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Permalink

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Journal

Biological reviews of the Cambridge Philosophical Society, 94(5)

ISSN

1464-7931

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Publication Date

2019-10-01

DOI

10.1111/brv.12525

Peer reviewed

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

3

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19

20 ABSTRACT

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

23Recent work indicates that incorporating these movements into ecosystem
24models can enhance our ability to predict the spatio-temporal distribution of
25nutrients. However, the role of animal behaviour in animal-mediated nutrient
26transport (i.e. active subsidies) remains under-explored. Here we review the
27current literature on active subsidies to show how the behaviour of active
28subsidy agents makes them both ecologically important and qualitatively
29distinct from abiotic processes (i.e. passive subsidies). We first propose that
30animal movement patterns can create similar ecological effects (i.e. press
31and pulse disturbances) in recipient ecosystems, which can be equal in
32magnitude to or greater than those of passive subsidies. We then highlight
33three key behavioural features distinguishing active subsidies. First,
34organisms can transport nutrients counter-directionally to abiotic forces and
35potential energy gradients (e.g. upstream). Second, unlike passive subsidies,
36organisms respond to the patterns of nutrients that they generate. Third,
37animal agents interact with each other. The latter two features can form
38positive- or negative-feedback loops, creating patterns in space or time that
39can reinforce nutrient hotspots in places of mass aggregations and/or create
40lasting impacts within ecosystems. Because human-driven changes can
41affect both the space-use of active subsidy species and their composition at
42both population (i.e. individual variation) and community levels (i.e. species
43interactions), predicting patterns in nutrient flows under future modified
44environmental conditions depends on understanding the behavioural
45mechanisms that underlie active subsidies and variation among agents'

46contributions. We conclude by advocating for the integration of animal
47behaviour, animal movement data, and individual variation into future
48conservation efforts in order to provide more accurate and realistic
49assessments of changing ecosystem function.

50

51*Key words:* animal behaviour, behavioural ecology, energy flow, mobile links,
52movement ecology, nutrient cycling, spatial subsidies.

53

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68I. INTRODUCTION: ANIMALS AS IMPORTANT VECTORS OF NUTRIENT 69TRANSPORT

70 The concentration of nutrients across multiple spatio-temporal scales
71establishes the foundation of ecosystem productivity and subsequent
72diversity within and across habitats. Geological processes such as tectonic
73movement and sedimentation determine the underlying distribution of
74essential resources (e.g. nitrogen, phosphorous, and carbon) that influence
75primary productivity and biomass (Cook & McElhinny, 1979; Vitousek, 2004;
76Elser *et al.*, 2007; LeBauer & Treseder, 2008; Vitousek *et al.*, 2013). This
77initial distribution is modified by environmental and physical factors ('passive
78subsidies'; Earl & Zollner, 2014), including wind, current, gravity and erosion
79(Zhao & Running, 2010; Cleveland *et al.*, 2013; Houlton & Morford, 2015;
80Morford, Houlton & Dahlgren, 2016). In addition to these abiotic processes,
81biotic vectors further redistribute nutrients through various mechanisms,
82mostly *via* animal movement (Fig. 1). Specifically, animals can displace
83resources, or serve as 'mobile links' (Jeltsch *et al.*, 2013), within and among
84ecosystems, generating nutrient inputs that are referred to as 'active
85subsidies' (Earl & Zollner, 2014). Active subsidies often differ in their physical
86form (nutrient composition, lability, etc.), which can influence the pathways
87by which these nutrient influxes enter ecosystems (Marcarelli *et al.*, 2011).
88Furthermore, animal vectors exhibit diverse behaviours that influence
89movement patterns and how nutrients are distributed. Ultimately, these
90behaviours allow active subsidies to be quantitatively important in

91ecosystem dynamics, but qualitatively different from passive subsidies in
92their nutrient deposition patterns.

93 There is an extensive body of research demonstrating that animals
94across taxa transport nutrients within and among ecosystems (e.g. Polis,
95Anderson & Holt, 1997; Helfield & Naiman, 2001; Bauer & Hoyer, 2014;
96Adame *et al.*, 2015). This literature shows that animals can redistribute large
97masses of nutrients in the environment by (1) consuming and transporting
98biomass (e.g. the deposition of waste products by migrating grazers such as
99wildebeest (*Connochaetes taurinus*; Holdo *et al.*, 2007) and (2) serving as the
100supply of biomass themselves (e.g. *via* predator consumption or
101decomposition of wildebeest carcasses; Subalusky *et al.*, 2017). Yet, while
102the impact of active subsidies in nutrient transportation has been
103convincingly demonstrated in many studies, empirical work has historically
104focused on the patterns of nutrient accumulation created by organism
105movement, neglecting the processes by which animal vectors (directly or
106indirectly) shape the ecosystem.

107 To address this limitation, recent work has explored how animal
108movement decisions influence the distribution of resources in space and
109time (e.g. Bauer & Hoyer, 2014; Earl & Zollner, 2017). This requires
110consideration of the factors that drive an organism's behaviour, such as
111characteristics of the external environment (e.g. initial nutrient distribution
112or presence of other agents). A recent framework argues that exogenous
113(external) factors such as mortality and competition risk, thermal

114conservation, and prey activity affect an animal's behaviour at multiple
115hierarchical levels, from instantaneous decision-making to annual activity
116patterns such as migration (McCann, Zollner & Gilbert, 2017). Collectively,
117such factors interact with other drivers and constraints (such as the
118organism's internal state, cognitive navigational capacity, and biomechanical
119motion capacity) to shape each movement path (Nathan *et al.*, 2008). For
120instance, wildebeest respond to external factors such as drying vegetation
121through mass migration, and their collective movement ultimately results in
122a relatively large nutrient influx into local river systems (Subalusky *et al.*,
1232017). Predictions regarding future influx into rivers depend on the size of
124the expected wildebeest population, the future environmental conditions
125affecting their migration, and their consequent movement decisions. Thus, a
126more mechanistic understanding of active subsidy transport is critical for
127projecting alterations in nutrient patterns on the landscape, especially in
128light of ongoing environmental change, which can alter community
129composition (Barnosky *et al.*, 2012; Dirzo *et al.*, 2014), reduce population
130sizes (Both *et al.*, 2006; Worm *et al.*, 2006) and affect the movements of
131various species (Tucker *et al.*, 2018). Consequently, an increasing body of
132literature now advocates modelling methods that consider animal movement
133when predicting the ecological impact of active subsidies (e.g. individual-
134based models, state-space models, hidden Markov models) (Earl & Zollner,
1352017; Subalusky & Post, 2018).

136 Here, we review the quantitative importance of active subsidies and
137their ability to generate substantial ecological effects (i.e. press and pulse
138disturbances). We then offer a complementary behavioural perspective that
139identifies three fundamental features that separate active subsidies from
140passive subsidies. (1) First, active subsidies can move counter-directionally
141to environmental gradients, transporting nutrients in directions that oppose
142major abiotic forces like gravity, prominent wind flows, and prevailing
143currents (e.g. salmon swimming upstream). (2) Second, active subsidy
144agents can respond to the patterns of nutrients in their environment,
145creating positive or negative feedbacks with the distribution of abiotic
146resources. (3) Third, active subsidy agents respond to the presence and
147behaviour of other organisms, creating positive or negative feedbacks with
148aspects of the biotic environment, including other active subsidy agents.
149Finally, we call attention to an area for future study by discussing the
150potential impact of individual behavioural variation on active subsidy
151distribution. With the support of several examples from the existing literature
152that highlight these concepts, we conclude that understanding the
153behavioural context of animal movement is essential for predicting and
154conserving resource patterns formed by active subsidies in rapidly changing
155environments.

156

157II. THE QUANTITATIVE IMPORTANCE OF ACTIVE SUBSIDIES

158 Recent work argues that the nutrient contributions from active
159subsidies can be of similar magnitude to those of passive subsidies, and are
160essential for many ecological systems (Earl & Zollner, 2017; Subalusky &
161Post, 2018). Even small organisms can show behaviours (e.g. emergence
162along the aquatic–terrestrial interface) that result in nutrient movements
163that are substantially greater than those generated by abiotic forces (Yang &
164Gratton, 2014). Similar evidence has been found in other systems with
165varying vector species (see Fig. 2). These impacts are highly dependent on
166the spatial and temporal scales of the subsidy’s movement behaviour and its
167interaction with prevailing passive nutrient-movement processes. For
168example, populations of flying insects selectively follow prevailing winds,
169effectively redistributing large amounts of biomass on a regional scale in
170combination with abiotic processes (Hu *et al.*, 2017).

171 In addition to sheer magnitude, active subsidy inputs can act like
172critical press or pulse perturbations within an ecosystem (defined below),
173depending largely on the temporal heterogeneity of animal movements
174(Bender, Case & Gilpin, 1984; Bauer & Hoyer, 2014; Allgeier, Burkepile &
175Layman, 2017). Press disturbances are created by continuous movements
176that lead to a sustained nutrient influx; these can occur when active subsidy
177nutrient transport is relatively consistent in time, driven by repeated
178patterns of activity (Wagner, Jones & Gordon, 2004; Fagan, Lutscher &
179Schneider, 2007) (Fig. 3A). For example, Brazilian cave-dwelling bats
180(*Hipposideros* and *Eonycteris* spp.) sustain entire cave ecosystems through

181their nightly roosting behaviour, since their guano provides nutrients to an
182otherwise energy-poor system (Ferreira & Martins, 1999; Poulson & Lavoie,
1832000; Fenolio *et al.*, 2006; Bird *et al.*, 2007; Kunz *et al.*, 2011). Parallel
184examples also exist in marine environments (Williams *et al.*, 2018). By
185contrast, pulse perturbations can occur when a less-common behaviour
186results in the instantaneous alteration of active subsidy behaviour or
187population density, and thus creates a flux of nutrients of large magnitude
188and short duration (Fig. 3B, C). For example, the mass migration of
189anadromous fishes can generate profound ecosystem impacts as they move
190nutrients from the marine environment to aquatic and terrestrial systems
191(Helfield & Naiman, 2001; Gende *et al.*, 2002; Varpe, Fiksen & Slotte, 2005;
192Childress & McIntyre, 2015). Similar effects can result from the population
193dynamics and movements of many other animals, including insects (Yang,
1942004; Yang & Gratton, 2014; Hu *et al.*, 2017) and mammals (Roman &
195McCarthy, 2010; Subalusky *et al.*, 2017). Depending on their frequency,
196pulses can be cyclic (within a regular interval) or irregular. Although the
197former is likely more predictable from the perspective of a consumer,
198irregular pulses (such as locust outbreaks) can produce greater shifts from
199baseline nutrient levels than mere seasonal changes (Fig. 3C). Thus,
200although it can be easy to ignore nutrient fluxes driven by animal behaviour
201as inconsistent or inconsequential when modelling community-level
202dynamics, it is important to note that presses and pulses generated by active

203subsidy input can be equally, if not more, instrumental to ecological
204processes as those of passive subsidies.

205

206**III. FEATURES THAT DISTINGUISH ACTIVE FROM PASSIVE SUBSIDIES**

207**(1) Counter-gradient and cross-habitat transport**

208 Passive subsidies (e.g. erosion, water flow) often follow a gradient of
209potential energy, such as downstream water flow. While there are
210exceptional examples where passively transported nutrients move against a
211gradient of potential energy (e.g. wildfire, volcanic eruptions and upwelling),
212these are generally localized events. Organisms, on the other hand, can
213widely and selectively redistribute resources by moving them in directions
214and/or to distances unachievable by most passive agents ('counter-gradient
215transport'; Table 1). For instance, animals frequently exhibit behaviours (e.g.
216foraging, migration, refuging, nesting, breeding) that drive them to move
217against the topographic slope of mountains and hills. Notably, multiple
218behaviours can simultaneously shape animal movements and are rarely
219mutually exclusive; for instance, foraging and mating often both drive
220migration patterns. In a classic example, spawning salmon (*Oncorhynchus*
221spp.) annually swim hundreds of kilometers upstream from the ocean,
222leading to doubling or tripling of the amount of nitrogen and phosphorous in
223certain spawning habitats (Helfield & Naiman, 2001; Holtgrieve & Schindler,
2242011; Deacy *et al.*, 2016). Although juveniles eventually migrate (disperse)
225back to the ocean, an estimated 85% of marine-derived nutrients from

226carcasses or eggs remain in the food web upstream, supporting both aquatic
227and terrestrial food webs (Moore & Schindler, 2004). Similarly, insects that
228exhibit hill-topping behaviour (i.e. aggregating on hills or cliffs to mate;
229Capinera & Skevington, 2008) could also serve as a subsidy to the regions in
230which they gather, although this potential nutrient influx has yet to be
231explicitly quantified.

232 Counter-gradient movement by animal vectors likely occurs in systems
233where food resources and critical habitat (e.g. for breeding or nesting) are
234separated by an energy gradient (e.g. uphill) or ecosystem boundary. A
235prominent example is the vertical movement of deep-diving whales (e.g.
236*Physeter macrocephalus* and *Balaenoptera physalus*) throughout the water
237column as they feed in deep ocean layers and then rise to the surface to
238breathe (known as the 'whale pump'; Fig. 4; Roman & McCarthy, 2010). In
239doing so, they move counter-directionally to the downward flux of key
240nutrients from the surface through the gravitational pull on aggregates and
241faeces (Roman & McCarthy, 2010). Through this process, cetaceans may
242transport up to 2.3×10^4 metric tons of nitrogen to the surface per year in
243areas such as the Gulf of Maine - more than all coastal point sources in that
244region (Roman & McCarthy, 2010). This movement may be particularly
245important in the open ocean because biological production here depends
246largely on nutrient dynamics within the photic zone (Longhurst & Harrison,
2471989). Nutrients from whale waste (i.e. nitrogen) are utilized in this area for
248growth and photosynthesis by phytoplankton, which are then consumed by

249zooplankton and fish to fuel the biological pump. Without animal movement,
250these limiting nutrients would be entirely dependent on seasonal upwelling,
251which is restricted in time and space. Thus, the counter-directional
252redistribution of nutrients as a result of whale feeding behaviour during
253migration serves to expand the otherwise seasonal nutrient influx temporally
254and the locations covered by passive subsidies spatially.

255 Counter-gradient movement of nutrients by active subsidy agents has
256important implications for ecosystem function over time. This is particularly
257true when organisms traverse ecosystem boundaries in ways that passive
258subsidies cannot, enhancing connectivity among systems. For instance, birds
259can serve as an important conduit of carbon across the marine-terrestrial
260ecosystem boundary (Anderson & Polis, 1999; Adame *et al.*, 2015;
261McFadden, Kauffman & Bhomia, 2016; Otero *et al.*, 2018). Classic examples
262are avian species that forage at sea and nest on islands relatively
263uninhabited by other organisms (Anderson & Polis, 1999). Unlike the passive
264exchange by ocean waves of nutrients between marine and terrestrial
265ecosystems at the island boundary, seabirds consistently forage beyond this
266boundary, moving ocean nutrients further onto land. On nutrient-limited
267islands (e.g. desert or mangrove; Fig. 5), this supply of guano to terrestrial
268plants can also significantly change the nutrient cycles within an island by
269relieving nutrient limitation (Adame *et al.*, 2015), and the increase in soil
270nitrogen and phosphorous concentrations has been shown to enhance plant
271growth and primary productivity (Anderson & Polis, 1999). On desert islands

272in particular, the effect of seabird roosting behaviour can lead to a 3- to 24-
273fold increase in populations of detritivores, herbivores, and predators, driving
274productivity and ecosystem-wide dynamics (Anderson & Polis, 1999). In
275these cases, daily foraging movements create an essential press-like
276disturbance for these ecosystems.

277 Furthermore, when animal vectors move along specific paths, they
278have the potential to transport nutrients more rapidly and over larger spatial
279scales than passive vectors. For example, the migration of sea turtles
280between foraging (i.e. marine habitat) and nesting grounds (i.e. coastal
281habitat) represents the long-distance movement of nutrients derived from
282the feeding grounds to selected coastal ecosystems (Bouchard & Bjørndal,
2832000), creating a nutrient hotspot *via* both egg content and hatchlings
284(Bouchard & Bjørndal, 2000). Some species of migrating turtles can transport
285nutrients over significantly greater distances, at a higher consistency, and
286over a much shorter time scale than any form of passive subsidy transport
287(e.g. currents). For example, leatherback turtles (*Dermochelys coriacea*) that
288feed on jellyfish in the Arctic Circle annually return thousands of kilometers
289to tropical beaches to nest (Bjørndal, 1997). This nutrient movement
290supports food webs in the recipient ecosystems, including detrital consumers
291as well as larger terrestrial predators such as ants, crabs, foxes, and
292raccoons (Fowler, 1979; Stancyk, 1995). Notably, the spatial distribution of
293this influx depends on nest-site-selection behaviour. For example,
294loggerhead turtles (*Caretta caretta*) nest further from dunes than other

295species, and thus the nutrients they transport may contribute less to dune
296vegetation than to other components of the ecosystem (Witherington, 1986;
297Bouchard & Bjørndal, 2000). Such targeted transport emphasizes the unique
298role of behaviour (in this case, habitat selection) in ecosystem subsidies
299(Subalusky & Post, 2018). Seasonal migrations, like those performed by sea
300turtles, can create pulsed or cyclic perturbations of nutrient availability
301within a habitat. Consequently, such counter-gradient movements have the
302potential to generate important ecosystem impacts that reflect those of
303passive subsidies (i.e. can be consistent or cyclical in nature), but differ in
304terms of their pathway.

305

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

308 Animal-mediated transport can also be reactive, driven by an
309organism's behavioural response to its physical environment (e.g.
310environmental structure, climate, existing resource distribution). Specifically,
311resource distribution both influences and is influenced by organism
312movement, and this can lead to positive- or negative-feedback loops in
313nutrient accumulation (Earl & Zollner, 2017; Subalusky & Post, 2018). This
314feature of active subsidies is likely most prominent when nutrient influxes
315affect the resources that agents directly use. Specifically, if a nutrient influx
316by an animal vector directly affects its own food source (e.g. for a herbivore)
317or habitat structure (e.g. for a tree-nesting species), this may generate a

318stronger feedback loop compared to situations in which habitat selection is
319not heavily influenced by nutrient input. However, the direction of the
320feedback loop (positive or negative) and magnitude of the subsidy input
321depend on the strength of drivers that influence the behaviour of the active
322subsidy (see Table 1 for examples).

323 Positive-feedback loops are generated when organisms aggregate in
324an area of high resource availability and continue to contribute to its
325productivity through fertilization. One of the best-studied outcomes of this
326feature is the formation of resource hotspots, in which organisms
327preferentially revisit areas where they have already deposited nutrients
328(reviewed in Earl & Zollner, 2017). In these cases, the active subsidy agents
329can create and/or respond to an influx of resources. This process has been
330observed when seabird preference for nesting on certain islands has resulted
331in significantly elevated levels of plant-available nitrogen surrounding areas
332of concentrated guano deposits (McCauley *et al.*, 2012; Adame *et al.*, 2015;
333Graham *et al.*, 2018). On nutrient-depleted mangrove islands, for example,
334seabirds improve the quality of their own habitat through the net influx of
335nutrient enrichment, rendering the islands more attractive to roosting
336seabirds and continuing to support – or even increasing suitability for –
337populations of these active subsidy agents (Adame *et al.*, 2015; Fig. 5).
338Feedback loops like this increase primary productivity and strengthen
339autotroph communities (e.g. plants), which not only attracts agent
340conspecifics, but also heterospecifics. For example, in the African savannah–

341 woodland system, the grassy remnants of former livestock corrals (once
342 fertilized by livestock dung) often form high-resource glade regions, which in
343 turn attract ungulate grazers (Augustine, 2003; Muchiru, Western & Reid,
344 2008). As they forage within this habitat, ungulates fertilize the area with
345 dung and urine, helping to maintain the productivity of the glade and attract
346 other species to the area even long after the initial active subsidy agents
347 have dispersed (Augustine, 2003; Muchiru *et al.*, 2008). These include superb
348 starlings (*Lamprotornis superbus*), which nest on acacia trees around the
349 outskirts of glades, taking advantage of the predictable insect abundance
350 found within glades to provision hatchlings, and thus emphasizing how active
351 subsidy movement influences both conspecific and heterospecific habitat use
352 (Rubenstein, 2007, 2016).

353 Conversely, negative-feedback loops occur when organisms actively
354 avoid certain locations and consequently limit nutrient influx from potential
355 active subsidies. Most simply, this can occur due to resource depletion, such
356 as when organisms spread nutrients from hotspots across a broader area
357 and consequently avoid the initial hotspot locations once the nutrients have
358 been depleted. On a small spatial scale, this takes place when frugivores
359 disperse seeds from a tree (a local hotspot), reducing the hotspot and
360 contributing to a more uniform distribution of resources as seeds from the
361 fruit are spread from their source (Côtés & Uriarte, 2013). Negative-
362 feedback loops may also be more complex, driven by biotic interactions as
363 well as behavioural responses to the environment across wider scales. For

364example, on tropical islets in the Central Pacific, invasive coconut trees
365(*Cocos nucifera*) tend to grow where they benefit from bird-transported
366nutrients (Young *et al.*, 2010). However, seabirds (e.g. *Sula* spp.) prefer to
367roost in native trees (*Pisonia grandis* and *Tournefortia argentea*) over these
368invasive plants (Young *et al.*, 2010). Thus, bird behavioural responses to
369coconut trees (i.e. repulsion) reduce the initial hotspot by reducing marine-
370derived subsidies in these locations and triggering nutrient-depletion
371patterns within the communities on these islands (Young *et al.*, 2010).
372Negative-feedback loops can also form in existing hotspots when these areas
373become saturated with nutrients to the point of toxicity ('subsidy overload';
374Dutton *et al.*, 2018), as in the case of eutrophication. For example, excessive
375amounts of nutrient deposition on seabird islands can lead to changes in
376species composition by killing certain plant species (Hogg & Morton, 1983;
377Ellis, Fariña & Witman, 2006). In general, since predicting when and how a
378feedback loop will form depends heavily on the system, considering the net
379impact of behavioural responses to existing nutrient distribution will require
380empirical work that is tailored to specific systems.

381

382**(3) Interactions among agents affect deposition patterns**

383 Animal movement is not only affected by abiotic factors, like the
384physical environment or existing resource distribution, but also by the
385distribution and movement of other agents (i.e. direct interactions between
386organisms). These may be conspecific or heterospecific, representing

387 competitors, mates, pathogens, prey or predators. Variation in behaviours as
388a result of other agents, like social attraction or anti-predator responses,
389 thus affects the movement patterns and ecological implications of active
390 subsidies. Furthermore, perturbations of the community composition (e.g.
391 through the introduction of an invasive species or local extinctions) can also
392 affect movement and the derived nutrient deposition patterns, again
393 highlighting how predictions from phenomenological models alone may
394 become inaccurate under changing environmental conditions.

395 Perhaps best studied is how predators influence subsidies through their
396 effect on prey population size and behaviour (Schmitz, Hawlena & Trussell,
397 2010; Strickland *et al.*, 2013). Most obviously, predation can directly affect
398 nutrient deposition within an ecosystem *via* consumptive effects. For
399 example, subsidies from wolf-killed carcasses in Yellowstone National Park
400 have been shown to create temporary hotspots by attracting scavenging
401 species such as ravens (*Corvus corax*), bald eagles (*Haliaeetus*
402 *leucocephalus*), and smaller carnivores (Ripple *et al.*, 2011). But
403 independently of consumptive effects, the ‘landscape of fear’ generated by
404 predator presence also shapes prey habitat preference, food choice, space
405 use and distribution (Laundré, Hernández & Ripple, 2010, Schmitz *et al.*,
406 2010). In turn, evasive behavioural responses to predator activity can affect
407 the distribution of nutrients across a landscape. For instance, after the
408 eradication of Yellowstone wolves (*Canis lupus*) in the early 20th century,
409 relatively uninhibited populations of ungulates nearly doubled the rate of net

410nitrogen availability among grasslands through waste products (Frank,
4112008). Several years following the reintroduction of grey wolves to the park,
412there was a notable decrease in net nitrogen availability in these grasslands.
413This change was likely driven by a shift in ungulate habitat-use patterns,
414rather than direct removal of these grazers by the reintroduced wolves
415(Frank, 2008). Thus, in situations where heterospecific interactions play a
416major role in agent movement, identifying the response (e.g. limited
417movement or altered patch use) will be critical for predicting how nutrient
418deposition will change in both space and time.

419 In addition to trophic-level interactions, conspecific interactions can aid
420in the formation of nutrient hotspots, particularly for species that utilize
421social information to make decisions about movement within and among
422habitats (i.e. 'ecology of information'; Clobert *et al.*, 2009; Schmidt, Dall &
423Van Gils, 2010). Specifically, social information generates correlations in
424behaviour and space use of multiple individuals (Gil *et al.*, 2018), thus
425affecting both the nature and magnitude of active subsidy nutrient
426distribution across a landscape. For instance, breeding-site selection by
427many social agents is often based on conspecifics, such as when the
428presence of nesting marine birds provides cues about local breeding
429conditions ('information barrier hypothesis'; Forbes & Kaiser, 1994; Schmidt
430*et al.*, 2010), deterring individuals from dispersal to a new habitat. In this
431case, we would hypothesize that the subsequent social aggregation likely
432drives hotspot formation *via* the accumulation of nutrients in these areas

433(Fig. 1). Central-place foraging behaviour by highly social animals can
434similarly cause the formation of nutrient hotspots *via* aggregation, especially
435if these central places remain stable over long periods (Clay *et al.*, 2013). For
436example, colonial canopy ants (*Azteca trigona*) that continually return to a
437collective home base following foraging bouts can alter nutrient composition
438of the leaf litter below their nests *via* a steady stream of nutrient-rich excreta
439falling on the forest floor (Clay *et al.*, 2013). In these cases, understanding
440how large, dense and spatially stable conspecific aggregations form is key
441for predicting the effect of social behaviour on nutrient influxes. Whether
442aggregating behaviour occurs on a daily (e.g. foraging or anti-predator
443response) or seasonal (e.g. breeding) basis would then determine the
444corresponding ecosystem effect (press or pulse), depending on whether the
445subsidy influx from this movement is consistent or cyclical.

446

447**IV. INDIVIDUAL DIFFERENCES AS A SOURCE OF VARIATION**

448 Although almost entirely overlooked by the ecological subsidy literature,
449individual variation of within-population space use likely plays a role in
450generating nutrient-deposition patterns. This variation can arise from a
451combination of external and internal factors (Nathan *et al.*, 2008). First,
452individuals might move differently simply because they occupy different
453habitats with differences in structure and composition. For example,
454individuals in resource-scarce areas might be forced to move more in search
455of these resources, resulting in longer transportation distances. Second,

456 differences in movement patterns can arise from variation in individual life
457 stage, sex, and morphology (Fraser *et al.*, 2001). For instance, winged-morph
458 insects readily disperse across distances and barriers that de-winged morphs
459 are physically unable to overcome (Roff, 1986). Furthermore, such
460 intraspecific differences can occur at multiple scales, reflecting variation
461 among populations (e.g. along a latitudinal gradient), or differences within a
462 population. Lastly, a growing body of literature is also linking differential
463 space-use patterns with variation in life-history traits or behavioural
464 strategies (Réale *et al.*, 2010; Sih *et al.*, 2012). Personality traits (defined as
465 within-individual consistency in behavioural responses across time or
466 contexts) may interact with environmental heterogeneity, resulting in
467 personality-dependent dispersal and space use that can affect various
468 ecological processes at the population and community levels (Cote *et al.*
469 2010a; Spiegel *et al.*, 2017; Villegas-Ríos *et al.*, 2017).

470 Evidence of consistent (phenotype-related) intra-population differences in
471 dispersal distance, home-range size, habitat selection and other space-use
472 axes is becoming more common in a wide range of taxa (Duckworth &
473 Badyaev, 2007; Cote *et al.*, 2010b; Harrison *et al.*, 2014; Spiegel *et al.*,
474 2015b; Patrick, Pinaud & Weimerskirch, 2017). Understanding these aspects
475 of behavioural phenotype can provide greater insight into an organism's role
476 in nutrient distribution, as they can potentially affect the distance, rate, and
477 amount of nutrients transported. For example, individual wandering
478 albatross (*Diomedea exulans*) vary in the ratio of their exploration-

479exploitation foraging behaviour (Patrick *et al.*, 2017). Thus, different
480individuals likely move nutrients between patches at different rates. In this
481case, one might expect exploiters (i.e. those that spend more time in
482restricted-area search) to contribute more to local transport and hotspot
483formation than explorers (i.e. those that spend more time in long-distance
484travel), while the latter could contribute more to long-range transport and
485ecosystem connectivity. Similarly, individual brown bears (*Ursus arctos*) vary
486in the time spent foraging at salmon (*Oncorhynchus* spp.) spawning sites
487(Deacy *et al.*, 2016). As previously mentioned, salmon are an important
488source of nutrients in upstream spawning habitats, and their consumers
489serve as the final link in transporting salmon-derived nutrients from marine
490and aquatic ecosystems to the terrestrial environment. Variation in salmon
491consumption by brown bears, as well as in post-consumption space use
492among individual bears (Leclerc *et al.*, 2016; Hertel *et al.*, 2019), would thus
493influence the extent to which cross-boundary active subsidy transport
494occurs.

495 Furthermore, variation in space use can lead to spatial structuring of
496phenotypes within a population (e.g. Duckworth & Badyaev, 2007; Cote *et*
497*al.*, 2010a; Spiegel *et al.*, 2017), which could then affect the spatial
498structuring of nutrient inputs. Examples of such spatial structuring are
499exemplified by non-native introductions, where individuals found on the
500invasion front have both morphological and behavioural differences
501compared to individuals in established areas (e.g. Gruber *et al.* 2017). In

502these cases, larger and bolder individuals commonly found at the dispersal
503front would be expected to deposit greater amounts of subsidies at further
504distances. Scenarios like this suggest that incorporating intraspecific
505differences in space use can help provide a better understanding of how the
506same population of animal vectors may simultaneously generate differing
507patterns of nutrient deposition within and among habitats.

508

509**V. CONSERVATION IMPLICATIONS**

510 There is increasing recognition that the materials exchanged *via*
511animal vector links should be incorporated into management decisions to
512maintain resilience and ensure future ecosystem function (Lundberg &
513Moberg, 2003). Previous work has highlighted some of the major implications
514of removing active subsidy agents in altered ecosystems (Subalusky & Post,
5152018). Among these, human-induced rapid environmental change (HIREC;
516Sih, Ferrari & Harris, 2011) can cause population reductions or even local
517extinctions, resulting in fewer active subsidy agents (Barnosky *et al.*, 2011;
518Dirzo *et al.*, 2014; Earl & Zollner, 2017; Subalusky & Post, 2018). For
519example, the movement of nutrients from sea to land *via* seabirds and
520anadromous fish has been reduced by 96% due to the loss of these species
521(Doughty *et al.*, 2016). The reduction of animal vector populations and
522subsequent active subsidy influxes also has a variety of indirect ecological
523effects. For instance, moth migration altered by changes in large-scale
524weather patterns affects the movement of Brazilian free-tailed bats

525(*Tadarida brasiliensis*), since these bats rely heavily on this seasonal
526resource to gain fat for their own autumn migrations (Krauel *et al.*, 2018).

527 Although the number of applied models incorporating organism
528movement is increasing (Holyoak *et al.*, 2008; Grüss *et al.*, 2011),
529understanding how behavioural responses change in altered environments
530can lend greater predictive power to changes in active subsidy nutrient
531distribution than considering movement patterns alone (Fraser *et al.*, 2018).
532For example, HIREC could reduce the extent of active subsidy agent
533movement by increasing fragmentation (i.e. creating physical barriers to
534movement) or by generating a plastic change in behavioural response (e.g.
535alterations in habitat use or home-range size). In addition, because many
536large species tend to travel further, they may exhibit higher sensitivity in
537behavioural responses to anthropogenic change, altering their movement
538more significantly and thus inhibiting their ability to act as active subsidies
539(Tucker *et al.*, 2018). Moreover, HIREC can affect the phenotypic composition
540within populations, through selection of certain life-history traits, behavioural
541types or morphologies (e.g. Cooke *et al.*, 2007; Biro & Post, 2008; Parsons,
542Morrison & Slater, 2010). For example, human harvesting selects against
543phenotypes with large size, fast growth rates, and high activity and boldness
544(Biro & Post, 2008; Huntingford, Mesquita & Kadri, 2013). At both local and
545broader scales, removal of more mobile phenotypes within certain species
546would limit nutrient distribution by active subsidy agents. Conversely, for
547recently introduced species, selection may favour bolder individuals that

548 might achieve greater dispersal distances (e.g. Duckworth & Badyaev, 2007)
549 and therefore transport nutrients further into novel environments. A third
550 scenario is also possible, by which more behaviourally plastic species or
551 individuals are best able to adapt to HIREC by calibrating their behaviour to
552 the current circumstances (e.g. Crowley *et al.*, 2019). For example, recent
553 modelling of Burmese python (*Python molurus bivittatus*) behaviour suggests
554 that species able to exhibit adaptively flexible dispersal behaviour are most
555 successful in population expansion (Mutascio *et al.*, 2017).

556 In general, one critical step for managers and policy-makers will be to
557 recognize the limitations of spatially restricted forms of management to
558 enact more proactive conservation measures for mobile animal vectors. For
559 such animals in the pelagic environment, including sharks and whales,
560 alternative options could include dynamic (i.e. mobile) or seasonal marine
561 protected areas to cover key locations in a given species' range (Game *et al.*,
562 2009). In terrestrial habitats, movement corridors could protect large
563 migratory or far-ranging species (Silveira *et al.*, 2014; Spiegel *et al.*, 2015a;
564 Belote *et al.*, 2016) such as raptors and insects. Regardless of management
565 form, given the alarming evidence of reduction in biomass and movement
566 ranges of various species exposed to increasing levels of anthropogenic
567 change, we suggest prioritizing conservation approaches that facilitate the
568 maintenance of active subsidy behaviour across taxa.

569

570 **VI. CONCLUSIONS**

571(1) The role of animal behaviour in the flow of resources has been
572underappreciated. Here we suggest that consideration of the behaviours that
573drive animal movement patterns can provide a better understanding of
574ecological processes.

575(2) Animal behaviours operate at various spatial and temporal scales, and
576can generate effects that are quantitatively similar to passive subsidies in
577nature (i.e. press and pulse perturbation) and, in some cases, can be equal
578or greater in magnitude.

579(3) Active subsidy transport processes differ qualitatively from those of
580passive subsidies in that they are behaviourally driven. Three features of
581animal behaviour highlight how active subsidy behaviours lead to nutrient-
582distribution patterns unachievable by passive subsidies: (1) animals can
583move against abiotic gradients; (2) animals respond to the distribution of
584nutrients they help form (e.g. positive-feedback loops and the formation of
585nutrient hotspots); (3) animals also interact with other heterospecific and
586conspecific active subsidy agents, altering their nutrient-deposition patterns.

587 (4) Individuals within populations of animal vectors often exhibit consistent
588behavioural differences, which can affect their movement patterns and
589generate variation in nutrient transport. While widely acknowledged in the
590context of movement and behaviour, these recent insights have been under-
591investigated in the context of active subsidies.

592(5) Lastly, it is important to consider animal behaviour when predicting
593ecosystem-wide responses to future environmental alteration. Specifically,

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

601

602

603 **VII. ACKNOWLEDGEMENTS**

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

609

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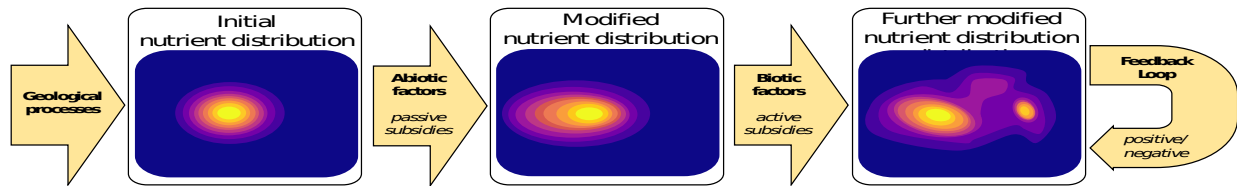
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1009 Table 1. Examples of behaviours that highlight various active subsidy
1010 features.

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

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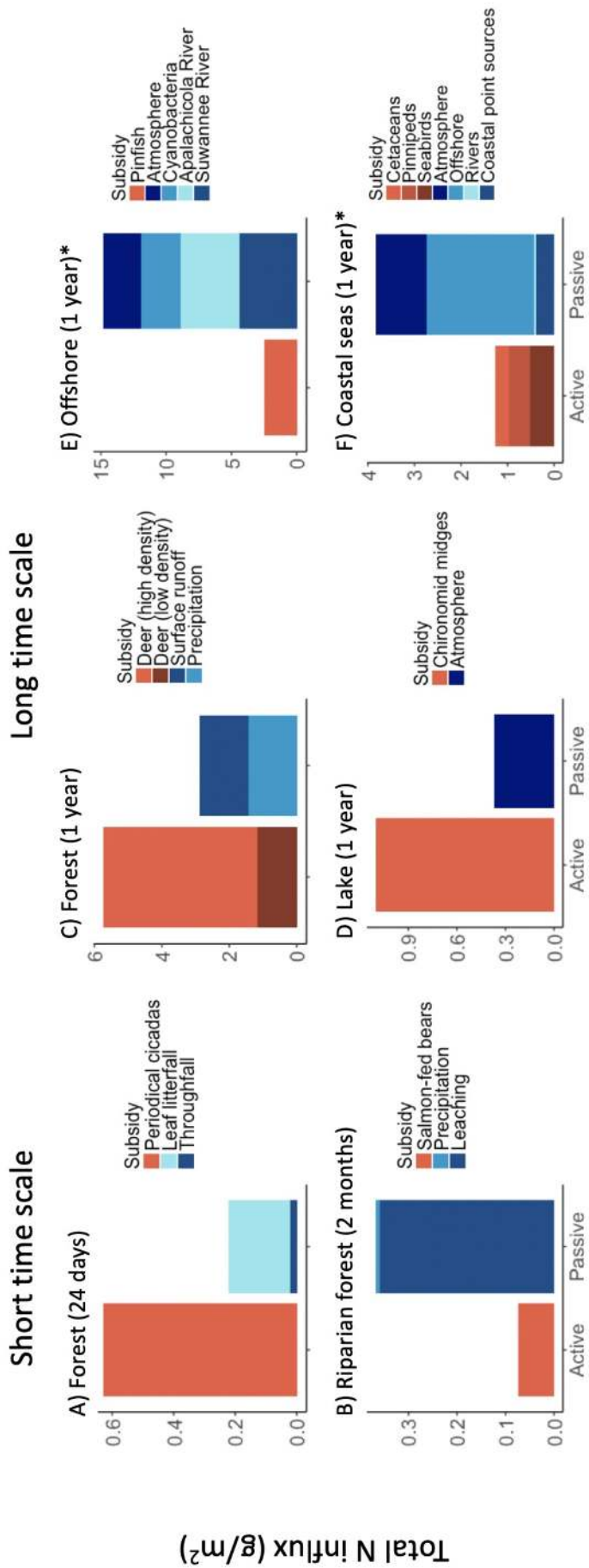


1014

1015 **Fig. 1.** The main forces shaping nutrient distributions. Initial distribution is a
1016 by-product of geological processes such as plate tectonics, volcanism and
1017 sedimentation (here, a hypothetical contour map, with warmer colours
1018 corresponding to higher concentrations of a certain nutrient, e.g. nitrogen or
1019 phosphorus). This distribution is reshaped by abiotic factors like erosion,
1020 ocean currents, wind, and gravity (here, creating an anisotropic peak shape).
1021 Animals respond to this distribution and further modify it by moving across
1022 local and regional scales. These movements often drive further
1023 heterogeneity (here, visualized as secondary peaks) at consistent hotspots of
1024 biological attractions or during pulses of nutrient flow such as at avian
1025 roosting colonies and in locust mass outbreaks. Finally, if animals respond
1026 continuously to resource distributions and the presence and behaviour of
1027 other organisms, this can generate feedback loops that further enhance
1028 heterogeneity.

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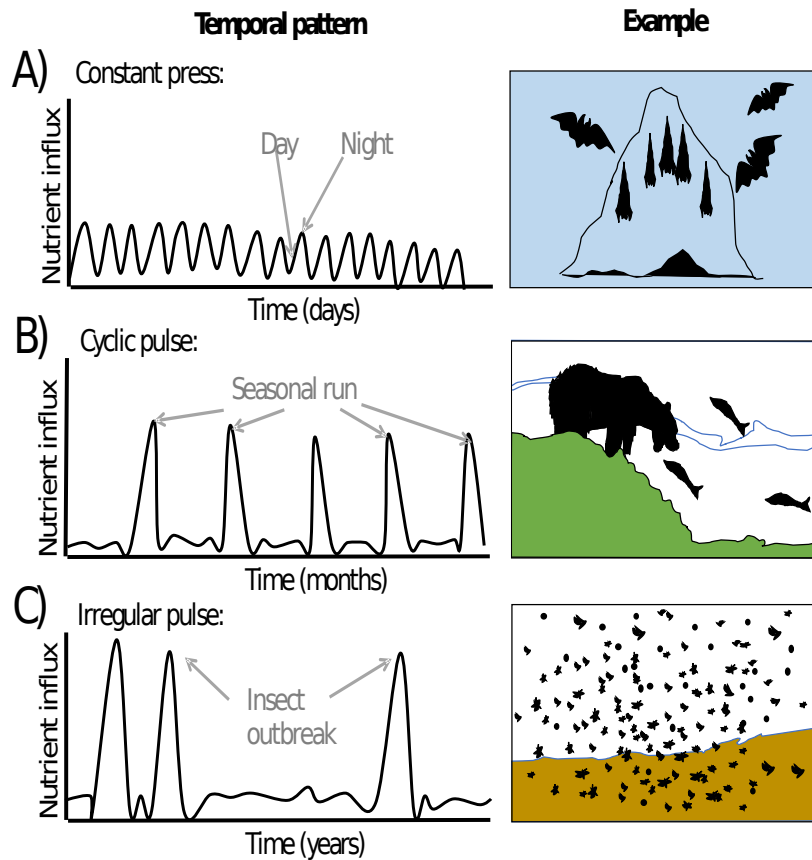
Total N influx (g/m²)

1032 **Fig. 2.** A quantitative comparison of net nitrogen influx by active (red) and
1033 passive (blue) subsidy sources in different ecosystems at various time
1034 scales. Active subsidies can generate pulses of events at shorter time scales:
1035 (A) in forest ecosystems, over the course of 24 days (Hamburg & Lin, 1998;
1036 Whiles *et al.*, 2001) and (B) in riparian forest ecosystems, over the course of
1037 2 months (Helfield & Naiman, 2006). Similarly, they can create a prolonged
1038 impact over the course of an entire year: (C) in forest ecosystems (Peterjohn
1039 & Correll, 1984; Seagle, 2003); (D) along the aquatic-terrestrial interface in
1040 lake systems (Yang & Gratton, 2014; Dreyer *et al.*, 2015); (E) in offshore
1041 regions (Nelson *et al.*, 2013); and (F) in coastal marine ecosystems (Sowles,
1042 2001; Townsend, 1998; Roman & McCarthy, 2010). In cases where a range of
1043 nitrogen-deposition values are available, we have included the most
1044 conservative estimates. Asterisks indicate log-transformed values.

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1049 **Fig. 3.** Variation in temporal dynamics of nutrient influx by active subsidies.

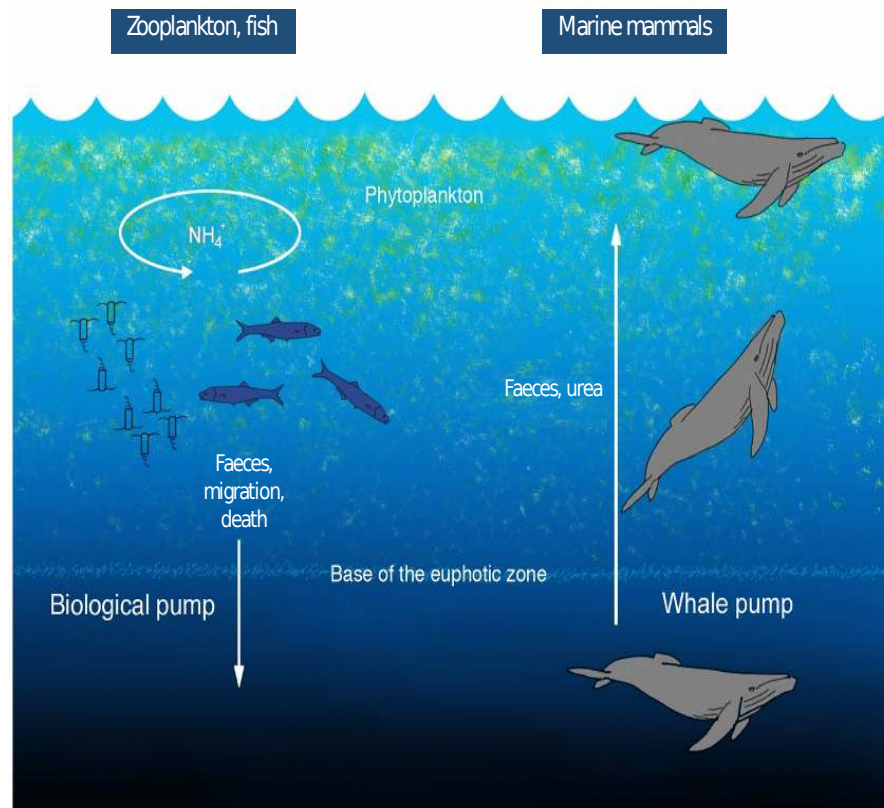
1050 (A) Constant press: bats provide relatively constant subsidies (with a daily
 1051 cycle). These subsidies support a community of guano-dependent consumers
 1052 and their predators. (B) Cyclic pulse: migrating salmon provide strong pulses
 1053 of nutrients with an accurate yearly cycle. These pulses support upstream
 1054 consumers and facilitate aggregations of generally solitary bears. (C)
 1055 Irregular pulse: locust migrations provide massive but non-cyclic active
 1056 subsidies that support communities in arid areas.

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1062 **Fig. 4.** The conceptual model of the whale pump (as presented by Roman &
1063 McCarthy, 2010). Great whales exhibit the key characteristics of active
1064 subsidy transport during their annual migrations, when they recycle nitrogen
1065 from deeper waters into the photic zone through a mechanism known as the
1066 'whale pump' (Roman & McCarthy, 2010). Cetaceans feed at depth (>100 m)
1067 on fish and zooplankton in the waters through which they migrate, but must
1068 rise to the surface to breathe, releasing nitrogen-rich urea and faecal plume
1069 material. Nutrients from the waste (i.e. nitrogen) are utilized in the photic
1070 zone for growth and photosynthesis by phytoplankton, which are then
1071 consumed by zooplankton and fish to fuel the biological pump. This serves as

1072a counter-directional vector to the downward flux of key nutrients from the
1073surface through the gravitational pull on aggregates and faeces, and the
1074vertical movement of zooplankton and fish (Roman & McCarthy, 2010).



1075

1076**Fig. 5.** Behavioural features of agents that affect active subsidies. Marine
1077birds act as a major transportation agent, bringing nutrients from the ocean
1078into terrestrial systems on certain islands. The release of ocean-derived
1079nutrients by birds is shown with orange arrows. This system demonstrates
1080three general features that make active subsidies (animal-mediated nutrient
1081transport) distinct from passive subsidies. (1) Birds transport nutrients
1082counter-directionally to gravity, beyond the reach of ocean waves. (2) Birds
1083respond to the nutrient distributions they generate, creating a positive-
1084feedback loop. For example, on mangrove islands like that pictured here,
1085nutrient influxes *via* guano at bird-aggregation sites create a nutrient

1086hotspot and facilitate growth of suitable roosting trees, which leads to
1087positive feedback for bird populations (Adame *et al.*, 2015). (3) Transport is
1088also influenced by interactions between conspecifics, creating a positive-
1089feedback loop. Many seabirds use social information to inform their
1090movement decisions, likely using the presence of conspecifics as a signal of
1091high-quality nesting habitat (Forbes & Kaiser, 1994; see text for details).
1092