviour highlight how active subsidy behaviours lead to nutrient-distribution patterns unachievable by passive subsidies: (1) animals can move against abiotic gradients; (2) animals respond to the distribution of nutrients they help form (e.g. positive-feedback loops and the formation of nutrient hotspots); (3) animals also interact with other heterospecific and conspecific active subsidy agents, altering their nutrient-deposition patterns.

(4) Individuals within populations of animal vectors often exhibit consistent behavioural differences, which can affect their movement patterns and generate variation in nutrient transport. While widely acknowledged in the context of movement and behaviour, these recent insights have been under-investigated in the context of active subsidies.

(5) Lastly, it is important to consider animal behaviour when predicting ecosystem-wide responses to future environmental alteration. Specifically,

human-induced rapid environmental change (HIREC) can interfere with the proposed behavioural features by altering not only the number of acting agents or the community composition, but also their space use and consequent nutrient-deposition patterns. Thus, integrating animal behaviour into predictive models of nutrient fluxes will help to assess more accurately the mechanisms that drive variation in nutrient cycling and how these will be disturbed in the future.

VII. ACKNOWLEDGEMENTS

We thank Andy Sih, Jenn Rehage and three anonymous reviewers for their helpful comments. We would also like to recognize Eric Van Cleave and Matthew Savoca, who provided valuable insights and reference suggestions. Finally, A.G.M. thanks Damien Caillaud and Nann Fangue for their guidance and mentorship.

VIII. REFERENCES

Adame, M.F., Fry, B., Gamboa, J.N. & Herrera-Silveira, J.A. (2015) Nutrient subsidies delivered by seabirds to mangrove islands. *Marine Ecology Progress Series* **525**, 15–24.

Allgeier, J.E., Burkepile, D.E. & Layman, C.A. (2017) Animal pee in the sea: consumer-mediated nutrient dynamics in the world’s changing oceans. *Global Change Biology* **23**, 2166–2178.

Anderson, W.B. & Polis, G.A. (1999) Nutrient fluxes from water to land: seabirds affect plant nutrient status on Gulf of California islands. *Oecologia* **118**, 324–332.

AUGUSTINE, D.J. (2003) Long-term, livestock-mediated redistribution of nitrogen and phosphorus in an East African savanna. *Journal of Applied Ecology* **40**, 137–149.

BARNOSKY, A.D., MATZKE, N., TOMIYA, S., WOGAN, G.O., SWARTZ, B., QUENTAL, T.B., MARSHALL, C., MCGUIRE, J.L., LINDSEY, E.L., MAGUIRE, K.C. & MERSEY, B. (2011) Has the Earth's sixth mass extinction already arrived? *Nature* **471**, 51–57.

BARNOSKY, A.D., HADLY, E.A., BASCOMPTE, J., BERLOW, E.L., BROWN, J.H., FORTELIUS, M., GETZ, W.M., HARTE, J., HASTINGS, A., MARQUET, P.A., MARTINEZ, N.D., MOOERS, A., ROOPNARINE, P., VERMEIJ, G., WILLIAMS, J.W., ET AL. (2012) Approaching a state shift in Earth's biosphere. *Nature* **486**, 52–58.

BAUER, S. & HOYE, B.J. (2014) Migratory animals couple biodiversity and ecosystem functioning worldwide. *Science* **344**, 1242552.

BELOTE, R.T., DIETZ, M.S., MCRAE, B.H., THEOBALD, D.M., MCCLURE, M.L., IRWIN, G.H., MCKINLEY, P.S., GAGE, J.A. & APLET, G.H. (2016) Identifying corridors among large protected areas in the United States. *PLoS ONE* **11**.

BENDER, T.J., CASE, E.A. & GILPIN, M.E. (1984) Perturbation experiments in community ecology: theory and practice. *Ecology* **65**, 1–13.

BIRD, M.I., BOOBYER, E.M., BRYANT, C., LEWIS, H.A., PAZ, V. & STEPHENS, W.E. (2007) A long record of environmental change from bat guano deposits in Makangit Cave, Palawan, Philippines. *Earth and Environmental Science Transactions of the Royal Society of Edinburgh* **98**, 59–69.

BIRO, P.A. & POST, J.R. (2008) Rapid depletion of genotypes with fast growth and bold personality traits from harvested fish population. *Proceedings of the Natinoal Academy of Sciences* **105,** 2919-2922.

BJØRNDAL, K.A. (1997) Foraging ecology and nutrition of sea turtles. In *The biology of sea turtles* (eds P.L. LUTZ & J.A. MUSICK), pp. 199–232. CRC Press, Boca Raton, FL.

BOTH, C., BOUWHUIS, S., LESSELLS, C.M. & VISSER, M.E. (2006) Climate change and population declines in a long-distance migratory bird. *Nature* **441**, 81.

BOUCHARD, S.S. & BJØRNDAL, K.A. (2000) Sea turtles as biological transporters of nutrients and energy from marine to terrestrial ecosystems. *Ecology* **81**, 2305–2313.

Capinera, J.L. & Skevington, J.H. (2008) Hilltopping. In *Encyclopedia of Entomology, Second Edition.* Kluwer Academic Publisher.

Capps, K.A. & Flecker, A.S. (2013) Invasive fishes generate biogeochemical hotspots in a nutrient-limited system. *PLoS ONE* **8**, e54093.

Childress, E.S. & Mcintyre, P.B. (2015) Multiple nutrient subsidy pathways from a spawning migration of iteroparous fish. *Freshwater Biology* **60**, 490–499.

Clay, N.A., Lucas, J., Kaspari, M. & Kay, A.D. (2013) Manna from heaven: refuse from an arboreal ant links aboveground and belowground processes in a lowland tropical forest. *Ecosphere* **4**, 1–15.

Cleveland, C.C., Houlton, B.Z., Smith, W.K., Marklein, A.R., Reed, S.C., Parton, W., Del Grosso, S.J. & Running, S.W. (2013) Patterns of new versus recycled primary production in the terrestrial biosphere. *Proceedings of the National Academy of Sciences* **110**, 12733–12737.

Clobert, J., Le Galliard, J.-F., Cote, J., Meylan, S. & Massot, M. (2009) Informed dispersal, heterogeneity in animal dispersal syndromes and the dynamics of spatially structured populations. *Ecology Letters* **12**, 197–209.

Cook, P.J. & McElhinny, M.W. (1979) A reevaluation of the spatial and temporal distribution of sedimentary phosphate deposits in the light of plate tectonics. *Economic Geology* **74**, 315–330.

Cooke, S.J., Suski, C.D., Ostrand, K.G., Wahl, D.H. & Philipp, D.P. (2007) Physiological and behavioral consequences of long-term artificial selection for vulnerability to recreational angling in a teleost fish. *Physiological and Biochemical Zoology* **80**, 480–490.

Côrtes, M.C. & Uriarte, M. (2013) Integrating frugivory and animal movement: a review of the evidence and implications for scaling seed dispersal. *Biological Reviews* **88**, 255–272.

Cote, J., Clobert, J., Brodin, T., Fogarty, S. & Sih, A. (2010a) Personality-dependent dispersal: characterization, ontogeny and consequences for spatially structured populations. *Philosophical Transactions of the Royal Society B: Biological Sciences* **365**, 4065–4076.

Cote, J., Fogarty, S., Weinersmith, K., Brodin, T. & Sih, A. (2010b) Personality traits and dispersal tendency in the invasive mosquitofish (*Gambusia affinis*). *Proceedings of the Royal Society of London B: Biological Sciences* **277**, 1571–1579.

Crowley, P.H., Trimmer, P.C., Spiegel, O., Ehlman, S.M., Cuello, W.S. & Sih, A. (2019) Predicting habitat choice after rapid environmental change. *The American Naturalist* **193**, 619–632.

Deacy, W., Leacock, W., Armstrong, J.B. & Stanford, J.A. (2016) Kodiak brown bears surf the salmon red wave: direct evidence from GPS collared individuals. *Ecology* **97**, 1091–1098.

Dirzo, R., Young, H.S., Galetti, M., Ceballos, G., Isaac, N.J.B. & Collen, B. (2014) Defaunation in the anthropocene. *Science* **401**, 401–406.

Doughty, C.E., Roman, J., Faurby, S., Wolf, A., Haque, A., Bakker, E.S., Malhi, Y., Dunning, J.B. & Svenning, J.-C. (2016) Global nutrient transport in a world of giants. *Proceedings of the National Academy of Sciences* **113**, 868–873.

Dreyer, J., Townsend, P.A., Hook, J.C., Hoekman, D., Vander Zanden, M.J. & Gratton, C. (2015) Quantifying aquatic insect deposition from lake to land. *Ecology* **96**, 499–509.

Duckworth, R.A. & Badyaev, A. V (2007) Coupling of dispersal and aggression facilitates the rapid range expansion of a passerine bird. *Proceedings of the National Academy of Sciences* **104**, 15017–15022.

Dutton, C.L., Subalusky, A.L., Hamilton, S.K., Rosi, E.J. & Post, D.M. (2018) Organic matter loading by hippopotami causes subsidy overload resulting in downstream hypoxia and fish kills. *Nature Communications* **9**, 1951.

Earl, J.E. & Zollner, P.A. (2014) Effects of animal movement strategies and costs on the distribution of active subsidies across simple landscapes. *Ecological Modeling* **283**, 45–52.

Earl, J.E. & Zollner, P.A. (2017) Advancing research on animal-transported subsidies by integrating animal movement and ecosystem modeling. *Journal of Animal Ecology* **86**, 987–997.

ELLIS, J.C., FARIÑA, J.M. & WITMAN, J.D. (2006) Nutrient transfer from sea to land: the case of gulls and cormorants in the Gulf of Maine. *Journal of Animal Ecology* **75**, 565–574.

Elser, J.J., Bracken, M.E., Cleland, E.E., Gruner, D.S., Harpole, W.S., Hillebrand, H., Ngai, J.T., Seabloom, E.W., Shurin, J.B. & Smith, J.E. (2007) Global analysis of nitrogen and phosphorus limitation of primary producers in freshwater, marine and terrestrial ecosystems. *Ecology Letters* **10**, 1135–1142.

Fagan, W.F., Lutscher, F. & Schneider, K. (2007) Population and community consequences of spatial subsidies derived from central-place foraging. *The American Naturalist* **170**, 902–915.

Fenolio, D.B., Graening, G.O., Collier, B.A. & Stout, J.F. (2006) Coprophagy in a cave-adapted salamander; the importance of bat guano examined through nutritional and stable isotope analyses. *Proceedings of the Royal Society B: Biological Sciences* **273**, 439–443.

Ferreira, R.L. & Martins, R.P. (1999) Trophic structure and natural history of bat guano invertebrate communities, with special reference to Brazilian caves. *Tropical Zoology* **12**, 231–252.

Forbes, L. & Kaiser, G.W. (1994) Habitat choice in breeding seabirds: when to cross the information barrier. *Oikos* **70**, 377–384.

Fowler, L.E. (1979) Hatching success and nest predation in the green sea turtle, *Chelonia Mydas*, at Tortuguero, Costa Rica. *Ecology* **60**, 946–955.

Frank, D.A. (2008) Evidence for top predator control of a grazing ecosystem. *Oikos* **117**, 1718–1724.

Fraser, D.F., Gilliam, J.F., Daley, M.J., Le, A.N. & Skalski, G.T. (2001) Explaining leptokurtic movement distributions: intrapopulation variation in boldness and exploration. *The American Naturalist* **158**, 124–135.

Fraser, K.C., Davies, K.T.A., Davy, C.M., Ford, A.T., Flockhart, D.T.T. & Martins, E.G. (2018) Tracking the conservation promise of movement ecology. *Frontiers in Ecology and Evolution* **6**, 1–7.

Game, E., Grantham, H., Hobday, A.J., Pressey, R.I., Lombard, A.T., Beckley, L.E., Gjerde, K., Bustamante, R., Possingham, H. & Richardson, A.J. (2009) Pelagic protected areas: the missing dimension in ocean conservation. *Trends in Ecology and Evolution* **24**, 360–369.

GENDE, S.M., EDWARDS, R.T., WILLSON, M.F. & WIPFLI, M.S. (2002) Pacific salmon in aquatic and terrestrial ecosystems. *American Institute of Biological Sciences* **52**, 917–928.

Gil, M., Hein, A., Spiegel, O., Baskett, M.L. & Sih, A. (2018) Social information links individual behavior to population and community dynamics. *Trends in Ecology and Evolution* **33**, 535–548.

Graham, N.A.J., Wilson, S.K., Carr, P., Hoey, A.S., JENNINGS, S. & McNeil, M.A. (2018) Seabirds enhance coral reef productivity and functioning in the absence of invasive rats. *Nature* **559**, 250–253.

Gruber, J., Brown, G., Whiting, M.J. & Shine, R. (2017) Is the behavioural divergence between range-core and range-edge populations of cane toads (*Rhinella marina*) due to evolutionary change or developmental plasticity? *Royal Society Open Science* **4**, 1–9.

Grüss, A., Kaplan, D.M., Guénette, S., Roberts, C.M. & Botsford, L.W. (2011) Consequences of adult and juvenile movement for marine protected areas. *Biological Conservation* **144**, 692–702.

Hamburg, S.P. & Lin, T.-C. (1998) Throughfall chemistry of an ecotonal forest on the edge of the Great Plains. *Canadian Journal of Forest Research* **28**, 1456–1463.

Harrison, P.M., Gutowsky, L.F.G., Martins, E.G., Patterson, D.A., Cooke, S.J. & Power, M. (2014) Personality-dependent spatial ecology occurs independently from dispersal in wild burbot (*Lota lota*). *Behavioral Ecology* **26**, 483–492.

Hata, H., Nishihira, M. & Kamura, S. (2002) Effects of habitat-conditioning by the damselfish *Stegastes nigricans* (Lacepède) on the community structure of benthic algae. *Journal of Experimental Marine Biology and Ecology* 280, 95–116.

Helfield, J.M. & Naiman, R.J. (2001) Effects of salmon-derived nitrogen on riparian forest growth and implications for stream productivity. *Ecology* **82**, 2403–2409.

Helfield, J.M. & Naiman, R.J. (2006) Keystone interactions: salmon and bear in riparian forests of Alaska. *Ecosystems* **9**, 167–180.

Hertel, A., Leclerc, M., Warren, D., Pelletier, F., Zedrosser, A. & Mueller, T. (2019) Don’t poke the bear: using tracking data to quantify behavioural syndromes in elusive wildlife. *Animal Behaviour* **147**, 91–104.

Hogg, E.H. & Morton, J.K. (1983) The effects of nesting gulls on the vegetation and soil of islands in the Great Lakes. *Canadian Journal of Botany* **61**, 3240–3254.

HOLDO, R.M., HOLT, R.D., COUGHENOUR, M.B. & RITCHIE, M.E. (2007) Plant productivity and soil nitrogen as a function of grazing, migration and fire in an African savanna. *Journal of Ecology* **95**, 115–128.

Holtgrieve, G.W. & Schindler, D.E. (2011) Marine-derived nutrients, bioturbation, and ecosystem metabolism: reconsidering the role of salmon in streams. *Ecology* **92**, 373–385.

Holyoak, M., Casagrandi, R., Nathan, R., Revilla, E. & Spiegel, O. (2008) Trends and missing parts in the study of movement ecology. *Proceedings of the National Academy of Sciences* **105**, 19060–19065.

Houlton, B. & Morford, S. (2015) A new synthesis for terrestrial nitrogen inputs. *Soil* **1**, 381–397.

Hu, K., Horvitz, N., Clark, S., Reynolds, D., Sapir, N. & Chapman, J.G. (2017) Mass seasonal bioflows of high-flying insect migrants. *Science* **354**, 1584–1586.

Huntingford, B., Mesquita, F. & Kadri, S. (2013) Personality variation in cultured fish: implications for production and welfare. In *Animal personalities: Behavior, physiology and evolution* (eds C. Carere & D. Maestripieri), pp. 414–440. University of Chicago Press, Chicago.

Jeltsch, F., Bonte, D., Pe'er, G., Reineking, B., Leimgruber, P., Balkenhol, N., Schröder, B., Buchmann, C.M., Mueller, T., Blaum, N., Zurell, D. & Thorsten, K.B. (2013) Integrating movement ecology with biodiversity research. *Movement Ecology* **1**, 1–13.

Krauel, J.J., Ratcliffe, J.M., Westbrook, J.K. & McCracken, G.F. (2018) Brazilian free-tailed bats (*Tadarida brasiliensis*) adjust foraging behaviour in response to migratory moths. *Canadian Journal of Zoology* **96**, 513–520.

Kunz, T.H., Braun de Torrez, E., Bauer, D., Lobova, T. & Fleming, T.H. (2011) Ecosystem services provided by bats. *Annals of the New York Academy of Sciences* **1223**, 1–38.

LAUNDRÉ, J.W., Hernandez, L. & Ripple, W.J. (2010) The landscape of fear: ecological implications of being afraid. *The Open Ecology Journal* **3**, 1–7.

Lebauer, D.S. & Treseder, K.K. (2008) Nitrogen limitation of net primary productivity in terrestrial ecosystems is globally distributed. *Ecology* **89**, 371–379.

Leclerc, M., Vander Wal, E., Zedrosser, A., Swenson, J.E., Kindberg, J. & Pelletier, F. (2016) Quantifying consistent individual differences in habitat selection. *Oecologia* **180**, 697–705.

Longhurst, A.R. & Harrison, W.G. (1989) The biological pump: profiles of plankton production and consumption in the upper ocean. *Progress in Oceanography* **22**, 47–123.

Lundberg, J. & Moberg, F. (2003) Mobile link organisms and ecosystem functioning: implications for ecosystem resilience and management. *Ecosystems* **6**, 0087–0098.

Marcarelli, A.M., Baxter, C. V., Mineau, M.M. & Hall, R.O. (2011) Quantity and quality: unifying food web and ecosystem perspectives on the role of resource subsidies in freshwaters. *Ecology* **92**, 1215–1225.

McCann, N.P., Zollner, P.A. & Gilbert, J.H. (2017) Temporal scaling in analysis of animal activity. *Ecography* **40**, 1436–1444.

McCauley, D.J., Desalles, P.A., Young, H.S., Dunbar, R.B., Dirzo, R., Mills, M.M. & Micheli, F. (2012) From wing to wing: the persistence of long ecological interaction chains in less-disturbed ecosystems. *Scientific Reports* **2**, 1–9.

McFadden, T.N., Kauffman, J.B. & Bhomia, R.K. (2016) Effects of nesting waterbirds on nutrient levels in mangroves, Gulf of Fonseca, Honduras. *Wetlands Ecology and Management* **24**, 217–229.

McIntyre, P.B., Flecker, A.S., Vanni, M.J., Hood, J.M., Taylor, B.W. & Thomas, S.A. (2008) Fish distributions and nutrient cycling in streams: can fish create biogeochemical hotspots. *Ecology* **89**, 2335–2346.

McNaughton, S.J., Banyikwa, F.F. & McNaughton, M.M. (1997) Promotion of the cycling of diet-enhancing nutrients by African grazers. *Science* **278**, 1798–1800.

Moore, J.W. & Schindler, D.E. (2004) Nutrient export from freshwater ecosystems by anadromous sockeye salmon (*Oncorhynchus nerka*). *Canadian Journal of Fisheries and Aquatic Sciences* **61**, 1582–1589.

Morford, S.L., Houlton, B.Z. & Dahlgren, R.A. (2016) Geochemical and tectonic uplift controls on rock nitrogen inputs across terrestrial ecosystems. *Global Biogeochemical Cycles* **30**, 339–349.

Muchiru, A.N., Western, D.J. & Reid, R.S. (2008) The role of abandoned pastoral settlements in the dynamics of African large herbivore communities. *Journal of Arid Environments* **72**, 940–952.

Mutascio, H.E., Pittman, S.E. & Zollner, P.A. (2017) Investigating movement behavior of invasive Burmese pythons on a shy–bold continuum using individual-based modeling. *Perspectives in Ecology and Conservation* **15**, 25–31.

Nathan, R., Getz, W., Revilla, E., Holyoak, M., Kadmon, R., Saltz, D., & Smouse, P. E., R, W.M. (2008) A movement ecology paradigm for unifying organismal movement research. *Proceedings of the National Academy of Sciences* **105**, 19052–19059.

Nelson, J.A., Stallings, C.D., Landing, W.M. & Chanton, J. (2013) Biomass transfer subsidizes nitrogen to offshore food webs. *Ecosystems* **16**, 1130–1138.

Otero, X.L., De La Peña-Lastra, S., Pérez-Alberti, A., Ferreira, T.O. & Huerta-Diaz, M.A. (2018) Seabird colonies as important global drivers in the nitrogen and phosphorus cycles. *Nature Communications* **9**, 246.

Parsons, D.M., Morrison, M.A. & Slater, M.J. (2010) Responses to marine reserves: decreased dispersion of the sparid *Pagrus auratus* (snapper). *Biological Conservation* **143**, 2039–2048.

Patrick, S.C., Pinaud, D. & Weimerskirch, H. (2017) Boldness predicts an individual's position along an exploration–exploitation foraging trade-off. *Journal of Animal Ecology* **86**, 1257–1268.

Peterjohn, W.T. & Correll, D.L. (1984) Nutrient dynamics in an agricultural watershed: observations on the role of riparian forest. *Ecology* **65**, 1466–1475.

Polis, G.A., Anderson, W.B. & Holt, R.D. (1997) Toward an integration of landscape and food web ecology: the dynamics of spatially subsidized food webs. *Annual Review of Ecology and Systematics* **28**, 289–316.

Polunin, N.V.. & Koike, I. (1987) Temporal focusing of nitrogen release by a periodically feeding herbivorous reef fish. *Journal of Experimental Marine Biology and Ecology* **111**, 285–296.

Poulson, T.L. & Lavoie, K.H. (2000) The trophic basis of subsurface ecosystems. In *Ecosystems of the World: Subterranean Ecosystems* (eds H. Wilkens, D.C. Culver & W.F. Humphreys), pp. 231–249. Elsevier Science.

Réale, D., Garant, D., Humphries, M.M., Bergeron, P., Careau, V. & Montiglio, P.O. (2010) Personality and the emergence of the pace-of-life syndrome concept at the population level. *Philosophical Transactions of the Royal Society Biological Sciences* **365**, 4051–4063.

Ripple, W.J., Wirsing, A.J., Beschta, R.L. & Buskirk, S.W. (2011) Can restoring wolves aid in lynx recovery? *Wildlife Society Bulletin* **35**, 514–518.

Roff, D.A. (1986) The evolution of wing dimorphism in insects. *Evolution* **40**, 1009–1020.

Roman, J. & McCarthy, J.J. (2010) The whale pump: marine mammals enhance primary productivity in a coastal basin. *PLoS ONE* **5**, e13255.

Rubenstein, D. (2016) Superb starlings: cooperation and conflict in an unpredictable environment. In *Cooperative breeding in vertebrates: Studies of ecoogy, evolution, and behavior* (eds W.D. Koenig & J.L. Dickinson), pp. 181–196. Cambridge University Press.

Rubenstein, D.R. (2007) Territory quality drives intraspecific patterns of extrapair paternity. *Behavioral Ecology* **18**, 1058–1064.

Sato, T., Watanabe, K., Kanaiwa, M., Niizuma, Y., Harada, Y. & Lafferty, K.D. (2011) Nematomorph parasites drive energy flow through a riparian ecosystem. *Ecology* **92**, 201–207.

Schmidt, K.A., Dall, S.R.X. & van Gils, J.A. (2010) The ecology of information: an overview on the ecological significance of making informed decisions. *Oikos* **119**, 304–316.

Schmitz, O.J., Hawlena, D. & Trussell, G.C. (2010) Predator control of ecosystem nutrient dynamics. *Ecology Letters* **13**, 1199–1209.

Seagle, S.W. (2003) Can ungulates foraging in a multiple-use landscape alter forest nitrogen budgets? *Oikos* **103**, 230–234.

Sih, A., Cote, J., Evans, M., Fogarty, S. & Pruitt, J. (2012) Ecological implications of behavioural syndromes. *Ecology Letters* **15**, 278–289.

Sih, A., Ferrari, M.C.O. & Harris, D.J. (2011) Evolution and behavioural responses to human-induced rapid environmental change. *Evolutionary Applications* **4**, 367–387.

Silveira, L., Sollmann, R., Jácomo, A.T.A., Diniz Filho, J.A.F. & Tôrres, N.M. (2014) The potential for large-scale wildlife corridors between protected areas in Brazil using the jaguar as a model species. *Landscape Ecology* **29**, 1213–1223.

Sowles, J. (2001) Nitrogen in the Gulf of Maine: sources, susceptibility, and trends. *NOAA/UNH Cooperative Institute for Coastal and Estuarine Environmental Technology, Gulf of Maine Council on the Marine Environment, & NOAA Ocean Service*.

Spiegel, O., Harel, R., Centeno-Cuadros, A., Hatzofe, O., Getz, W.M. & Nathan, R. (2015a) Moving beyond curve fitting: using complementary data to assess alternative explanations for long movements of three vulture species. *The American Naturalist* **185**, 44–54.

Spiegel, O., Leu, S.T., Bull, C.M. & Sih, A. (2017) What’s your move? Movement as a link between personality and spatial dynamics in animal populations. *Ecology Letters* **20**, 3–18.

Spiegel, O., Leu, S.T., Sih, A., Godfrey, S.S. & Bull, C.M. (2015b) When the going gets tough: behavioural type-dependent space use in the sleepy lizard changes as the season dries. *Proceedings of the Royal Society of London B: Biological Sciences* **282**, 20151768.

Stancyk, S.E. (1995) Non-human predators of sea turtles and their control. In *Biology and conservation of sea turtles* (ed K.A. Bjorndal), pp. 139–152. Smithsonian Institution Press, Washington, D.C.

Strickland, M.S., Hawlena, D., Reese, A., Bradford, M.A. & Schmitz, O.J. (2013) Trophic cascade alters ecosystem carbon exchange. *Proceedings of the National Academy of Sciences* **110**, 11035–11038.

Subalusky, A.L., Dutton, C.L., Rosi-Marshall, E.J. & Post, D.M. (2015) The hippopotamus conveyor belt: vectors of carbon and nutrients from terrestrial grasslands to aquatic systems in sub-Saharan Africa. *Freshwater Biology* **60**, 512–525.

Subalusky, A.L., Dutton, C.L., Rosi, E.J. & Post, D.M. (2017) Annual mass drownings of the Serengeti wildebeest migration influence nutrient cycling and storage in the Mara River. *Proceedings of the National Academy of Sciences* **114**, 7647–7652.

Subalusky, A.L. & Post, D.M. (2019) Context dependency of animal resource subsidies. *Biological Reviews* **94**, 517–538.

Townsend, D.W. (1998) Sources and cycling of nitrogen in the Gulf of Maine. *Journal of Marine Systems* **16**, 283–295.

Tucker, M.A., Böhning-Gaese, K., Fagan, W.F., Fryxell, J.M., Van Moorter, B., Alberts, S.C., Ali, A.H., Allen, A.M., Attias, N., Avgar, T., Bartlam-Brooks, H., Bayarbaatar, B., Belant, J.L., Bertassoni, A., Beyer, D., et al. (2018) Moving in the Anthropocene: global reductions in terrestrial mammalian movements. *Science* **359**, 466–469.

Varpe, Ø., Fiksen, Ø. & Slotte, A. (2005) Meta-ecosystems and biological energy transport from ocean to coast: the ecological importance of herring migration. *Oecologia* **146**, 443–451.

Villegas-Ríos, D., Réale, D., Freitas, C., Moland, E. & Olsen, E.M. (2017) Individual level consistency and correlations of fish spatial behaviour assessed from aquatic animal telemetry. *Animal Behaviour* **124**, 83–94.

Vitousek, P.M. (2004) *Nutrient cycling and limitation: Hawaii as a model system*. Princeton University Press, Princeton.

Vitousek, P.M., Menge, D.N.L., Reed, S.C. & Cleveland, C.C. (2013) Biological nitrogen fixation: rates, patterns and ecological controls in terrestrial ecosystems. *Philosophical transactions of the Royal Society of London. Series B, Biological sciences* **368**, 20130119.

Wagner, D., Jones, J.B. & Gordon, D.M. (2004) Development of harvester ant colonies alters soil chemistry. *Soil Biology and Biochemistry* **36**, 797–804.

Whiles, M.R., Callaham, Jr., M.A., Meyer, C.K., Brock, B.L. & Charlton, R.E. (2001) Emergence of periodical cicadas (*Magicicada cassini*) from a Kansas riparian forest: densities, biomass and nitrogen flux. *American Midland Naturalist* **145**, 176–187.

Williams, J.J., Papastamatiou, Y.P., Caselle, J.E., Bradley, D. & Jacoby, D.M.P. (2018) Mobile marine predators : an understudied source of nutrients to coral reefs in an unfished atoll. *Proceedings of the Royal Society of London B: Biological Sciences* **285**, 20172456.

Witherington, B.E. (1986) Human and natural causes of marine turtle clutch and hatchling mortality and their relationship to hatchling production on an important Florida nesting beach. Thesis. University of Central Florida, Orlando, Florida, USA.

Worm, B., Barbier, E., Beaumont, N., Duffy, J.E., Folke, C., Halpern, B.S., Jackson, J.B.C., Lotze, H., Micheli, F., Palumbi, S.R., Sala, E., Selkoe, K., Stachowicz, J. & Watson, R. (2006) Impacts of biodiversity loss on ocean ecosystem services. *Science* **314**, 787–790.

Yang, L.H. (2004) Periodical cicadas as resource pulses in North American forests. *Science* **306**, 1565–1567.

Yang, L.H. & Gratton, C. (2014) Insects as drivers of ecosystem processes. *Current Opinion in Insect Science* **2**, 26–32.

Young, H.S., McCauley, D.J., Dunbar, R.B. & Dirzo, R. (2010) Plants cause ecosystem nutrient depletion via the interruption of bird-derived spatial subsidies. *Proceedings of the National Academy of Sciences* **107**, 2072–2077.

Zhao, M. & Running, S.W. (2010) Drought-induced reduction in global terrestrial net primary production from 2000 through 2009. *Science* **329**, 940–943.

Table 1. Examples of behaviours that highlight various active subsidy features.

1011

Nature of active subsidy	**Behaviour**	**Examples**	**References**
Counter-gradient transport	Migration/dispersal	Salmon spawning upstream	Helfield & Naiman (2001); Gende *et al.* (2002); Holtgrieve & Schindler (2011)
	Migration	Sea turtles migrating to nesting grounds, bringing ocean nutrients onto land	Bouchard & Bjørndal (2000)
	Foraging	'Whale pump' (see Fig. 4)	Roman & McCarthy (2010)
	Foraging	Pelagic birds foraging off islands, bringing ocean nutrients onto land	Anderson & Polis (1999); Adame *et al.* (2015); McFadden *et al.* (2016)
	Foraging	Hippopotamus daily foraging forays	Subalusky *et al.* (2015)
	Foraging	Reef sharks foraging in offshore waters	Williams *et al.* (2018)
Responding to resources	Habitat selection	Seabirds nesting on islands with suitable vegetation	Adame *et al.* (2015); Young *et al.* (2010); Graham *et al.* (2018)
	Foraging	Ungulates utilizing hotspots fertilized by their activity	Augustine (2003) McNaughton *et al.* (1997)
	Foraging	'Whale pump' (see Fig. 4)	Roman & McCarthy (2010)
	Habitat modification	Damselfish farming	Polunin & Koike, (1987); Hata *et al.* (2002)
Interacting with other agents	Habitat selection	Shoaling fish	McIntyre *et al*. (2008); Capps & Flecker (2013)
	Habitat selection	Central-place foraging in colonial ants	Clay *et al.* (2013)
	Anti-predator response	Changes in grasshopper foraging behaviours	Strickland *et al.* (2013)
	Anti-predator response	Alteration of ungulate space use	Frank (2008)
	Anti-predator response	Bats in caves during the day	Bird *et al*. (2007); Kunz *et al*. (2011)
	Parasite manipulation	Invertebrates jumping into streams	Sato *et al.* (2011)

1012

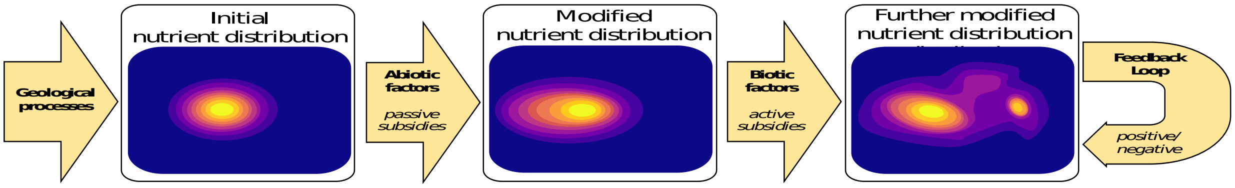

Fig. 1. The main forces shaping nutrient distributions. Initial distribution is a by-product of geological processes such as plate tectonics, volcanism and sedimentation (here, a hypothetical contour map, with warmer colours corresponding to higher concentrations of a certain nutrient, e.g. nitrogen or phosphorus). This distribution is reshaped by abiotic factors like erosion, ocean currents, wind, and gravity (here, creating an anisotropic peak shape). Animals respond to this distribution and further modify it by moving across local and regional scales. These movements often drive further heterogeneity (here, visualized as secondary peaks) at consistent hotspots of biological attractions or during pulses of nutrient flow such as at avian roosting colonies and in locust mass outbreaks. Finally, if animals respond continuously to resource distributions and the presence and behaviour of other organisms, this can generate feedback loops that further enhance heterogeneity.

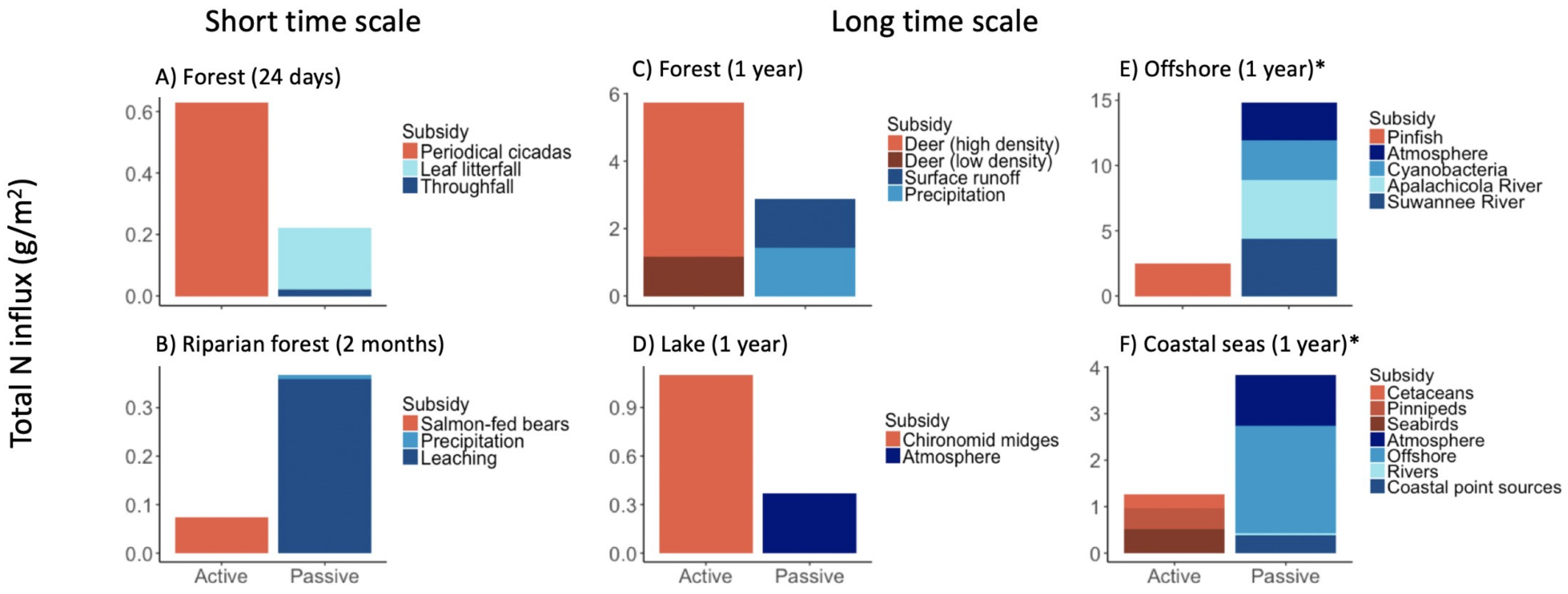
Short time scale
Long time scale
Total N influx (g/m²)
A) Forest (24 days)
0.6
0.4
0.2
0.0
Subsidy
Periodical cicadas
Leaf litterfall
Throughfall
C) Forest (1 year)
6
4
2
0
Subsidy
Deer (high density)
Deer (low density)
Surface runoff
Precipitation
E) Offshore (1 year)*
15
10
5
0
Subsidy
Pinfish
Atmosphere
Cyanobacteria
Apalachicola River
Suwannee River
B) Riparian forest (2 months)
0.3
0.2
0.1
0.0
Active
Passive
Subsidy
Salmon-fed bears
Precipitation
Leaching
D) Lake (1 year)
0.9
0.6
0.3
0.0
Active
Passive
Subsidy
Chironomid midges
Atmosphere
F) Coastal seas (1 year)*
4
3
2
1
0
Active
Passive
Subsidy
Cetaceans
Pinnipeds
Seabirds
Atmosphere
Offshore
Rivers
Coastal point sources

Fig. 2. A quantitative comparison of net nitrogen influx by active (red) and passive (blue) subsidy sources in different ecosystems at various time scales. Active subsidies can generate pulses of events at shorter time scales: (A) in forest ecosystems, over the course of 24 days (Hamburg & Lin, 1998; Whiles *et al*., 2001) and (B) in riparian forest ecosystems, over the course of 2 months (Helfield & Naiman, 2006). Similarly, they can create a prolonged impact over the course of an entire year: (C) in forest ecosystems (Peterjohn & Correll, 1984; Seagle, 2003); (D) along the aquatic–terrestrial interface in lake systems (Yang & Gratton, 2014; Dreyer *et al*., 2015); (E) in offshore regions (Nelson *et al*., 2013); and (F) in coastal marine ecosystems (Sowles, 2001; Townsend, 1998; Roman & McCarthy, 2010). In cases where a range of nitrogen-deposition values are available, we have included the most conservative estimates. Asterisks indicate log-transformed values.

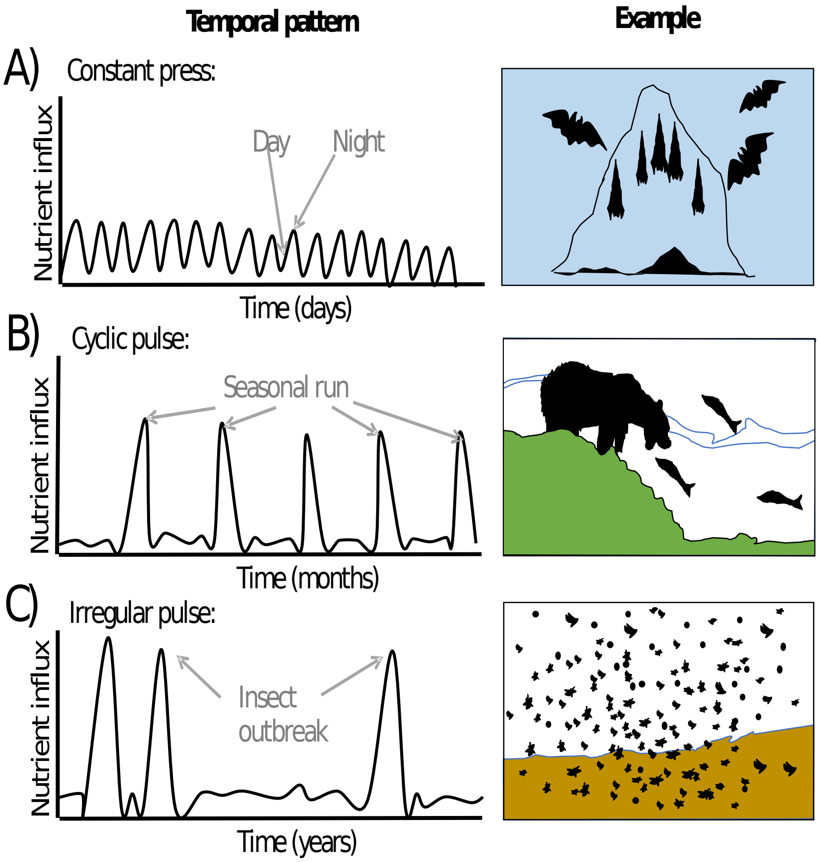

Fig. 3. Variation in temporal dynamics of nutrient influx by active subsidies. (A) Constant press: bats provide relatively constant subsidies (with a daily cycle). These subsidies support a community of guano-dependent consumers and their predators. (B) Cyclic pulse: migrating salmon provide strong pulses of nutrients with an accurate yearly cycle. These pulses support upstream consumers and facilitate aggregations of generally solitary bears. (C) Irregular pulse: locust migrations provide massive but non-cyclic active subsidies that support communities in arid areas.

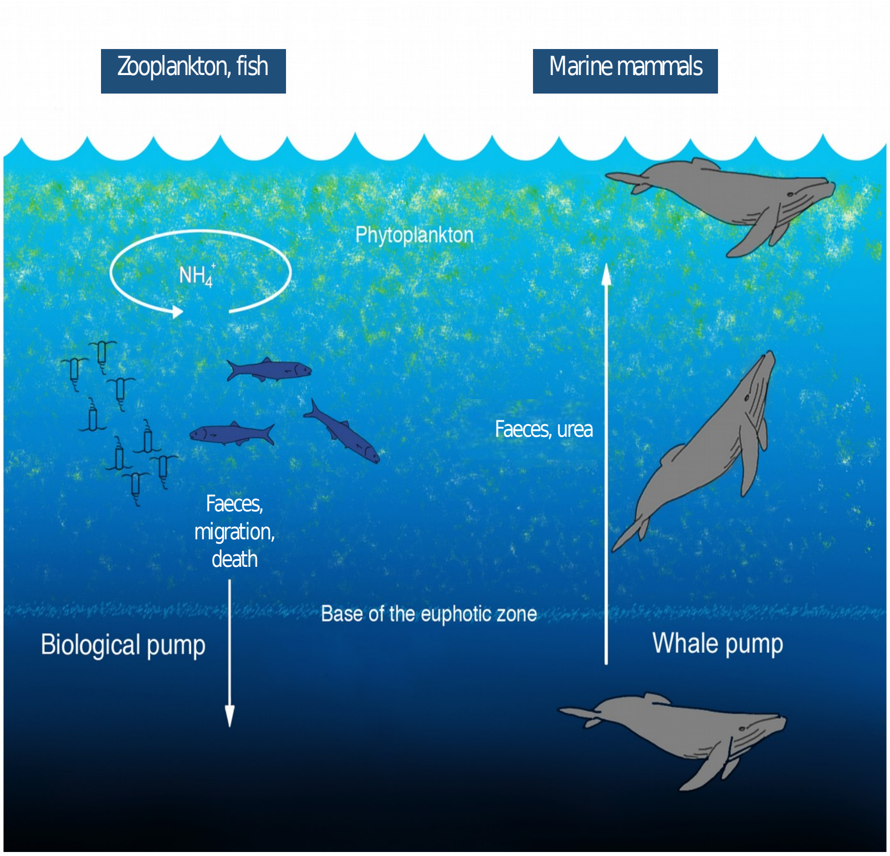

Fig. 4. The conceptual model of the whale pump (as presented by Roman & McCarthy, 2010). Great whales exhibit the key characteristics of active subsidy transport during their annual migrations, when they recycle nitrogen from deeper waters into the photic zone through a mechanism known as the 'whale pump' (Roman & McCarthy, 2010). Cetaceans feed at depth (>100 m) on fish and zooplankton in the waters through which they migrate, but must rise to the surface to breathe, releasing nitrogen-rich urea and faecal plume material. Nutrients from the waste (i.e. nitrogen) are utilized in the photic zone for growth and photosynthesis by phytoplankton, which are then consumed by zooplankton and fish to fuel the biological pump. This serves as

a counter-directional vector to the downward flux of key nutrients from the surface through the gravitational pull on aggregates and faeces, and the vertical movement of zooplankton and fish (Roman & McCarthy, 2010).

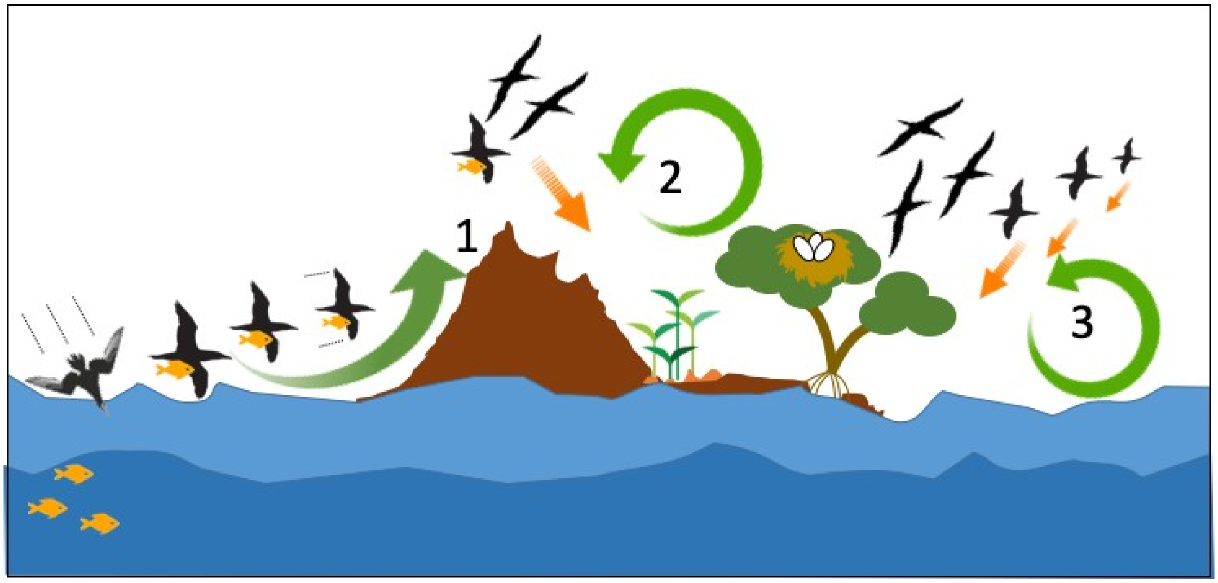

Fig. 5. Behavioural features of agents that affect active subsidies. Marine birds act as a major transportation agent, bringing nutrients from the ocean into terrestrial systems on certain islands. The release of ocean-derived nutrients by birds is shown with orange arrows. This system demonstrates three general features that make active subsidies (animal-mediated nutrient transport) distinct from passive subsidies. (1) Birds transport nutrients counter-directionally to gravity, beyond the reach of ocean waves. (2) Birds respond to the nutrient distributions they generate, creating a positive-feedback loop. For example, on mangrove islands like that pictured here, nutrient influxes *via* guano at bird-aggregation sites create a nutrient

hotspot and facilitate growth of suitable roosting trees, which leads to positive feedback for bird populations (Adame *et al*., 2015). (3) Transport is also influenced by interactions between conspecifics, creating a positive-feedback loop. Many seabirds use social information to inform their movement decisions, likely using the presence of conspecifics as a signal of high-quality nesting habitat (Forbes & Kaiser, 1994; see text for details).