A methodological roadmap to quantify animal-vectored spatial ecosystem subsidies

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Keywords: Meta-ecosystem theory, animal movement, biogeochemistry, ecosystem ecology, stoichiometry, remote sensing

Abstract

Ecosystems are open systems connected through spatial flows of energy, matter, and nutrients. Predicting and managing ecosystem interdependence requires a rigorous quantitative understanding of the drivers and vectors that connect ecosystems across spatio-temporal scales. Animals act as such vectors when they transport nutrients across landscapes in the form of excreta, egesta, and their own bodies. Here, we introduce a methodological roadmap that combines movement, foraging, and ecosystem ecology to study the effects of animal-vectored nutrient transport on meta-ecosystems. The meta-ecosystem concept — the notion that ecosystems are connected in space and time by flows of energy, matter, and organisms across boundaries — provides a theoretical framework on which to base our understanding of animal-vectored nutrient transport. However, partly due to its high level of abstraction, there are few empirical tests of meta-ecosystem theory, and while we may label animals as important mediators of ecosystem services, we lack predictive inference of their relative roles and impacts on diverse ecosystems. Recently developed technologies and methods — tracking devices, mechanistic movement models, diet reconstruction techniques and remote sensing — have the potential to facilitate the quantification of animal-vectored nutrient flows and increase the predictive power of meta-ecosystem theory. Understanding the mechanisms by which animals shape ecosystem dynamics may be important for ongoing conservation, rewilding, and restoration initiatives around the world, and for more accurate models of ecosystem nutrient budgets. We provide conceptual examples that show how our proposed integration of methodologies could help investigate ecosystem impacts of animal movement. We conclude by describing practical applications to understanding cross-ecosystem contributions of animals on the move.

Introduction

Ecosystems and animal nutrient cycling

Flows of energy, nutrients, matter, and organisms crisscross landscapes worldwide, connecting intrinsically open ecosystems over space and time. The advancement of meta-ecosystem theory (Loreau *et al.* 2003; Leroux & Loreau 2008; Massol *et al.* 2011; Marleau *et al.* 2014) has aided our understanding of the influence of these spatial exchanges in both donor and recipient ecosystem functioning (Gounand *et al.* 2018b). Classic ecosystem theory holds that the spatial flow of organic and inorganic matter from source to recipient locations is largely passive, coming for example from *in situ* weathering of parent geological material, release from riverine sediments, wind-born dust, or rain-driven and snowmelt-driven run-off (Chapin *et al.* 2012). Nevertheless, there is growing appreciation that ecosystems also receive subsidies via animal movement (Vanni, 2002; Atkinson, Capps, Rugenski, & Vanni, 2017; Schmitz et al., 2018; Mcinturf, Pollack, Yang, & Spiegel, 2019). Such movement can result in an influx of new prey or predators to recipient locations, pulses of animal-transported nutrients in dung and urine, or the accumulation of organic matter via decomposition of carcasses deposited in recipient locations (henceforth, animal-vectored subsidies; Earl & Zollner 2017; Mcinturf *et al.* 2019). Whenever biotic—such as animal-vectored subsidies—or abiotic processes influence the structure and functioning of ecosystems, they are deemed ecosystem controls (Weathers *et al.* 2012). Theory predicts that animals can exert top-down control on ecosystems via subsidies, the magnitude of which could sometimes be equal to bottom-up (Leroux & Loreau, 2008; Allen & Wesner, 2016).

Increasingly, migratory populations of large bodied species are recognized for playing an especially important role as landscape-scale vectors of ecosystem subsidies (Bauer & Hoye 2014). Yet at the same time, across the globe, their populations are in decline (Wilcove & Wikelski 2008; Dirzo *et al.* 2014) and their movement is increasingly constrained by human activities (Tucker *et al.* 2018). The implications of such effects on top-down control over ecosystem functioning at broad spatial scales remain uncertain, but estimates suggest they can be substantial (Doughty *et al.* 2016). Hence, an important avenue of new research in ecosystem ecology is empirically resolving the relative importance of animal-vectored vs. passive subsides on ecosystem functioning. We are at an opportune scientific and technical juncture to begin synthesizing advances made in disparate fields.

78 The empirical challenge in understanding and attributing how much control animals exert over
79 ecosystem functioning is to quantify spatial flows of different kinds of animal-vectored subsidies
80 (i.e. excretion, egestion, carcass deposition, reproductive material). While theory is in place to
81 identify the different components that need measuring to obtain a coherent understanding of this
82 phenomenon (Leroux & Loreau, 2008; Earl & Zollner, 2017; Gounand et al. 2018; Schmitz et al.,
83 2018), it remains largely conceptual and offers few insights into how to operationalize empirical
84 measurement. Here, we address this limitation by offering a methodological road map that
85 discusses the various measurements that need to be integrated to develop a coherent picture of
86 the quantitative effects of animals on nutrient dynamics across ecosystems. There is now
87 unprecedented ability to characterize functional and structural properties of ecosystems
88 including topography, vegetation community composition, and habitat structure across vast
89 spaces (Bergen *et al.* 2009; Pettorelli *et al.* 2018). Likewise, movements of a wide range of
90 animal species can be monitored remotely (Kays, Crofoot, Jetz, & Wikelski, 2015; Wilmers et
91 al., 2015a), which can facilitate quantification of the net effects of animals on nutrient and
92 material transport. New DNA-based and isotopic analyses can resolve dietary nutrient sources.
93 Additionally, these nutrient sources and fates can be mapped spatially using nutrient distribution
94 modeling (West et al. 2010; Sitters *et al.* 2015; Leroux *et al.* 2017). While ripe for integration,
95 these methods and technologies continue to be deployed separately in research that examines
96 different components of animal movement and resource use within ecosystems. We show here
97 how these different methods can be used jointly to give a coherent, theory-driven understanding
98 of the ecosystem consequences of animal-vectored nutrient flows across landscapes.
99
100 **Materials and Methods**
101
102 **Meta-ecosystem models to understand animal-vectored subsidies**
103
104 The series of measurements we discuss are motivated by ecological theory on meta-ecosystem
105 dynamics. A multitrophic version of such an ecosystem model can be used to consider how
106 internal dynamics of ecosystems are connected by regional flows of materials and organisms
107 between the ecosystems (Marleau *et al.* 2014). To identify the processes that need to be
108 measured, we consider a model configured as a four trophic level food chain (Fig. 1), which
109 describes the dynamics of a single abiotic nutrient or element (N), a plant (P), a herbivore (H),
110 and a carnivore (C) within and between i local ecosystems that together create the meta-
111 ecosystem. This structure is intended for simple illustrative purposes to show how to relate the

112 dynamical systems model to the salient ecosystem and spatial processes that need to be
113 measured. The model can be made more complex by considering multiple nutrients to make it
114 stoichiometrically explicit (Leroux *et al.* 2012; Cherif & Loreau 2013) as well as multiple species
115 among trophic levels (McCann *et al.* 2005). Such granularity is beyond the scope of this paper.
116 Instead, we use this theoretical framework specifically to identify salient processes (and inherent
117 variables) that need to be measured to obtain a quantitative understanding the role of animals in
118 connecting and shaping the structure and functioning of local ecosystems across spatial scales.
119 The model reveals two salient processes that need to be considered: trophic interactions and
120 nutrient translocation and deposition. These two processes can be subdivided into five more
121 finely resolvable spatial components (Fig.1) that require detailed measurement. Hence, our
122 roadmap focuses on measuring these five components.
123
124 Trophic interactions within ecosystem i determine nutrient uptake and assimilation by
125 herbivores and carnivores (Fig. 1) that may vary in size, and habitat structure within an
126 ecosystem determines species spatial occurrences and the nature of their interactions (Schmitz
127 et al. 2017). Thus, an accounting of animal spatial interactions will require analysis of: (1) the
128 spatial extent and spatial grain size for analysis of the focal animal species and their
129 interdependent predators or prey/resources (i.e., spatial trophic food chain structure) in relation
130 to (2) the habitat structure within and between source and recipient local ecosystems. Moreover,
131 animals can be selective in their choice of resources, necessitating further spatial analyses of
132 (3) the resources selected by animals in source and recipient locations. Nutrient translocation
133 and deposition in ecosystems will depend on (4) the movement rates and directional spatial
134 flows of animal species and animal-vectored nutrients, and (5) the amounts and spatial
135 deposition rate of animal transported nutrients or materials, which can include the animals' own
136 body mass, waste products, reproductive material, and dispatched prey. Each of these
137 components can be measured with its own set of technologies (Fig. 2). We next provide a brief
138 review of these tools and of their potential use in the context of measuring animal-vectored
139 subsidies.
140
141 ***(1) Spatial trophic structure***
142 The first step to understanding how animal movement shapes ecosystems is to describe the
143 geographic domain over which focal animals roam and their trophic position within food chains,
144 including the scope of interactions with predators and resources (Fig. 2). These factors will
145 determine the geographic area and spatial grain of interest, the animals' habitat domain within

146 that area, and any ecosystem effects the animal could have within said domain through
147 cascading impacts on associated food webs. The habitat domain is the spatial extent of habitat
148 space used within a species' broader home range that is relevant to interspecific interactions,
149 e.g., areas used for foraging or avoiding predation (Schmitz *et al.* 2017).
150
151 Characterizing the spatial grains at which animals interact with other species and their
152 environment is crucial to understanding their distributions. Animal movement can be described
153 at fine spatial scales (e.g. responses to environmental resources such as foraging [see section
154 3]) or at coarser scales, such as their broad home range (introduced in section 4) (Mertes *et al.*
155 2020). Fine and coarse spatial grains have been termed "response grain" and "occupancy
156 grains", respectively (Mertes *et al.* 2020). To quantify an animal's response grain, first passage
157 time analysis can be employed. These are defined as the time it takes an animal to cross a
158 circle with a defined radius -- and as such scale dependent -- and can quantify the time duration
159 of an individual animal present within such a circle (Fauchald & Tveraa 2003). First passage
160 time allows estimating the spatial scale at which an individual animal focuses its search efforts
161 (i.e. by plotting variance in first passage time against the spatial scale, Fauchald & Tveraa 2003,
162 Fig. 2 bottom left panel). As such, hierarchical scales of animal habitat selection (Johnson 1980;
163 Mertes & Jetz 2017; Mertes *et al.* 2020) should drive the spatial resolution of remote sensing
164 products selected for analysis, not the other way around. This is especially relevant for animal
165 movement data, which are typically measured at finer spatio-temporal resolutions than data
166 from remotely sensed imagery (Remelgado *et al.* 2017, 2019). The habitat domain can be
167 measured using movement data by tracked individuals across a landscape, to calculate an
168 animals utilization distribution and probabilities of spatial locations associated with foraging and
169 migration behaviour across a landscape (Schmitz et al. 2017). A three-dimensional utilization
170 distribution could be estimated if vertical movements are tracked, e.g. movement in forest
171 canopies (McLean *et al.* 2016).
172
173 Species interactions can alter animal movement behaviour, which can in turn impact ecosystem
174 nutrient dynamics (Schmitz, Hawlena, & Trussell, 2010; Schmitz et al., 2018). Hence
175 consideration of the amount and spatial domain of animal vectored subsidies needs to consider
176 species embeddedness within food chains. Moreover, such consideration will enhance the
177 appreciation that animal vectored subsidies can trigger the rearrangement of food chains or
178 initiate novel trophic interactions (Montagano *et al.* 2019). Generally in this context, primary
179 producers have a trophic position of 1, primary consumers have a trophic position of 2,

secondary consumers have a trophic position of 3, and so on (Leroux & Loreau 2012). Yet there are many animals that occupy trophic positions between these discrete designations. For example, an omnivore may consume mostly primary consumers, but also some secondary consumers and therefore have a trophic position between 2 and 3 (Kelson et al 2020). We discuss how stable isotopes may be used to determine trophic position in section 3, which is important to resolve the nature and source of nutrients (e.g. largely plant-based vs. largely animal-based) that comprise subsidies (see section 3, Kelson et al. 2020).

(2) Habitat structure within and between source and recipient locations

Habitat structure and topographic features, within and between source and recipient locations, shape animal movement and nutrient transport within habitat domains (Leroux & Loreau, 2008; Gounand, Little, Harvey, & Altermatt, 2018; Schmitz et al., 2018). A spatially accurate characterization of these fundamental ecosystem attributes is key to understanding why, how, and where animals move over the landscape (Fig. 2). Earth observation via satellite, airborne, or drone imagery provides an important basis for developing such a characterization (Allan *et al.* 2018; Pettorelli *et al.* 2018). Remotely sensed landcover maps (i.e. forest, grassland, urban) can be used to delineate ecosystem boundaries and assess how these change through time. Advances of LiDAR (Light Detection and Ranging) make it possible to characterize vertical habitat structure and above-ground vegetation biomass within and across ecosystem boundaries. Furthermore, ecosystem productivity can be remotely measured and represented as vegetation indices (de Araujo Barbosa *et al.* 2015; Pettorelli *et al.* 2018). Topographic products, such as slope and topographic ruggedness (Amatulli *et al.* 2018), can resolve passive abiotic flow pathways to pinpoint where nutrients may end up on the landscape (e.g., flow down concave and into convex surfaces; Lindeman, 1942; Leroux & Loreau, 2008). Finally, LiDAR estimates are becoming available from the Global Ecosystem Dynamics Investigation (GEDI) mounted on the International Space Station, which measures forest structure and above-ground biomass density across the globe (Hancock *et al.* 2019)

More finely resolved structure can be obtained within habitats using hyperspectral technologies to collect hundreds of bands across the electromagnetic spectrum which distinguish unique ‘fingerprints’, referred to as spectral signatures for different kind of environmental features (Stuart *et al.* 2019). Such spectral signatures can be related to spatial patterns in plant functional diversity, vegetation elemental composition, and plant density (Knyazikhin *et al.* 2013;

Jetz *et al.* 2016; Schneider *et al.* 2017; Durán *et al.* 2019). Further, endmember extraction from multispectral imagery can be used to extract information on subpixel features, e.g., to identify signatures of water availability and abundance (Xie *et al.* 2016) .

Remotely sensed environmental products have different pixel resolution, commonly referred to as 'grain size'. Accessing and utilizing a plethora of remote sensing products is facilitated through geoprocessing tools such as Google Earth Engine, the Movebank Env-Data system, and the getspatialdata package (Pettorelli *et al.* 2014; Clark *et al.* 2016; Wegmann 2017). We list a collection of remote sensing products available to study ecosystem features across source and recipient locations in Table 1. Regardless of the product used, coherent understanding requires a grain size that aligns with the grain size of measurement of animal movement.

(3) Resources available to and selected by animals in source and recipient locations

Characterization of species habitat domains and structure can next be used to determine why animals move where they do, and what resources they use in source and recipient locations (Fig. 2). This can be accomplished using resource selection functions (RSF; Boyce *et al.* 2002) and step selection functions (SSF; Fortin *et al.* 2005). Generally, these functions associate environmental variables with locations used by individual animals and compare these with randomly generated points representing locations available to, but not used by, them (Michelot *et al.* 2019). Both methods estimate the probability of animal presence as a function of environmental covariates. SSF can be used further to predict future movement paths of animals, while RSF predicts spatial patterns of species occurrences over spatio-temporal scales (Michelot *et al.* 2019). Parameters from SSF can highlight whether animals avoid or are attracted to certain landscape features or resources. For example, SSF analysis reveals that in Etosha National Park, Namibia, elephants avoided areas with high tree biomass and were attracted to water sources and grassland patches with long term patterns of productivity (Tsalyuk *et al.* 2019). This could indicate that waterholes and grasslands receive more animal-vectored subsidies from elephants when compared to steep areas or dense forests. Such behavioural information would improve mechanistic predictions of nutrient redistribution by these wide-ranging megafauna which are known to play a large effect on regional carbon budgets (Berzaghi *et al.* 2018).

Resource selection is a hierarchical process (Courbin et al. 2013). While RSF and SSF are broad-scale measures of animal movement and habitat use, more finely resolved measures are needed to understand which food items are used by animals and their nutritional values within different locations. This understanding of animal food consumption and eventual processing and deposition (in body material, or as urine and fecal matter) can provide an understanding of where and how nutrients removed from donor ecosystems end up in recipient ecosystems. Additionally, the identity of consumed resources directly impacts the quantity and quality of nutrients deposited by animals (Subalusky & Post 2018).

Traditionally, dietary analyses have been performed based on physical dissection and microhistological analyses of stomach contents and fecal matter (Holechek et al., 1982, Joly, 2018). These methods, however, often require either opportunistic sampling of carcasses or destructive harvesting of live animals. DNA-metabarcoding provides an alternative, as it allows for the identification of materials consumed using fecal matter alone (Kartzinel *et al.* 2015; see Deagle et al., 2019 for an overview of DNA-metabarcoding methods). DNA-metabarcoding can shed important insights into the trophic ecology of source and recipient sites, and how consumption, and thus acquisition and transport of nutrients, can change in time and space (Pansu *et al.* 2019). For example, Atkins et al. (2019) combined GPS tracking data of bushbuck (*Tragelaphus sylvaticus*) with DNA-metabarcoding of fecal samples to show that herbivores occupy new habitats and forage on novel food items after extirpation of their predators. Bushbuck presence further changed plant community composition (demonstrated by comparing plant composition in exclosure and control plots) (Atkins *et al.* 2019). A playback experiment of predator sounds was able to revert bushbuck behaviour as they perceived predation risk (Atkins *et al.* 2019).

Stable isotopes, such as $\delta^{15}N$, $\delta^{13}C$, and $\delta^{18}O$, are also powerful tools in elucidating the trophic position (Ben-David et al., 2012), diet, and foraging location of a focal species in a non-invasive manner (Newsome *et al.* 2010; Kristensen *et al.* 2011). In general animals are enriched by ~3‰ of nitrogen and ~1‰ of carbon compared to what they eat, providing an estimate of trophic position (Post 2002). Therefore, trophic position can be discerned by using the isotopic signature (i.e. $\delta^{15}N$) of the consumer, of the ecosystem's primary producers, and a discrimination factor for the change in $\delta^{15}N$ enrichment between the ecosystem's trophic levels (Kelson *et al.* 2020). Using stable isotopes could also be a cost-effective way to identify the correct primers when conducting DNA-metabarcoding. For example, while white-tailed deer are

primarily herbivores, there is some evidence that they sometimes consume animal matter (Ellis-Felege *et al.* 2008). If stable isotopes revealed that deer have an omnivorous diet, DNA-metabarcoding could be used to discern exactly what animal material they consumed.

Stable isotopes can also be used to arrive at approximate estimates of diet. The isotopic signatures of food items (for example, C3 and C4 plants) often vary from one another. Therefore, examining the isotopic signature in bone, tooth, or feces has shown a successful method of coarsely understanding diet (Ben-David & Flaherty 2012). We recommend using stable isotopes to determine diet if DNA-metabarcoding is not financially possible, when using samples that have degraded and DNA-metabarcoding is no longer possible, or when a broad understanding of diet is sufficient for the question at hand For an extensive overview of using stable isotopes for ecological research, see Ben-David & Flaherty (2012), Hobson et al., (2019), and West *et al.* (2010).

(4) The movement rates and directional patterns of animal species and subsequently translocated nutrients

Animals can transport nutrients along and against biophysical gradients (Earl & Zollner, 2017; Mcinturf et al., 2019). Therefore, an understanding of animal movements will elucidate the nature and scale of consequent nutrient transfer (Fig. 2). Patterns of animal movement are directly related to the degree of connectivity (c_{ij}, Fig. 1) among local ecosystems as well as the movement rates of the animals (d_H, d_C, Fig. 1), which depend on the topography of the biophysical gradient. Advances in animal tracking technologies – dubbed biologging – offer possibilities to study internal (e.g., physiology, metabolism, reproduction) and external (e.g., social, environmental) drivers of animal movement (Nathan *et al.* 2008). Biologging enables quantification of the space-use and resource requirements of animals (Kays *et al.* 2015; Hays *et al.* 2019). The frequency with which animals visit certain areas (e.g., waterholes, fruit bearing tree, latrines) can be estimated via first passage times and recursive analysis (Mahoney & Young 2017; Bracis *et al.* 2018; Mertes *et al.* 2020).

Migrations are among the greatest examples of animal movement. Extensive research has explored their direction, length, and drivers (Dechmann *et al.* 2017; Somveille *et al.* 2018, 2019). Locations of an animal's track can be classified into specific movement strategies (i.e. disperser, migrator, nomad, central place forager) by segmentation methods (Bastille-Rousseau *et al.*

2016; Edelhoff *et al.* 2016), thus setting the stage for further analysis. Fine-scale animal behaviour (i.e. foraging, rest, travel) can be resolved in GPS data using behavioural change point analysis, expected-maximum binary clustering methods (Garriga *et al.* 2016), and state-space models (Patterson *et al.* 2008). A promising approach combining state-space and continuous time correlated random walk models (Michelot & Blackwell 2019) allows estimating behavioural states when using tracking data that are not sampled at regular time intervals, which is a common occurrence with biologging data.

Modern biologging tags are comprised of GPS units, accelerometers, and additional on-board sensors. Accelerometers estimate change in velocity of body postures over time and can classify behavioural states of wild animals, including hunting, killing, resting (Brown *et al.* 2013; Williams *et al.* 2014), and even scent marking (Bidder *et al.* 2020). Accelerometers also allow quantifying energy expenditure of animals and of specific behaviours. Common methods for such energy expenditure are two closely linked metrics; Overall Dynamic Body acceleration (ODBA) and Vectorized sum of the Dynamic Body Acceleration (VeDBA) (Wilson *et al.* 2006, 2020). We refer to Joo, Boone, Clay, & Patrick, (2019) for a review on animal movement analysis.

Movement ecology increasingly studies fine scale behaviours such as foraging or sociality (Strandburg-Peshkin *et al.* 2015; Bennison *et al.* 2018) that can determine fine scale spatial heterogeneity in nutrient release, a process not yet considered in the current literature on animal-vectored subsidies (Gounand *et al.* 2018b). At the same time, movement ecology rarely quantifies the scale, scope, and magnitude of animal-mediated nutrient transfers.

(***5) The amounts and deposition rate of animal transported nutrients or material***

Remote sensing offers quantitative measures of ecosystem structure at broad geographic scales. Collecting environmental data in the field provides detailed information that is essential and complementary to remote sensing to understand how local microclimate influences ecosystem dynamics and the distribution of animals and the resources they consume (Zellweger *et al.* 2018) (Fig. 2, right panel). Local observations identify how trophic interactions and community structure vary across habitats and environmental gradients. For example, one could measure a site's microtopography (slope, elevation, roughness), surrounding vegetation type and cover. The development of methods to account for such micro-environmental variation

is necessary to facilitate realistic representations of environmental conditions experienced by organisms. Downscaled remote sensing products show promise in providing such fine spatial detail (Maclean *et al.* 2019; Maclean 2020) and, once overlaid with animal locations, enable identification of habitats that are source and recipient locations for animal-vectored nutrient subsidies.

Animal vectored subsidies involve several processes, including consumption, excretion, egestion, and deposition of carcasses and parturition material (McSherry & Ritchie 2013; Subalusky & Post 2018; Wenger *et al.* 2019). For example in the Maasai Mara National Park Reserve, Kenya, every day Hippopotamus egest approximately 36 tons of wet biomass consumed in terrestrial ecosystems into the Mara river, approximately 15 % of the dissolved organic carbon loading from the upstream catchment (Subalusky *et al.* 2015). Also in the Mara, mass drowning of wildebeest contributes ~18% of the total dissolved organic carbon to the river ecosystem (Subalusky *et al.* 2017).

Standard biogeochemical methods, which include analyses that quantify elemental composition of materials, can be used to characterize the stoichiometry and total nutritional composition of food items (Vanni et al., 2002). Additionally, these methods can assess nutrient quality and quantity of animal-deposited material (e.g. egesta, excreta, carcasses) as well as the magnitude of nutrient influx into the surrounding environment through *in situ* measurement of various soil and plant properties (e.g., pH, soil texture, plant community composition, soil and plant nutrient content) at sites of animal activity (i.e. see Bump et al., 2009, Risch *et al.* 2020). Finally, given that stable isotope that come from animal tissues and excreta are isotopically enriched compared to their diet, enriched plant and soil materials surrounding the deposition can indicate deposition and use of animal-vectorized subsidies (Bump et al 2009a). Such enrichment may also help parse out passive from active subsidy input.

The tracing and mapping of spatial nutrient flows and deposition can be aided by using stoichiometric distribution models (StDMs). Such models predict the geospatial distribution of nutrients in forage items (Leroux *et al.* 2017). Similar to a species distribution model and point Poisson process models, a resource – in this case a forage item's nutrient content, either absolute (g/m^2; i.e. quantity) or relative (carbon:nitrogen ratio; i.e. quality) – can be defined as the abundance of a given nutrient (nitrogen, phosphorus or carbon) in location x_i which is predicted by a vector of environmental covariates $z(_{xi})$, their coefficients β_i, and an error term ε.

383 StDMs map the distribution of nutrients in ways that can be overlaid with animal spatial habitat
384 domains, to reveal how animals respond to spatial variation in resource distribution across a
385 landscape (Leroux *et al.* 2017) and may create microsites of heterogeneity where subsidies are
386 transported against stoichiometric gradients in the broader landscape.
387

388 **From diverse data sources, to a coherent message - A road map for integrating methods**

389 The current technological and methodological juncture allows us to go beyond understanding
390 the drivers of animal movement. We now have the tools to enhance our understanding of the
391 ecosystem-wide consequences of animal movements, generating inference on the timing,
392 directionality, and magnitude of animal mediated subsidies on both donor and recipient
393 ecosystems. Our road map identifies five steps needed to develop such a coherent picture and
394 is presented in Figure 2. We illustrate the value of this road map with two case studies, one of a
395 herbivore and one of a top predator, discussing how methods from these five steps can be
396 integrated to understand how animals on the move influence their ecosystems at fine scales.
397

398 ***Case Studies***

399 **Measuring nutrient loading by Galapagos tortoises during their seasonal migration**

400 Galapagos tortoises (*Chelonoidis porteri*) are ecosystem engineers due to their seed dispersal
401 abilities, trampling of vegetation, and transport of nutrients (Gibbs *et al.* 2010; Blake *et al.* 2012;
402 Ellis Soto 2020). Coupling tortoise tracking data with remotely sensed NDVI has identified that
403 giant tortoises undergo seasonally recurring migrations in response to averages of long-term
404 environmental conditions (Bastille-Rousseau *et al.* 2019). Behavioural observations revealed
405 that tortoises preferentially feed on an agricultural crop (guava, *Psidium guajava*) when
406 migrating from higher to lower elevation areas (Blake *et al.* 2015). By preferentially feeding on
407 guava in agricultural areas, tortoises translocate guava seeds and nutrients into other habitats
408 during their downslope migration, resulting in the spread of guava as an invasive species and
409 posing a challenge to the maintenance of natural plant communities in Galapagos National Park
410 (Ellis-Soto *et al.* 2017). The distribution of guava has been mapped through local vegetation
411 sampling plots and drone and remote sensing imagery (Rivas-Torres *et al.* 2018; Laso *et al.*
412 2019). Coupling tortoise movement patterns, resource selection, and habitat structure makes it
413 possible to quantify giant tortoise vectored nutrient transfer in Santa Cruz Island, Galapagos.

Santa Cruz Island shows a distinct zonation of vegetation. Dry xerothermic plants dominate the low elevations of the national park, with rainfall and the presence of introduced species (e.g., guava) increasing with elevation (Itow 2003). During their downslope migration, adult tortoises can migrate from agricultural areas at higher elevations into the lowlands of the Galapagos National Park (identified through net square displacement, Suppl. Material 1). Overlapping home ranges (Winner *et al.* 2018) of tagged tortoises located in the lowlands inside the national park can reveal core areas of tortoise utilization distributions, providing a picture of spatial trophic structure. Using this core area, a stratified sampling of surrounding vegetation, soil samples, and description of microtopography can help understand nutrient composition, microbial activity and abiotic properties of selected areas in an attempt to further characterize habitat structure. Such measurements could be compared with samples obtained in areas where tortoises are absent, serving as a control plot (i.e. via exclosures or randomly selecting points outside the tortoise core area) to further isolate animal impacts on biogeochemical cycles and ecosystem fluxes.

Given their different photosynthetic pathways (C3 and CAM, respectively) guava likely contains a different isotopic signature (Sage & Zhu 2011) than the tortoises' most-consumed xerothermic plant at lower elevations of the National Park, the *Opuntia echios* cacti. Thus, stable isotope analysis of fecal matter containing guava could disentangle contributions by tortoises during their migrations from a donor ecosystem (agricultural areas) to a recipient ecosystem (lowlands of the Galapagos National Park) and make spatially explicit predictions of this animal-vectored nutrient flux. Finally, all of these measures can be combined to develop a nutrient budget for the lowland ecosystem of the Galapagos National Park and include the downslope migration of *C. porteri* as the mechanism for vectored subsidy (Fig. 3, Fig. 4). Such nutrient ecosystem budgets often attempt to quantify the flows of nutrients through different pools providing an understanding of how these flows may impact ecosystem functioning (Loreau & Holt 2004). Coupling an assessment of nutrient loading with past and present tortoise population numbers could provide a baseline for ongoing conservation initiatives aimed at restoring degraded island habitats by reintroducing giant tortoises to act as ecosystem engineers (Gibbs *et al.* 2010; Hunter *et al.* 2020). We provide the necessary code to replicate steps detailed in this conceptual tortoise example (Suppl. Material 1).

Quantifying how *Canis lupus* creates landscape heterogeneity through prey hunting and killing

Predators can have profound cascading impacts on ecosystem nutrient dynamics mediated by their effects on prey mortality and space use (Fig. 5). For example, the hunting behaviour of wolves (*Canis lupus*) and the subsequent deposition of prey carcasses may create nutrient hotspots across a landscape, creating heterogeneity in nutrient distribution as carcasses decompose at sites with high rates of predation (Bump *et al.* 2009a; Joseph *et al.* 2009). To explore this, a recursive analysis (Bracis *et al.* 2018) based on how often animals return to specific landscape areas defined by a determined circular radii — which could be chosen based on grain sizes identified from First Passage Times (Mertes *et al.* 2020) — display where and how collared wolves revisit areas in their range. Coupling accelerometer and animal location data can identify hunting, eating, and killing by predators in the wild through behavioural classification and ground-truthing GPS clusters at presumed kill sites (Williams *et al.* 2014; Wang *et al.* 2015). These methodologies can pinpoint the exact coordinates and time of hunting and killing events and therefore quantify the movement of the nutrients through these processes. Once a carcass's presence is identified, camera traps can provide insight into how the predation behaviours of top predators may have cascading impacts on subsidizing scavengers and invertebrates (Perrig *et al.* 2017; Cunningham *et al.* 2018).

Using a stratified sampling scheme of plant and soil characteristics, it is also possible to quantify the nutrients deposited by the carcasses, explore the spatial diffusion of those nutrients, and estimate how long those nutrients stay in the local system before leaching away or being scavenged. These sites can be compared to measurements collected in randomly selected points, which may serve as a control treatment. Assessing the plant community composition and cover will help identify whether killing behaviour of predators leads to changes in plant composition, while soil samples collected below carcasses can be used to compare microbial activity and nutrient availability between carcass and control sites (Metcalf *et al.* 2016; Risch *et al.* 2020). Both total soil and plant nutrient concentration as well as enriched $\delta^{15}N$ in plant and soil samples can be used to identify and quantify the impact of this animal vectorized subsidy (Bump *et al.* 2009b; Holtgrieve *et al.* 2009; Barton *et al.* 2016). This conceptual study design highlights how predators could concentrate nutrients at kill sites, contributing to landscape heterogeneity with potential knock-on effects on scavenger and plant community distribution. Such knowledge is key for understanding the ecosystem consequences of predator loss (Ripple *et al.* 2014).

Moving forward: Future Directions

481
482 We have illustrated how individual studies may productively integrate disparate fields and tools
483 to address specific questions about animal-vectored nutrient subsidies within a study system.
484 These disciplines and methodologies can be united to address larger questions about animals
485 and nutrient transport in diverse systems and at multiple scales. Below, we identify the next
486 frontiers in ecological research, which can be resolved through synergistic research linking
487 animal movement and nutrient transport.
488
489 **Improve tracing and mapping of animal vectorized subsidies**
490
491 We see opportunities to improve predictions of animal vectored subsidies based on advances of
492 Species Distribution Modeling (SDM) such as incorporating a priori expert knowledge (Merow *et*
493 *al.* 2016) and joint species distribution modeling (jSDM) (Pollock *et al.* 2014). Such expert
494 knowledge can represent species geographic ranges or species specific elevational ranges as
495 known from field guides. Expert knowledge could enter StDM's in the form of a statistical offset
496 which has been shown to improve model predictions from SDM's (Ellis-Soto *et al.* n.d.; Merow
497 *et al.* 2016). Such offset is independent of the predictor variable (nutrient quantity or quality) and
498 would provide *a priori* expectations of how resources are distributed across a study region
499 rather than assuming an equal likelihood for each cell in a landscape. StDMs could also
500 incorporate soil nutrient maps derived from coarse scale remote sensing (soilgrids database) as
501 an offset reflecting the a priori expectation of a nutrient concentration in a cell. We refer to
502 Merow, Wilson, & Jetz, (2017) for specifics about deploying offsets in logistic regression, but the
503 motivation is that expert information can provide estimates that are complementary to point
504 estimates that could predict nutrient quantity (g/m^2) or nutrient ratios (C:N).
505
506 jSDMs predict spatial occurrences of entire communities of species, rather than distributions of
507 single species, as in SDM (Pollock *et al.* 2014). StDMs could be similarly extended to consider
508 the distribution of multiple individual nutrients (not just their ratios). Particularly, we see potential
509 in adapting jSDM developments from Generalized joint attribute modelling (Clark *et al.* 2017),
510 Bayesian Ordination and Regression Analysis of Multivariate Abundance Data (Hui 2016), and
511 Spatial factor analysis (Thorson *et al.* 2015) to develop joint StDM. Such jStDM could be
512 overlapped with autocorrelated kernel density estimators (Fleming *et al.* 2015) to investigate
513 how animal space use relates to spatial stoichiometry.
514

We see potential in building upon mechanistic models of animal movement and seed and nutrient dispersal to map the distribution and magnitude of animal vectored subsidies (Bampoh *et al.* 2019; Kleyheeg *et al.* 2019; van Toor *et al.* 2019). These models couple animal movement and gut retention with remotely sensed land cover information to create spatially explicit maps of nutrient dispersal. Such models have provided insights about how extinct and extant animals have influenced nutrient translocations at coarse spatial scales across the globe (Doughty *et al.* 2016; Doughty 2017). These estimates could be refined by incorporating movement models such as allometric random walks (Hirt *et al.* 2018) and individual based movement models (Bampoh *et al.* 2019), rather than coarser lateral diffusion movement models which have hitherto been used.

Estimating animal-mediated nutrient translocation within a home range

Core areas where individuals within groups or populations might have strongest animal-vectorized subsidies effects can be identified using home range overlap indices between individuals. Such overlap indices may be simple convex hulls around individual home ranges to describe population ranges or more sophisticated utilization distributions based on bias-corrected Bhattacharyya coefficient as shown by Winner et al., (2018). RSFs of individuals with overlapping home ranges could reflect how these animals utilize resources across long-term timescales.

Behavioural pattern identification could characterize a suite of animal behaviours within home ranges (e.g., forage, rest, fight, prey capture; Kie *et al.* 2010) to identify how animals transport nutrients at shorter timescales (Fig. 3). Revisitation and accelerometer analysis hold promise to identify feeding sites, scent marking sites or latrines (Bracis *et al.* 2018; Bidder *et al.* 2020). High urine concentration at latrines could influence plant communities, soil nutrient loads, and microbial communities, constituting a nutrient hotspot. Other methods estimate nest locations and reproductive output from telemetry data (Picardi *et al.* 2019; Bidder *et al.* 2020). Such behavioural identification can identify where animals assimilate or excrete resources and under which conditions animals act as nutrient sources (bring more nutrients in than they consume, i.e. high urine concentration at latrines or high offspring mortality at nests) or sinks (have a negative net effect on nutrient concentrations at the site). Calculating integrated step selection functions (Avgar *et al.* 2016) using exclusively animal locations that were associated with foraging behaviour (Nathan *et al.* 2012) could identify such nutrient sources. Habitat selection

549 could be explored at fine detail by using drones to create study-site specific landcover maps
550 (Strandburg-Peshkin *et al.* 2017).
551
552 **Animal-vectored subsidies in the Anthropocene**
553
554 In human-modified landscapes, animals find themselves crossing a matrix of fragmented
555 habitats and human pressures (i.e. population density, infrastructure and agricultural areas) that
556 vary in permeability. Human modification of landscapes, such as urban development of roads or
557 C4 plant monocultures for agriculture, can alter diet and nutrient transfer by animals (Magioli *et*
558 *al.* 2019). For example, Roe deer (*Capreolus capreolus*) in central France routinely act as
559 vectors for large quantities of artificially-introduced nitrogen, which they obtain by foraging in
560 agricultural areas, which are deposited near resting sites in forested areas (Abbas *et al.* 2012).
561 In New Mexico, USA, snow geese (*Chen caerulescens*) perform daily foraging trips from wildlife
562 refuges to agricultural areas to feed on corn and alfalfa. This nutrient translocation was shown
563 to increase phosphorous nutrient loadings up to 75% in wetland ponds (Kitchell *et al.* 1999).
564 Thus, animals can link natural areas with human modified landscapes and modify the nutrient
565 budgets of ecosystems.
566 Mechanistic models of animal vectored subsidies (Bampoh *et al.* 2019) could predict
567 how nutrient budgets of ecosystems are altered by the removal of species, such as large bodied
568 animals (Bello *et al.* 2015; Sobral *et al.* 2017), or specific individuals (i.e. elephant bulls in
569 Kruger National Park (Davies & Asner 2019)), or animal introductions (goat introduction in the
570 Galapagos (Bastille-Rousseau *et al.* 2017)). These models could identify causal links between
571 ecosystem functioning and animal mediated subsidies. Such knowledge would provide evidence
572 to rewilding initiatives aiming to restore lost ecosystem services through animal reintroductions
573 (Falcon Wilfredo & Hansen 2018; Lundgren *et al.* 2018).
574
575 **Conclusion**
576
577 Understanding how animals move through both natural and human dominated landscapes to
578 influence ecosystem properties and functions is in need of concerted analysis. To this end, we
579 have provided a methodological road map that draws together methods of analysis across
580 disciplinary fields. We show how, when combined, these can lead to integrative, coherent
581 understanding of how animal vectored subsidies drive spatial ecosystem structure and
582 functioning. It is through the integration and collaboration of disciplines that we can address and

understand the importance of this type of nutrient transport in a spatially explicit manner. We hope that the introduced methodological roadmap will facilitate empirical studies that quantify how much the fluxes of nutrients from one pool to another across landscapes can be attributed to animal-vectored subsidies.

Acknowledgments: We thank Kevin Winner, Steven Blake, Brett Jesmer, Ruth Yvonne Oliver and Nathalie Sommers for helpful feedback on this publication. The authors declare no competing interests. This work was supported by a Rufford Small Grant to D.E.S. and a GRFP to K.M.F. under NSF grant no. DGE-1752134. O.J.S. acknowledges funding from the Yale School of the Environment. The authors declare no conflict of interest. All authors conceived the ideas and designed methodology; D.E.S conducted all necessary data analysis; D.E.S and K.M.F. led the writing of the manuscript. D.E.S. and O.J.S. created the figures of the manuscript. All authors contributed to this work and provided final approval for publication.

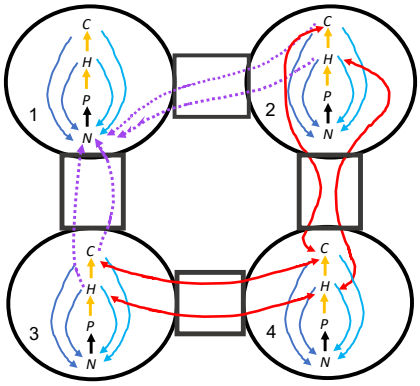
Figures

$$\frac{dN_i}{dt} = \mathrm{I} - \mathrm{E}N_i - \mathrm{U}(N_i, P_i) + \epsilon \mathrm{M}(P_i) + \chi_H \mathrm{L_H}(H_i) + \chi_C \mathrm{L_C}(C_i) + \gamma_H \mathrm{W}(P_i, H_i) + \gamma_C \mathrm{W}(H_i, C_i) + \mathrm{d_H} \sum_{j=1}^{n} c_{ij}\gamma_H \mathrm{W}(P_j, H_j) + \mathrm{d_C} \sum_{j=1}^{n} c_{ij}\gamma_C \mathrm{W}(H_j, C_j)$$

$$\frac{dP_i}{dt} = U(N_i, P_i) - \mathrm{M}(P_i) - \mathrm{W}(P_i, H_j)$$

$$\frac{dH_i}{dt} = (1-\gamma_H)\mathrm{W_H}(P_i, H_i) - \mathrm{L_H}(H_i) + \mathrm{d_H} \sum_{j=1}^{n} c_{ij} H_j - \mathrm{W_C}(H_i, C_i)$$

$$\frac{dC_i}{dt} = (1-\gamma_C)\mathrm{W_C}(H_i, C_i) - \mathrm{L_C}(C_i) + \mathrm{d_C} \sum_{j=1}^{n} c_{ij} C_j$$



Ecosystem model component	Spatial measurements needed (sections)
Trophic interactions within and between local ecosystems	(i) The spatial extent and spatial grain size of animal movement (ii) Habitat structure shaping where animals move (iii) Available and selected resources
Nutrient translocation and deposition due to within-ecosystem carcass and nutrient deposition and between ecosystem nutrient deposition	(iv) Movement rates directional spatial flow of animals and nutrients (v) Amount of animal carcass and nutrients deposited spatially

Figure 1: Meta-ecosystem model characterizing the trophic structure and dynamics of nutrients (N), plants (P), herbivores (H) and carnivores (C) within and between four local ecosystems. In the model carnivore abundance changes as a function of assimilated intake of herbivore biomass within ecosystem i (1- γ_C)$W_C(H_i, C_i)$, where γ_C is the degree of inefficiency in assimilation, loss due to natural mortality at rate $L_C(C_i)$, and gain due to migration from another local ecosystem $d_C \sum_{(j=1)} c_{ij}C_j$, where d_C is the movement rate of a carnivore and c_{ij} is the spatial connectivity between two local ecosystems (where high values reflect high connectivity and hence high ease of flow). Herbivore abundance changes as a function of assimilated intake of plant biomass (1- γ_H)$W_H(P_i, H_i)$, loss due to natural mortality at rate $L_H(H_i)$, loss due to predation at rate $W_C(H_i, C_i)$ and gain due to migration from another local ecosystem $d_H \sum_{(j=1)} c_{ij}H_j$. Plant biomass changes as a function of nutrient uptake at rate $U(N_i, P_i)$, loss due to senescence at rate $M(P_i)$ and herbivory at rate $WH(P_i, H_i)$. Finally nutrient abundance changes due to global inputs I from weathering of parent geological material, release from riverine sediments, wind-born dust, or rain-driven and snowmelt-driven run-off, loss due to leaching out of the ecosystem EN_i and plant uptake at rate $U(N_i, P_i)$, and

additions due to recycling of plant material $\epsilon M(P_i)$, herbivore and carnivore carcasses at rates $\chi_H L_H(H_i) + \chi_C L_C(C_i)$, and release of unassimilated consumption by herbivores an carnivores (e.g. egesta) at rates $\gamma H W(P_i, H_i) + \gamma C W(H_i, C_i)$. Local ecosystem nutrient budgets are also subsidized by unassimilated nutrient release as herbivores and carnivores migrate among local ecosystems $d_H \sum_{(j=1)} c_{ij} \gamma_H W P_j, H_j) + d_C \sum_{(j=1)} c_{ij} \gamma_C W(H_j, C_j)$. These components describing nutrient dynamics can ultimately be grouped according to two broad spatial processes: spatial trophic interactions and spatial nutrient translocation and deposition. These spatial processes can be further decomposed into five subprocesses that require different methodologies to measure. A coherent picture of spatial nutrient dynamics can be developed when data from the five subprocess measurements are combined into a dynamic map that portrays spatial animal movement and nutrient flow in relation to the biophysical features within and between local ecosystems across a landscape. Model and illustration adapted from Marleau et al. (2014).

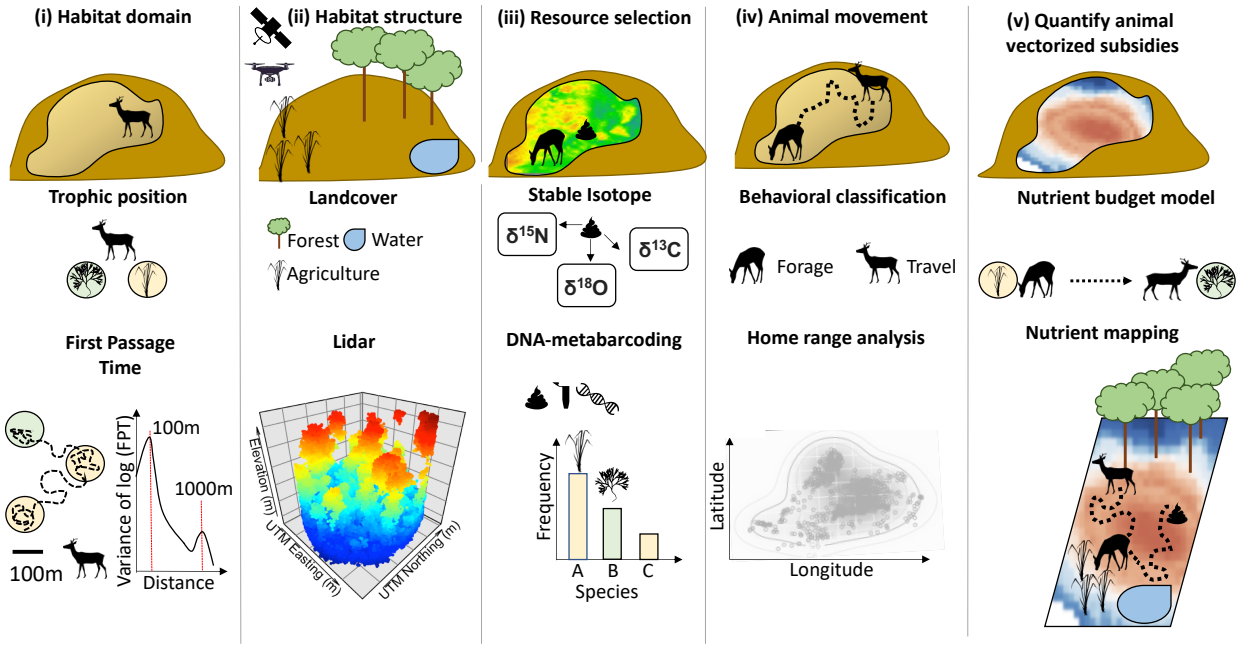
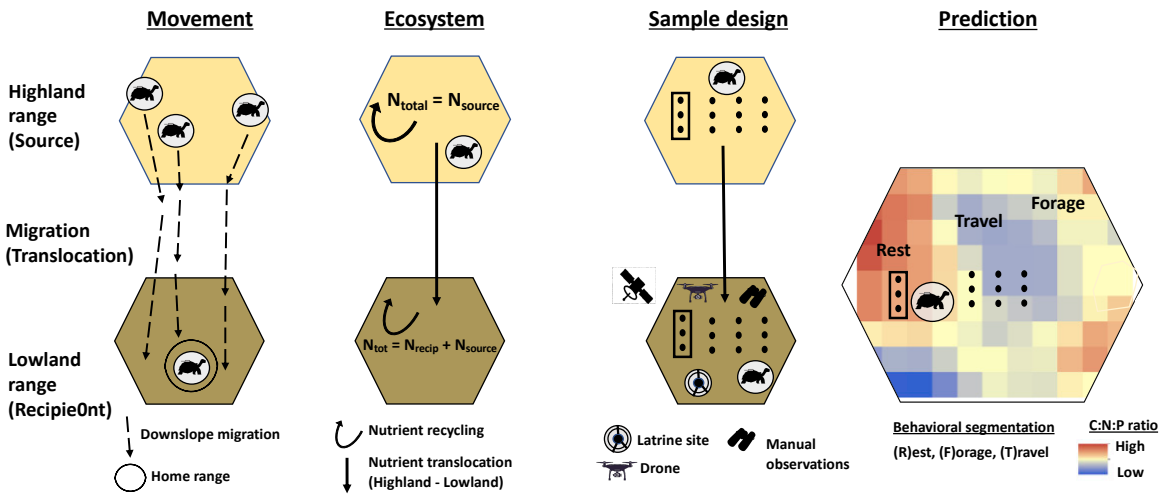


Figure 2: Conceptual demonstration of integrating different disciplines (sections 1,-4) for quantifying animal vectorized subsidies across a landscape (section 5). (i) The habitat domain helps understand the trophic position. In our hypothetical example, a roe deer (*Capreolus capreolus*) travels across yellow patches containing agricultural areas and a green patch with forested area. A first passage time analysis would reveal the scale of roe deer selection to be

strongest at approximately 100m. With this knowledge we can proceed on estimating the trophic positions and interactions at that scale, choosing subsequent remote sensing products at the same spatial scale. If we were to select a scale of 1000m – where extensive remove sensing products are available (Table 1), we would see a weaker response of animals selecting their environment. (ii) The habitat structure of our study region can be identified through remotely sensed products, such as landcover maps. In this example, agriculture and water would be convex ecosystems and likely receive abiotic inputs from forest leaves (concave ecosystem) due to runoff. Convex and concave can be defined with elevation products or with Lidar to obtain a 3D matrix of the environment across which animals navigate (i.e. against elevation gradients during animal upslope movement). Lidar imagery was created using the rLidar and rGedi packages. Habitat and environmental information (ii) can then be used as response variables to understand how animals select and avoid resources and associated habitat structures, using resource selection. Such resource use map is displayed in (iii) with green colors indicating hotspots of habitat selection by our animal. Further, DNA-metabarcoding (iii) of animal fecal matter in the study region can reveal the trophic position and the resources consumed and deposited at great taxonomic detail. Understanding the stoichiometry of resources consumed through stable isotopes (iii) provides insights into the composition and type of nutrients that are moved by animals. (iv) Detailed information of roe deer movement obtained through GPS collars reveals detailed space use of individuals (i.e. their home range) which can be overlaid with the habitat structure of the landscape. Behavioural change point analysis (iv) based on movement data could classify animal behaviour into foraging and travel. Coupling behavioural classification and animal movement with faecal sampling for DNA-metabarcoding and stable isotope can reveal sources (foraging locations) and sinks (excretion locations) of roe deer-vectorized subsidies. (v) Integrating the different methodologies described, allows quantifyng animal-vectorized subsidies through spatial modelling such as Stoichiometric Distribution Models (section v; Leroux et al. 2017). Importantly, coupling such models with abiotic nutrient deposition rates (e. g. leaching), allows us to contextualize the magnitude and direction of biotic nutrient deposition rates. We could thus begin including animal vectorized subsidies into ecosystem nutrient budget models (in our hypothetical case the roe deer brings nutrients from the agricultural matrix into the forest ecosystem). Integrating these steps (i-v) allows us to paint a picture of the landscape in which the ecological consequences of moving animals are incorporated into cross-ecosystem models. Silhouettes were obtained from the PhyloPic website (phylopic.org).



669

670 **Figure 3:** Integration of diverse disciplines and methodologies to characterize animal-vectored
671 subsidies; in this case nitrogen recycling and translocation by Galapagos tortoises (*Chelonoidis*
672 *porteri*) in time and space. (a) Movement determines the timing and direction of animal arrival
673 and departure of ecosystems. (b) Ecosystem nutrient budgets incorporate inputs from outside
674 ecosystem boundaries, such as animal-vectorized subsidies. (c) Careful sample design helps
675 elucidating drivers and predict consequences of nutrient transport by animals. Coupling large
676 extent (remote sensing, drones) with local field measurements (manual, drones) and animal
677 population estimates, allows (d) quantifying magnitude and flow of animal-vectorized subsidies
678 in a spatially explicit manner and estimate what proportion of total nutrients are being mobilized
679 by animals on the move. Tortoise silhouettes were obtained from the PhyloPic website
680 (phylopic.org).

681

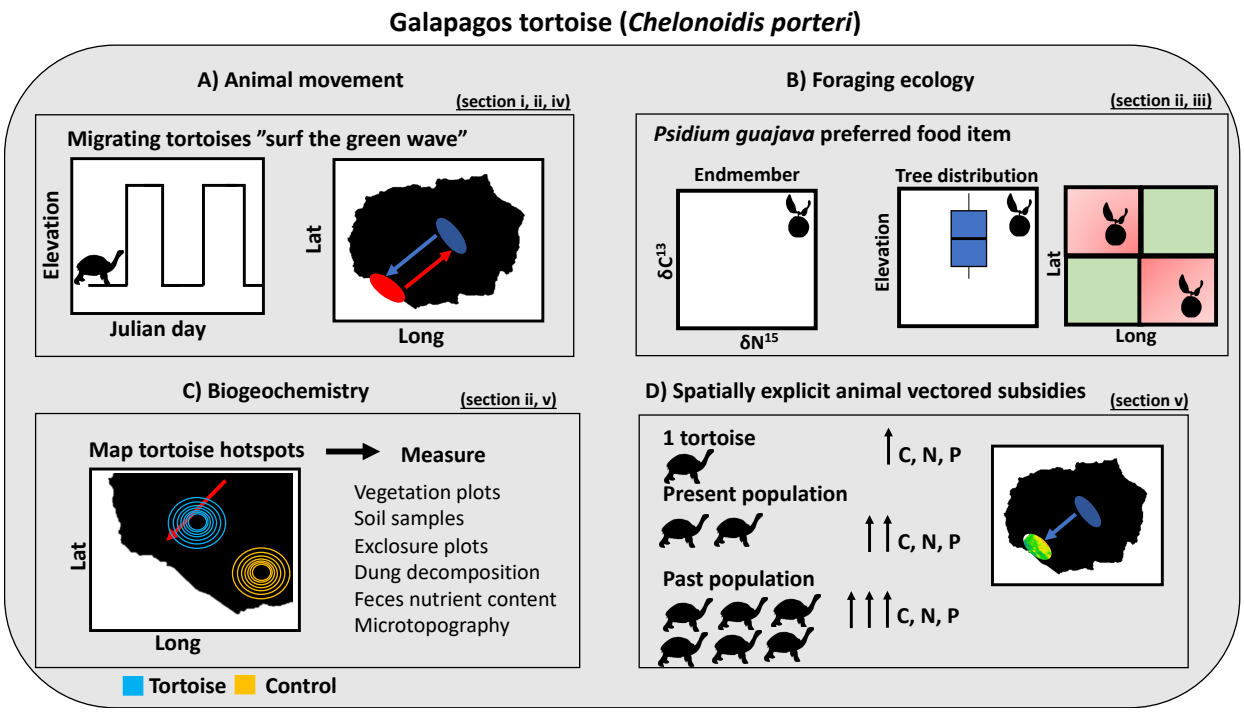


Figure 4: Conceptual example of studying nutrient transport of giant tortoises (*Chelonidis porteri*) in Santa Cruz Island. Integrating known movement patterns and foraging behaviour of this species with the distribution and nutritional composition of food items, it is possible to design an experiment to estimate the influence of tortoises transporting nutrients to the Galapagos National Park boundaries during their downslope migration. Silhouettes were obtained from the PhyloPic website (phylopic.org).

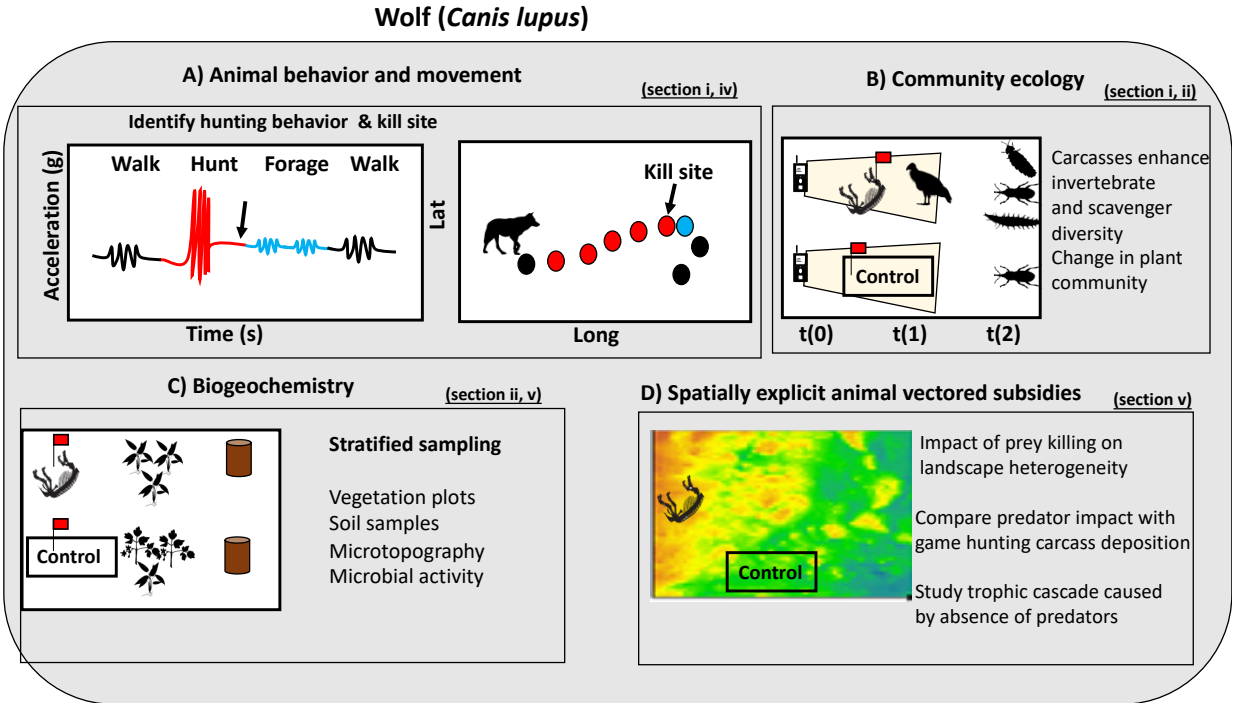


Figure 5: Conceptual example to identify killing sites of Wolfes (*Canis lupus*) with biologging technologies and quantify how predators drive landscape heterogeneity. Identifying kill sites allows studyng how carcass presence affects local biogeochemistry and community composition when compared to control locations. Silhouettes were obtained from the PhyloPic website (phylopic.org).

Table 1: Collection of applicable remote sensing products for animal mediated subsidies. We elucidate the spatio-temporal resolution and grain size of these products.

Appendix – Supplementary Material

Supplementary Material 1: Necessary code to perform movement ecology and remote sensing analysis of the Galapagos tortoise example

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