Understanding anthropogenic impacts on zoogeochemistry is essential for ecological restoration

Running title: Zoogeochemistry in ecological restoration

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Abstract

Ecological restoration is critical for climate and biodiversity resilience over the coming century. Today, there is strong evidence that wildlife can significantly influence the distribution and stoichiometry of elements across landscapes, with subsequent impacts on the composition and functioning of ecosystems. Consequently, any anthropogenic activity that modifies this important aspect of zoogeochemistry, such as changes to animal community composition, diet, or movement patterns, may support or hinder restoration goals. It is therefore imperative that the zoogeochemical effects of such anthropogenic modifications are quantified and mapped at high spatiotemporal resolutions to help inform restoration strategies. Here, we first discuss pathways through which human activities shape wildlife-mediated elemental landscapes and outline why current frameworks are inadequate to characterize these processes. We then suggest improvements required to comprehensively model, validate, and monitor element recycling and redistribution by wildlife under differing wildlife management scenarios and discuss how this might be implemented in practice through a specific example in the southern Kalahari Desert. With robust ecological forecasting, zoogeochemical impacts of wildlife can thus be used to support ecological restoration and nature-based solutions to climate change. If ignored in the restoration process, effects of wildlife on elemental landscapes may delay, or even prevent, restoration success.

Keywords

Biogeochemistry, conservation, ecosystem services, ecosystem restoration, nature-based solutions, rewilding, wildlife management, zoogeochemistry

Implications for practice

- Wildlife play a key role in recycling and redistributing nutrients and pollutants across landscapes, but human activities can modify these important zoogeochemical processes.
- Current modelling frameworks are inadequate to characterize anthropogenic impacts on zoogeochemistry in restoration projects. Improved models are needed, which resolve individual-scale idiosyncrasies, dynamic feedbacks, multi-element interactions, and integration with other ecological processes.
- Emerging viewpoints and technologies offer exciting opportunities to quantify and monitor element distributions and stoichiometries by wildlife at fine spatiotemporal scales.
- Together, advancements outlined here can help align wildlife management decisions to support restoration attempts in ways that are more effective, efficient, ethical, and natural.

Introduction

Terrestrial wildlife modulate carbon (C) and other element cycles through myriad pathways, referred to as zoogeochemical processes (*sensu* Schmitz et al. 2018). For example, animals can directly accelerate and decelerate biogeochemical cycles by altering the quantity and quality of resource flows to the soil pool via consumption, digestion, defecation, and urination (Hobbs 1996; Schrama et al. 2013). Similarly, animals can indirectly modulate element cycles by changing abiotic and microbial drivers, such as through altered fire regimes and soil compaction (Schrama et al. 2013; Schmitz et al. 2018). This ability of wildlife to mobilize key nutrients, as well as harmful pollutants, has been shown to influence many ecosystem processes including plant productivity, carbon storage, and community structure (Subalusky & Post 2018; McInturf et al. 2019, Ferraro et al. 2022). As a result, wild animals are increasingly recognised for their many zoogeochemical impacts and as potentially important agents within nature-based solutions to climate change (Malhi et al. 2022).

Recently, the United Nations issued a rallying call for the revival of ecosystems throughout the world as part of its Decade on Ecosystem Restoration, providing opportunities for large-scale ecosystem restoration (Svenning, 2020). However, whether the zoogeochemical impact of restored wildlife populations facilitates or impedes restoration goals is dependent upon local abiotic conditions, ecological context and management actions (figure 1). To date, wildlife restoration has been subject to significant comment and debate, which far outstrips scientific research (Lorimer et al. 2015). It is essential that future conservation practice is instead underpinned by robust scientific evidence, including the zoogeochemical impacts of wildlife communities. Here, we argue that particular attention must be paid to the role of human activities in altering the zoogeochemistry of nutrient and pollutant cycles in restoration projects. Human activities can modify zoogeochemical processes in a multitude of ways. For example, in oligotrophic landscapes where animal movement is restricted, wildlife managers often maintain wildlife health by providing supplementary resources (Murray et al. 2016), thereby augmenting wildlife diets, population densities, and concomitant impacts on ecosystem fertility and stoichiometry. By contrast, in eutrophic landscapes, issues relating to excessive nutrient loading and stoichiometric imbalances preside. In this case, wildlife may thwart restoration attempts by importing elements from eutrophic surrounding landscapes such as crop fields and water sources (Post et al. 1998; Abbas et al. 2012). Given the myriad ecological impacts of elemental recycling and redistribution by animals (Subalusky & Post, 2018), it is imperative that this aspect of zoogeochemistry is accurately quantified and mapped at high spatiotemporal resolutions during ecological restoration projects (Ellis-Soto et al. 2021).

In this article, we first outline various ways in which human activities disrupt element recycling and redistribution by wildlife. We then explain why current frameworks that attempt to characterize these processes are inadequate to inform restoration projects, and suggest necessary improvements to comprehensively model, validate and monitor zoogeochemistry across multiple trophic levels (soils, plants, animals). Whilst we focus on the role of animals in directly recycling and redistributing elements across landscapes via their excreta and carcasses (Doughty et al. 2016; le Roux et al. 2020; Villar et al. 2021), we recognise that wildlife have many additional indirect effects on biogeochemical cycles, including through ecosystem engineering, trampling, and seed dispersal (see Bello et al. 2015; Schmitz et al. 2018; Malhi et al. 2022). Further, while most zoogeochemical research to date focuses on limiting nutrients (e.g. nitrogen [N], phosphorus [P]), we extend our review to include pollutants (e.g. arsenic [As], lead [Pb]), as either can critically reshape the composition and function of ecosystems (Schlesinger & Bernhardt, 2013; Kraus et al. 2020).

With robust scientific forecasting, wildlife can thus be used to support ecological restoration and nature-based solutions to climate change (figure 1). If ignored in the restoration process, effects of wildlife on elemental landscapes may delay, or even prevent, restoration success.

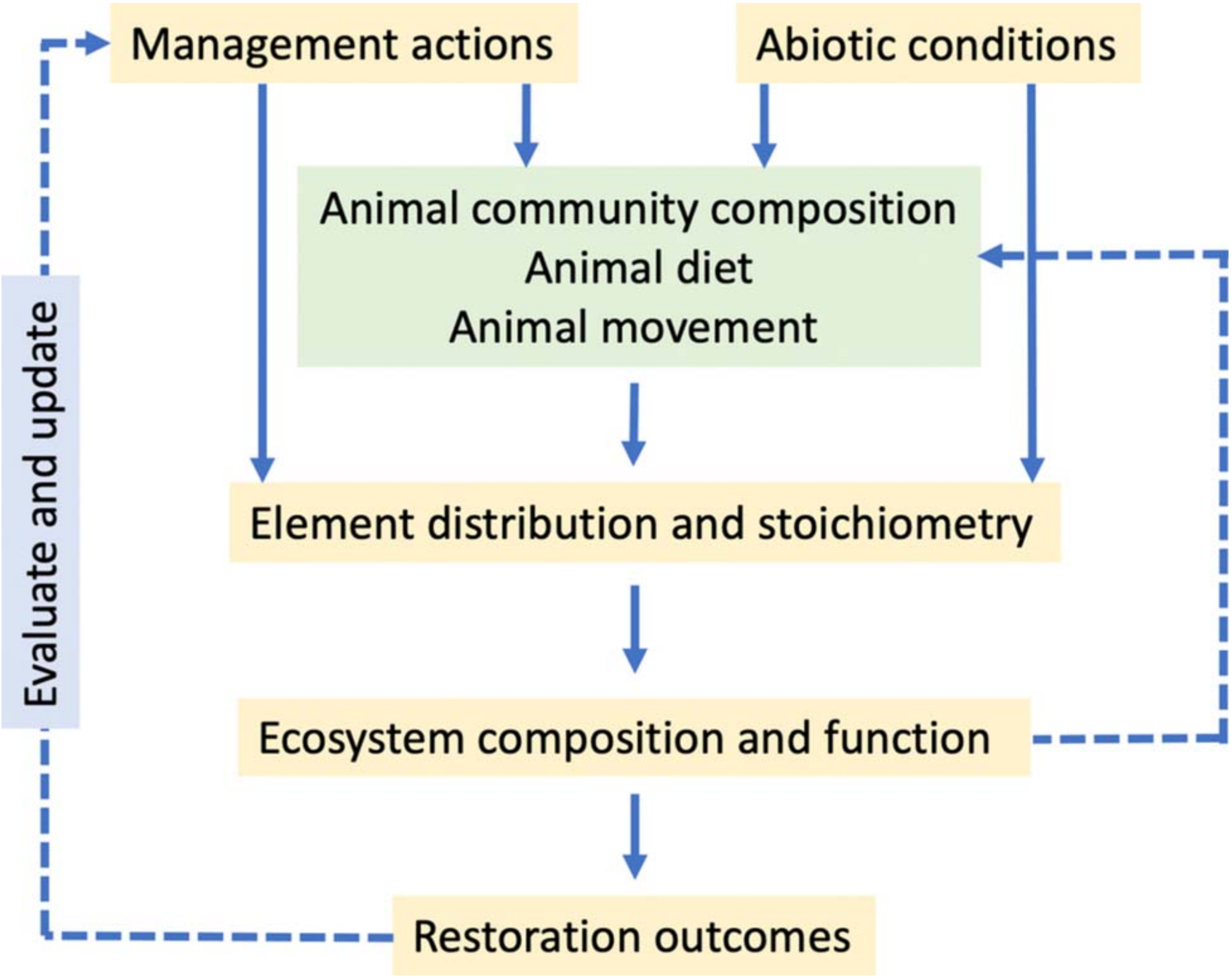


Fig. 1. Schematic diagram showing how abiotic conditions (e.g. climate, geology, etc.) and management actions influence elemental recycling and redistribution by wildlife, which can support or hinder restoration processes. Feedback processes are highlighted with dashed lines.

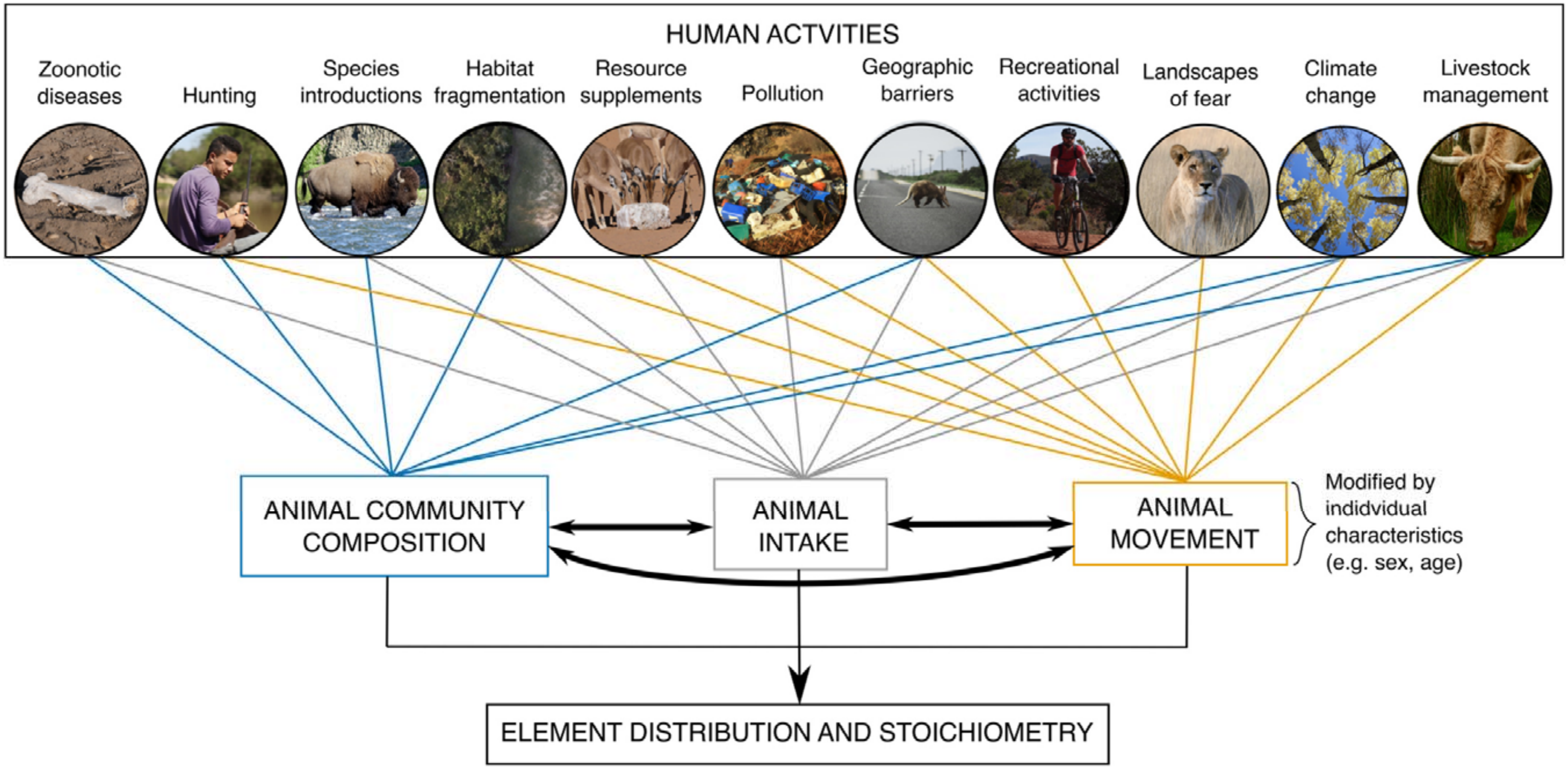


Fig. 2. Anthropogenic effects on the zoogeochemistry of nutrient and pollutant cycles. Colored lines represent direct links between human activities and animal community composition (blue), intake (gray), and movement (orange), which synergistically impact the distribution and stoichiometry of elements across restoration landscapes. Photos taken by A. Abraham and S. Abraham.

Anthropogenic impacts on element redistribution and stoichiometry by wildlife

Human activities can substantially alter zoogeochemical processes through direct impacts on wildlife or changes to their environment, notably through changes to 1) wildlife community size and composition, 2) element geographies, stoichiometries and wildlife intake, and 3) wildlife movement and activity patterns (figure 1). There is, however, significant synergy and feedback between these pathways, which can result in complex outcomes for landscape element distribution and stoichiometry (figure 2).

A: Wildlife community size and composition

Direct human actions such as hunting, species introductions, habitat degradation, forestry and the management of livestock and zoonotic diseases have profoundly reshaped the composition and abundance of animal communities throughout the world. In particular, large vertebrates have been prone to extinctions and range contractions due to their low population densities, slow reproductive rates, and increased likelihood of human-wildlife conflict (Dirzo et al. 2014). Critically, because of their greater mobility and longer gut passage times, this group is also considered disproportionately important for lateral element transport and have previously been referred to as the planet's "nutrient arteries" (Wolf et al. 2013). Today, wild vertebrate biomass has been severely reduced and is now dwarfed 18:1 by human biomass and their domestics (Bar-On et al. 2018). As a result, global nutrient transport by wild vertebrates may be <10% today compared to the late-Pleistocene (Doughty et al. 2016). Other key wildlife guilds, including reptiles, fish, and arthropods, have similarly been affected by human actions such as climate change, habitat loss, erection of physical barriers, and pollution (Twinning et al. 2016; Sánchez-Bayo & Wykhuys, 2019).

Anthropogenic changes to wildlife composition and abundance can also reshape ecosystem stoichiometry. Selective absorption and retention of required elements from an animal's diet affects the element ratios in the subsidies that are subsequently deposited (carcasses and excreta), modifying the stoichiometry of the ecosystems into which they enter. Different wildlife groups can therefore modify ecosystem stoichiometry differently. For example, stoichiometric differences in the diet of large vertebrate browsers and grazers lead to stoichiometric differences in their resource subsidies (faeces), which can ultimately influence competitive advantages between N_2-fixing trees and grasses (Sitters & Olde Venterink, 2021). Similarly, differences in the faecal stoichiometry of piscivorous and herbivorous birds has shown to differentially stimulate phytoplankton growth in freshwater systems (Petkuviene et al. 2019), whilst greater demands for P and calcium (Ca) to support larger bone structures may also modify resource subsidies by larger animals (le Roux et al. 2020).

Together, any human actions that selectively extirpate, reduce, or promote certain species, can therefore critically reshape the chemistry of an ecosystem. This has important implications for restoration projects, where management decisions often involve eradication, population management, or reintroductions. For example, megaherbivores and large carnivores play an important role in zoogeochemistry (le Roux et al. 2018; Monk & Schmitz, 2021), but these trophic groups face substantial restoration challenges (Lorimer et al. 2015).

B: Element geographies, ecological stoichiometries, and wildlife intake

Human activities can directly influence the distribution and availability of nutrients and pollutants to wildlife via many pathways, including agricultural fertilization, supplemental provisioning, resource extraction, pollution, modified diet selection, and altered abiotic fluxes such as atmospheric deposition and hydrological cycles (Birnie-Gauvin et al. 2017; Murray et al. 2016; Kraus et al. 2020). There are few landscapes today where human activities have not substantially influenced elemental distribution and stoichiometry (Schlesinger & Bernhardt, 2013; Kraus et al. 2020). Accordingly, the quantity and stoichiometric ratio of elements ingested by wildlife is often substantially modified by humans, leading to changes in zoogeochemistry. For example, Abbas et al. (2012) demonstrated that by feeding on and redistributing nutrients from fertilized agricultural fields, roe deer (*Capreolus capreolus*) markedly alter the N and P budgets of nearby forests in Europe. Similarly, Post et al. (1998) showed that geese (*Chen caerulescens* and *Chen rossii*) feeding in agricultural areas supply 40% of the N and 75% of the P entering nearby wetlands and that changes in local crop management can drastically alter the magnitude of these fluxes.

Human activities have also reshaped the distribution of and exposure to pollutants for wildlife. Sites of high pollutant concentration, such as landfills or mines, may nevertheless attract wildlife due to the availability of other resources (Sach et al. 2020). Consequently, animals can play an important role in transporting pollutants such as heavy metals into restoration sites. For example, Martín-Vélez et al. (2021) recently quantified the transport of several metal elements including As, Pb, and copper (Co) by lesser black-backed gulls (*Larus fuscus*) from mining and landfill sites into a Ramsar wetland conservation site in Spain. Such long-term deposition of heavy metals (e.g. 77g Pb ha^{-1} yr^{-1}) may compromise aquatic communities and ecological processes at this site. Similarly, elevated concentration of pollutants in elephant (*Loxodonta africana*) faeces near mining sites suggests they play an important role in distributing heavy metals in South Africa (Sach et al. 2020). Animals in higher-trophic levels, such as predators and scavengers, are important vectors of pollutants due to bioaccumulation of these elements in their bodies and excreta (Webster et al. 2021a). Further research is required to determine the contribution of lower-trophic organisms, including invertebrates (Monchanin et al., 2021).

Critically, any anthropogenic modification to wildlife element intake has important implications for animal digestive physiology, health, and reproduction (Birnie-Gauvin et al. 2017), which generates dynamic feedbacks between wildlife community composition, abundance, and the elemental landscape (see Section 2A). For an in-depth discussion on this topic we refer readers to the comprehensive review of wildlife nutrition in a changing world by Birnie-Gauvin et al. (2017).

C: Wildlife movement and activity patterns

Human activities impact wildlife movement in many ways. Here, we define four broad categories:

I. **Physical and disruptive barriers:** Static human infrastructure such as fences, roads, towns, and dams directly reduce animal movement, increase habitat fragmentation, and reduce ecosystem connectivity (Jakes et al. 2018). Even where physical barriers do not exist, disruptive linear features in the landscape, such as roads, have been shown to reduce animal home-range size (Seigle-Ferrand et al. 2022). Where animals congregate in large numbers, C storage and N fixation can be impeded (Veldhuis et al. 2019a). Currently, many restoration projects restore isolated pockets of habitat without restoring connectivity. Although this is often unavoidable, restoration practitioners should be aware that impeded element flows resulting from physical and disruptive barriers may compromise restoration success.

II. **Spatial and temporal distribution of resources:** Anthropogenic nutrient hotspots or hot moments (pulses of nutrients into an environment; *sensu* McClain et al. 2003) can generate patterns of directional wildlife movement towards, and concentration around, resources such as waterholes, landfills, compost facilities, bird feeders, or supplemental mineral blocks (Birnie-Gauvin et al. 2017; Murray et al. 2016). Similarly, anthropogenic depletion of resources or toxification of an environment with pollutants can shape movement patterns directionally away from ecosystems, with concomitant impacts for zoogeochemistry (Young et al. 2010). As wildlife subsequently influence elemental distribution and stoichiometries themselves, feedback patterns may also emerge (McInturf et al. 2019).

III. **Landscapes of fear:** Human disturbances strongly shape animal use of space and movement dynamics. For example, many species reduce their movement by >50% in areas with a high human footprint (Tucker et al. 2018). Fear towards humans may lead large predators to become more nocturnal and perform more energetically costly movements to avoid humans across landscapes (Gaynor et al. 2018). Likewise, access to concentrated mineral resources by herbivores is diminished where there is a perceived increase in vulnerability to hunting (Blake et al. 2013). Humans also exert a strong control on natural landscapes of fear via predator management. Where present, natural predators may generate spatial element heterogeneity in landscapes via the distribution of carcasses (Bump et al. 2009) and important non-consumptive effects on prey such as habitat selection and activity times (Veldhuis et al. 2020; Monk & Schmitz, 2021), although megaherbivores may escape these pressures (le Roux et al. 2018). As such, if size-dependent differences in elemental demand leads to variations in zoogeochemical impact (see Section 2A), differential response of prey species to predation will create further chemical heterogeneity. Consequently, whether a restoration project chooses to restore carnivores may have far reaching consequences to element distribution and stoichiometry.

IV. **Climate change, habitat fragmentation, and habitat loss:** Anthropogenic climate change is driving a geographical redistribution of plants and animals globally (Pecl et al. 2017). Similarly, habitat loss and fragmentation modify animal movement (Hadley & Betts, 2009) and thereby wildlife impacts on biogeochemistry. Animals that undertake long migrations (Wilcove & Wikelski, 2008) or are water-dependent (Veldhuis et al. 2019b) are particularly vulnerable to these anthropogenic forces, threatening their roles as important vectors of allochthonous nutrients into ecosystems (Childress et al. 2014).

The above anthropogenic factors can be static (e.g. road infrastructure) or dynamic (e.g. seasonal provision of supplementary resources). Animals have been shown to exhibit a high degree of behavioural flexibility with changing circumstances. This is well exemplified by the responses of wildlife communities throughout the world to COVID-19 induced lockdowns (Bates et al. 2020). Consequently, predicting how anthropogenic factors shape zoogeochemical processes during restoration projects is complex, whereby different factors may enhance or oppose each other (figure 2). In Box 1 we provide an example of how different wildlife management strategies may interact to potentially influence wildlife-mediated impacts on landscape element distribution and stoichiometry in a restoration site located in the southern Kalahari Desert, South Africa.

Current frameworks to model animal element redistribution

There are numerous studies examining wildlife-mediated element redistribution. However, most of these focus on just one or two idiosyncratic animal species (Subalusky & Post, 2019; Abraham et al. 2022a) and few explicitly explore anthropogenic influences on element redistribution (but see Post et al. 1998; Abbas et al. 2012; Martín-Vélez et al. 2021). Whilst the choice of these species is usually driven by unique characteristics particularly pertinent to the transport or recycling of elements (e.g. high consumption rates or long gut passage times), the collective impacts of *all* animals must be evaluated in order to understand the collective zoogeochemical role played by wildlife in ecological restoration projects. Inherently, attempts to model element

Box 1. Future modelling, validation and monitoring of anthropogenic impacts on zoogeochemistry at Tswalu Kalahari Reserve

Tswalu Kalahari Reserve (TKR; 120,000ha) is a 25-year ecological restoration project in the southern Kalahari Desert, South Africa (https://tswalu.com/tswalu-foundation). TKR was previously farmland, but now has a full complement of large vertebrate herbivores, predators and scavengers native to the region. The goal of TKR is to (i) restore the natural environment, (ii) re-establish and protect biodiversity, and (iii) maintain the Kalahari's characteristic ecological processes. As a nutrient-poor, arid environment (mean annual precipitation is ~300mm yr^{-1}), wildlife plays a critical role in recycling and redistributing nutrients within the reserve. For example, sociable weavers (*Philetairus socius*) and brown hyaenas (*Parahyaena brunnea*) have been shown to create 'islands of fertility' at their nest and latrine sites in TKR respectively (Pryang et al. 2020; Abraham et al. 2022b), with implications for tree growth and animal activity (Pryang et al. 2020; Lowney & Thomson, 2022). Consequently, any modification to these or other zoogeochemical processes by TKR wildlife management may impact the attainment of restoration goals.

Possible anthropogenic influences on zoogeochemistry at TKR

1. **Electrified fences**: TKR is fenced to reduce disease transmission and human-wildlife conflict. However, this prevents large scale animal migrations in response to nutrient shortage. An internal fence further splits TKR into two separate sections.
2. **Offsite wildlife removals**: To prevent overgrazing, large vertebrate herbivores are periodically removed from TKR, with concomitant loss of nutrients in their bodies (Abraham et al. 2021b). For some elements (e.g. P), this loss may be >50% of abiotic inputs.
3. **Mineral lick provision:** To offset nutritional deficits, wildlife managers provide supplementary mineral (P, Ca, K, Mg; ~25,000kg yr^{-1}) and salt (Na; ~10,000kg yr^{-1}) at ~25 point sources distributed throughout TKR. Camera trap studies highlight that larger herbivores disproportionately access these mineral resources and inter-species dynamics are modified at these sites (unpublished data).
4. **Landscapes of fear:** Large carnivore guilds are managed differently between the two sections of TKR, maintaining lion (*Panthera leo*) presence in one section, and spotted hyaena (*Crocuta crocuta*), cheetah (*Acinonyx jubatus*) and African wild dog (*Lycaon pictus*) presence in the other. Different predators have been shown to elicit different responses in prey behaviour at TKR (Makin et al. 2018) and may shift herbivore community composition towards predominantly larger-bodied species (le Roux et al. 2019) with cascading impacts on mineral demand.
5. **Airstrip**: TKR has a private airstrip to facilitate guest transport and helicopter flights. However, heavy metal deposition (Webster et al. 2021b) and noise pollution (Alquezar & Macedo, 2019) near the airstrip may alter wildlife element intake and movement patterns and therefore element intake and redistribution.
6. **Tourism and security**: Although tourist density in TKR is relatively low, road networks and vehicle disturbance can modify wildlife movement patterns and habitat use due to landscapes of fear, with subsequent impacts for nutrient redistribution (Shannon et al. 2017).

Modelling zoogeochemistry at TKR

The above human activities and infrastructure may exert an important collective influence on element recycling and redistribution by large vertebrate fauna at TKR (figure 3). Zoogeochemical modelling offers the opportunity to quantify and map how such static and dynamic anthropogenic modifications change the chemical landscape of TKR over coming decades. Where modelled outcomes negatively impact restoration processes, management strategies can be realigned or management actions designed to counteract the impact can be implemented. Some required data to model zoogeochemistry can be obtained using remote sensing (e.g. digital elevation model at 30m resolution for physical land structure).

However, many datasets must be collected *in situ*. TKR already collect many important data to help inform management decisions, including precipitation (~40 rainfall gauges across the reserve), large herbivore (>10kg) abundance and habitat mapping (Tokura et al. 2018). Additional datasets particularly required to facilitate robust zoogeochemical modelling include:

1. Current element distribution and stoichiometry
2. Estimates of major abiotic fluxes for focal elements
3. Presence of potential organic/synthetic pollutants
4. Wildlife diets and movement patterns
5. Faecal and urine concentration measurements
6. Annual management reports

To facilitate efficient transfer of data and knowledge from conservation practitioners to ecosystem modellers, wildlife managers should prepare and format all data for analysis and integration with models. Biologists and environmental scientists can then generate robust biogeochemical forecasts, for communication back to key stakeholder groups (figure 4).

Validation and monitoring of zoogeochemistry at TKR

Model forecasts are imperfect and must be rigorously validated before being used to help inform wildlife decision making. Similarly, monitoring frameworks should be put in place to observe the impacts of changing landscape chemistry over time, with collected data used to iteratively improve model performance and provide confidence in model outputs over time (figure 4). These validation and monitoring data could include, but are not limited to:

1. Element concentrations and ratios in soils, plants and wildlife excreta
2. Wildlife body condition
3. Baseline wildlife exclusion areas
4. Vegetation surveys (composition and abundance)
5. Wildlife movement patterns

redistribution by all animals within an ecosystem are more complex and there remains a paucity of studies that attempt to do so.

Current models used to estimate this zoogeochemical process by diverse animal communities are often based on differential equations that utilize allometric relationships between body mass and key characteristics such as metabolic rate, population density, and daily movement to estimate element diffusivity for each species (Wolf et al. 2013). This diffusivity coefficient has then been applied to databases of mammal ranges and body mass to generate spatially explicit maps of past and current element transport (e.g. Doughty et al. 2013; Doughty et al. 2016). Whilst this suite of models has allowed us to appreciate the importance of animals as agents within local and global biogeochemical cycles in a computationally efficient manner (Schmitz et al. 2018; Abraham et al. 2022a), there are several shortcomings. These include issues related to poorly mapped underlying element distributions (Wolf et al. 2013), a bias towards large vertebrate herbivores (Doughty et al. 2016), compound effects of using inaccurate mass-based scaling parameters such as gut passage time (Abraham et al. 2021a), unrealistic movement strategies which are approximated to Brownian motion (Wolf et al. 2013), and no feedback between animals and their elemental environment – an important relationship that drastically impacts animal movement (McInturf et al. 2019). As a result, precise estimation of how human activities influence element recycling and redistribution by animals in any one place is inherently uncertain, which has precluded the application of these models for modern-day wildlife and landscape management. Consequently, there have been calls for more sophisticated representations of zoogeochemistry in ecosystem models (Ellis-Soto et al. 2021).

Future modelling directions

Modelling human influence on element recycling and redistribution by wildlife requires a meta-ecosystem approach, linking anthropogenic activities to flows of energy, elements, and organisms (Loreau et al. 2003). Below we outline three key areas, whereby improved modelling will facilitate a deeper understanding of how the zoogeochemical impacts of animal communities can support or hinder restoration projects.

A. **Element distribution, stoichiometries, and availability:** An understanding of present-day spatial element distribution in soils and plants is critical for forecasting how wildlife management decisions may impact zoogeochemistry. Point field measurements are essential and can be mapped across landscapes by statistically integrating various drivers of spatial variation. Increasingly, machine learning methods are applied to the prediction of element distribution at high-spatial resolution (e.g. 30m; Hengl et al. 2021). To map wildlife-mediated impacts on ecosystem stoichiometry, it is important to represent multiple elements simultaneously. In this respect, Stoichiometric Distribution Models (StDMs) offer a framework to spatially resolve suites of elements using field data (Leroux et al. 2017). Alternatively, analysis of multi- or hyper-spectral data collected from drones, aircraft or satellites offers landscape-wide mapping of critical elements such as N, P, Ca and magnesium (Mg) with robust accuracy ($R^2 = 0.61$-0.88; Asner et al. 2017; Thomson et al. 2018). Current zoogeochemical models do not differentiate between the availability of discrete elemental resource stocks for different animal species (e.g. concentration and stoichiometric differences between C3 and C4 plants). Yet, this critically determines element intake of different animal diets, with implications for zoogeochemical processes (Balluffi-Fry et al. 2022). Resolving access to different element pools for grazers, browsers, frugivores, insectivores, scavengers, and carnivores is key for future modelling practices.

B. **Individual-scale processes:** Resolving important zoogeochemical processes at an individual-scale is essential for robustly modelling the spatiotemporal dynamics of zoogeochemistry in restoration projects. For example, space use and nutritional requirements vary based on species, age, sex, reproductive or lactation status, digestive physiology, and environmental conditions (Suttle, 2010), whilst individual memory can further impact movement patterns (Ranc et al. 2022). Moreover, these characteristics are dynamic and interactive, triggering feedback patterns that are not easily captured when modelling population averages (McInturf et al. 2019). Agent-based models (ABMs) provide one opportunity to model individuals – in this case individual animals – with the ability to perform dynamic decision-making tasks based on a changing environment.

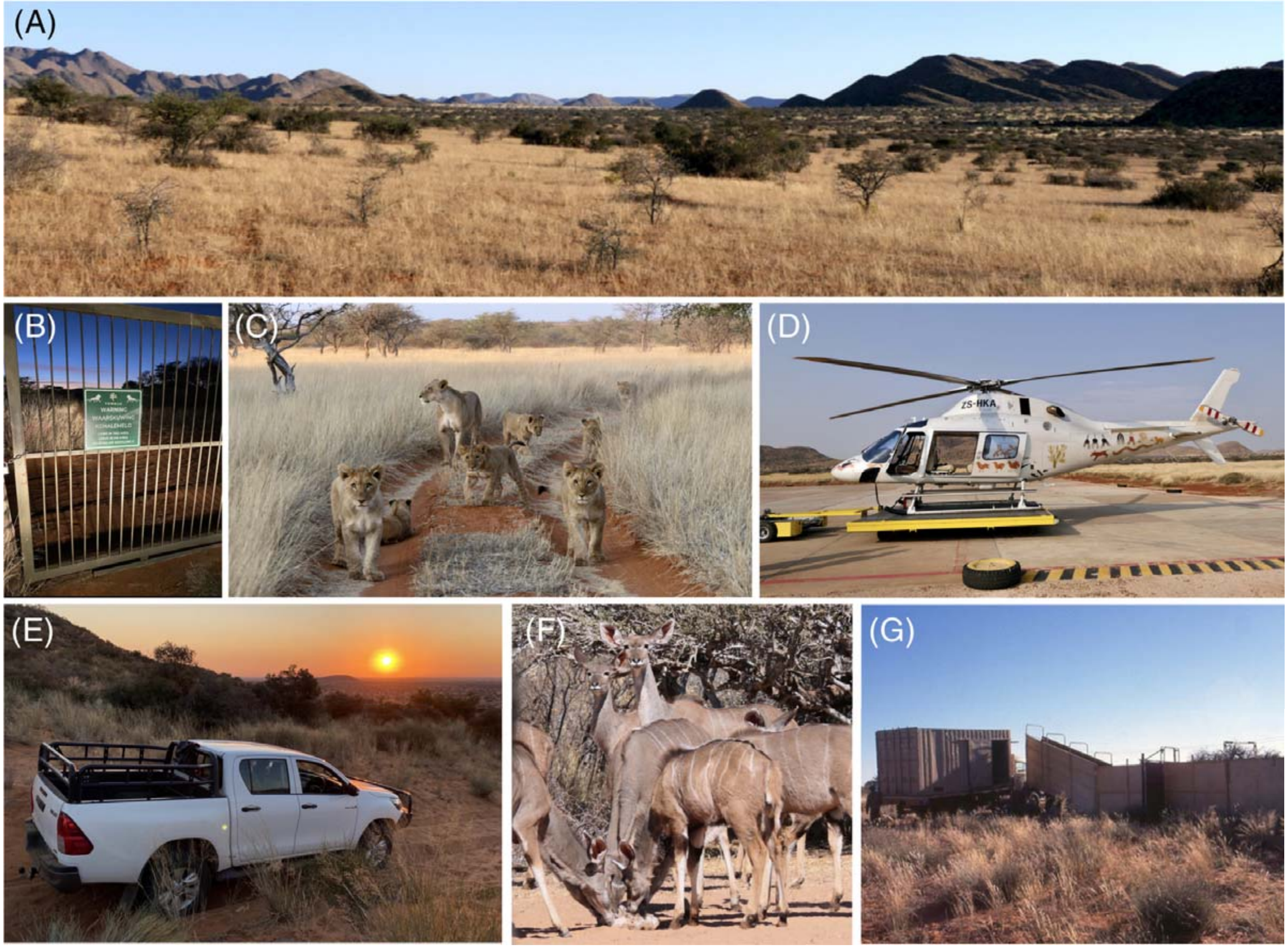
Consequently, many of the limitations of previous nutrient redistribution models, such as realistic animal movement and resource selection, can be overcome. Ferraro et al. (2022) insightfully demonstrate the advantages of ABMs for modelling zoogeochemistry. By tying empirical data of nutrient fluxes from the literature to animal movement, this model illustrated the landscape-level zoogeochemical effects of animals on the move. Their results indicate not only do large herbivores increase landscape-level and local-level heterogeneity, but also that the heterogeneity created by zoogeochemical effects may be important to sustaining wildlife populations. Additionally, their model indicates that previous nutrient budgeting models, which averaged the impact of an animal over a home range, miss important nuances in how individuals shape the zoogeochemistry of a landscape. Somveille & Ellis-Soto (2022) further build a spatially explicit predictive modelling framework that accounts for intraspecific variation in migratory behaviour of Galapagos giant tortoises (*Chelonoidis porteri*) and link this with long-distance seed dispersal events of invasive guava fruits across Santa Cruz Island, Galapagos. These fine-scale spatial predictions may serve as a baseline to estimate the zoogeochemical effects of hundreds of millions of guava seeds dispersed annually by giant tortoises (Ellis-Soto et al. 2017). However, both of these models focus on one species (caribou/giant tortoise) and one propagule (N/guava seeds). In highly dynamic, biodiverse systems (e.g. tropical forests), individual-scale effects and idiosyncrasies may still “average out” (Doughty et al. 2013). Yet, we argue that over the spatiotemporal resolution that restoration managers are concerned (metres-kilometres; months-years), as well as the discrete nature of management actions (e.g., the reintroduction of specific individuals or the removal of a fence), these individual-scale nuances will likely remain important. This is especially the case in high-latitude and arid systems, where individual contributions have longer-lasting impacts (Malhi et al. 2022). For example, representing individual scavengers is key for determining if elements from carcasses stay *in situ* (Bump et al. 2009) or are transported to specific latrines and den sites (Abraham et al. 2022b). The capacity of ABMs to provide predictions of on-the-ground change will also aid in the design of monitoring protocols by highlighting which ecosystem changes to monitor allowing for more adaptive management strategies. Moreover, the bottom-up construction of ABMs (creating a system from the decisions and interactions of its individual components) makes it a useful hypothesis-generating tool, allowing scientists to match their understanding of reality with reality itself. This occurs by making explicit all the assumptions that underlay our understanding of a system, revealing which aspects of the system, as modelled, are likely to be most influential and which are likely to interact with each other. However, ABMs can be computationally expensive, precluding their utilization at large (e.g. continental) scales. In this case, ABMs may serve as an intermediary or sub-component model that elicit key feedbacks within larger models, similar to the approach of novel food web models (e.g. Kadoya et al. 2018). Alternatively, trait-based approaches of modelling dispersal effects of animal communities within larger general ecosystem models (e.g. Harfoot et al. 2014; Bello et al. 2015; Schmitz & Leroux, 2020), offer promise.

C. **Key feedbacks and integration with other ecological processes:** Modelling anthropogenic influence on element recycling and redistribution in isolation may lead to incorrect restoration forecasts due to feedbacks within the ecosystem (McInturf et al. 2019). Element distribution has reciprocal relationships with many ecological processes such as primary productivity and animal activity (McInturf et al. 2019). Feedbacks between these ecological processes may lead to unintended conservation problems such as occurred during the classic example of introduced piscivorous fish to control harmful algal blooms (see DeMelo et al. 1992). For example, following one of the largest dam removal projects in history, the Elwha River restoration project in Washington State, USA, faced many challenges. This included the consideration of nutrient availability, seed dispersal, water retention, and shading for efficient plant growth of previously inundated riparian habitat. However, neglecting impacts of wildlife on restoration processes overlooked critical ecological interactions and drivers of restoration progress. For example, ungulates which transport nutrients and seeds from mature forest to restoration areas ultimately supressed plant growth through herbivory (McCaffrey et al. 2018). In contrast, the addition of log piles by managers to protect plants from herbivory provided habitat for birds and other wildlife, thereby initiating a subsidiary nutrient input. Such impacts by animals are instrumental in driving restoration, but reflect complex trade-offs in management decisions. It is therefore essential that potentially important processes such as soil compaction or overgrazing are either (i) explicitly incorporated in the zoogeochemistry framework, or (ii) that results of element distribution and stoichiometry are coupled with other vegetation, carbon or biodiversity models. For example, to understand how modified landscape chemistry influences grazing impacts on soil carbon storage, element distribution and stoichiometry results could be coupled with the SNAPGRAZE carbon dynamics model (Ritchie, 2020) for more integrative restoration forecasts.

The above suggestions are certainly not exhaustive. We encourage researchers to creatively build upon the ideas suggested here to further integrate modelling approaches with empirical data to refine the forecasting of element distribution and stoichiometry in restoration projects over time (figure 3).

Emerging viewpoints, technologies, and datasets for zoogeochemistry

In order to implement many of the above model improvements, adequate and robust information is needed. Emerging viewpoints, technologies, and datasets provide exciting opportunities for scientists to assemble the diverse data required to parameterize and validate models. For instance, indigenous perspectives are increasingly being incorporated into effective restoration and rewilding initiatives (Ban et al. 2018). First, indigenous knowledge can enhance understanding of past histories of human-wildlife relationships (Trisos et al. 2021), providing insights into long-term impacts on zoogeochemistry (Doughty et al. 2013). Second, traditional ecological knowledge can often provide accurate assessments of key information such as wildlife abundance and movement patterns (Braga-Pereira et al. 2022), which can be used in concert with, or in place of empirical data. For example, large vertebrate animals, such as bison (*Bison bison*), play a crucial role in several indigenous cultures, that have intimate knowledge of their ecology (Taschereau Mamers, 2020).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(F)
(G)

Fig. 3. The restoration of Tswalu Kalahari Reserve, South Africa, highlighting the reserve landscape (A) and six possible ways in which human activities and infrastructure impact ecosystem zoogeochemistry via fencing (B), predator management (C), airstrip pollution (D), vehicles and the road network (E), provision of mineral licks (F), and off-site wildlife removal (G). Photos A–F taken by A. Abraham. Photo G taken by J du P Bothma (University of Pretoria).

New technological advancements further improve the ability of scientists to quantify impacts of wildlife on chemical landscapes. These include handheld elemental analysers such as X-Ray Fluorescence (XRF) that can generate high volumes of field data, low-cost GPS tracking technologies for measuring animal movement (Kays et al. 2022), and eddy covariance towers that can disentangle methane emissions from animals (Stoy et al. 2021). Importantly, artificial intelligence (AI) can now be used to analyse the vast quantities of data that are generated by new technologies. For example, the Megadetector computer vision software (Tuia et al. 2022) can automatically identify animals and humans in camera trap images with high accuracy, reducing human labor and error. Similarly, advancements in eDNA and DNA barcoding can be used to track species presence and monitor diets across landscapes and through time (Beng & Corlett, 2020).

To monitor the impact of entire populations of wildlife across larger spatial scales, remote sensing products from drones, airplanes, and satellites offer unprecedented opportunities. For example, recently collected Global Ecosystem Dynamics Investigation (GEDI) LiDAR provides new insights into vegetation structure, facilitating research into how wildlife use and shape their environment at the landscape-scale (Burns et al. 2020). Similarly, the proposed 2024 surface biology and geology mission by the National Aeronautics and Space Administration (NASA) aims to deploy multi- and hyperspectral sensors that will offer opportunities to assess nutrient concentrations and stoichiometry in plants across most of the world at 60m resolution (Cawse-Nicholson et al. 2021). This novel data will provide sub-monthly temporal insights into forage quality available to wildlife. Coupling these, and other remotely-sensed datasets, with wildlife occurrence data can help accurately estimate the impact of wildlife on nutrient redistribution (*sensu* Ellis-Soto et al. 2021).

Ideally, where possible all aspects of zoogeochemical models should be parameterised using site-specific data. However, logistical and financial difficulties often prevent this. In the absence of site-specific data, newly published datasets can be leveraged. For example, Abraham et al. (2021a) collated a wide database on gut passage time in endotherms (n=391 species), a critical parameter to estimate element redistribution by large vertebrate animals. Similarly, new data repositories allow improved parameterization of ecosystem composition, whilst >1000 animal species are currently being tracked with animal tracking technologies, offering insights into wildlife space use and movement patterns (Kays et al. 2022). The volume of such animal movement data is currently doubling nearly every two years (Kays et al. 2022). Many other databases on plant (e.g. TRY database; Kattage et al. 2020) and animal functional traits (e.g. EltonTraits; Wilman et al. 2014) or faecal element concentrations (e.g. Dung Data Depository with >10,000 measurements from 44 mammalian herbivore species in 10 countries; le Roux et al. in prep) may also be useful.

Implementing and communicating zoogeochemistry for better restoration practices

Within the restoration process, modelling can be used to help identify the best course of action by simulating possible outcomes before action is taken (Restoration Actions, figure 3). However, all those involved in the process of imagining, modelling, and implementing restoration initiatives, must interrogate the underlying motivations and scope of any specific project, which can impact decisions made throughout the restoration processes, including at the modelling stage. By approaching restoration with clearly stated values and motivations, scientists and managers can create ethical restoration schemes based on sound policies and effective research (Ferraro et al. 2021; Nelson et al. 2021). It is also essential that all restoration projects that scientists develop strong connections between practitioners and conservation academics to exchange ideas, expertise and leverage existing datasets to maximise forecasts of potential restoration outcomes (Pretty & Smith, 2004). Modelling for restoration is improved when all important factors are identified and incorporated (Data Inputs, figure 3), and utilizing existing databases can help identify important data gaps. Given that models can be highly tailored to specific systems, conservation practitioners can help facilitate and improve efforts to effectively resolve zoogeochemical processes at their site by collating required datasets (for example see the hypothetical example in Box 1). After the relevant features are added to a model, the impact of various restoration decisions can be modelled producing elemental distribution maps for each potential restoration plan (Elemental Distribution and Stoichiometry Modelling, figure 4).

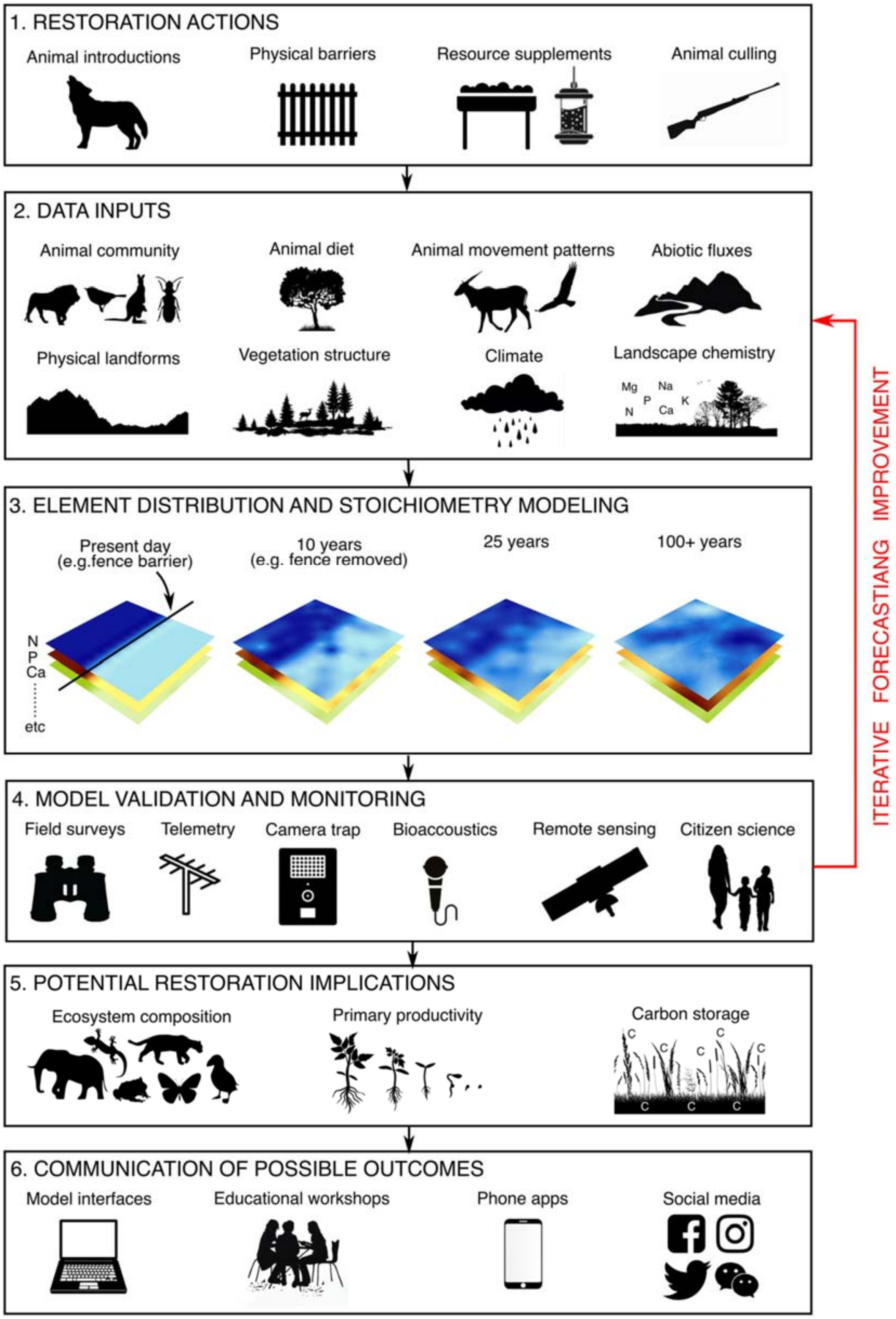

Fig. 4. Six-point workflow for understanding how different restoration options may impact the distribution and stoichiometry of elements throughout a landscape and how these outcomes can aid in creating successful restoration schemes. Red arrows show how information from initial model outputs and monitoring efforts can be used to iteratively improve model performance and restoration decision making. Animal silhouettes taken from http://phylopic.org/.

Ecosystems are complex and ecological forecasting is never perfect. It is therefore essential that validation monitoring frameworks are put in place to identify erroneous or over-simplified assumptions, ensure that model predictions are useful and to record verifiable impacts over time (Validation and Monitoring, figure 3). In this process, it is important to ensure that there is collective agreement on what successful zoogeochemical outcomes look like. For example, keeping animal-vectored pollutant levels below set thresholds (Martín-Vélez et al. 2021) or maintaining a certain degree of elemental heterogeneity within the landscape. There are a plethora of field-based (e.g. wildlife observations, sample measurement, bioacoustics) and remotely-sensed (e.g satellite) methods that can be used for validation and monitoring purposes. This data can be collected by diverse groups including indigenous peoples, ecologists, GIS specialists, wildlife managers, and citizen scientists. Data collected throughout restoration projects can be iteratively fed back into the modelling process to improve model forecasting (*sensu* Dietze et al. 2018), and highlight missing dynamics overlooked in earlier model versions (Data Inputs, figure 3). Consequently, the impacts of different wildlife management actions on element distribution and stoichiometry can be honed over time and management decisions revaluated and realigned to reach restoration goals (figure 1).

The outputs of an iterative modelling effort can help discern potential restoration implications for each intervention in concrete metrics, such as increases or decreases to primary productivity, or changes in ecosystem composition and dynamics (Restoration Implications, figure 4). Upon completion and validation of modelling exercises, generated information needs to be distilled into comprehensible and communicable language for each stakeholder group (Communication, figure 4). There is an exhaustive literature on communicating science to stakeholder groups that we do not go into here. However, dynamic model interfaces that illustrate outcomes of different management decisions may be particularly helpful.

Conclusion

Restoration of wildlife is critical for climate and biodiversity resilience over the coming century (Arias et al. 2021; Malhi et al. 2022), yet predicting successful schemes and understanding possible ecosystem outcomes is complicated by anthropogenic effects. Within restoration projects, wildlife plays a key zoogeochemical role, which can support or hinder restoration processes. For stakeholder groups to make informed wildlife management decisions that account for critical zoogeochemical processes, improved methodologies are needed that both consider anthropogenic influences and wildlife feedbacks. In this paper, we outline how zoogeochemical models may be improved to better forecast the impact of wildlife-mediated element recycling and redistribution in restoration projects. Improved models should consider how management decisions affect animal community composition, diet, and behaviour to forecast subsequent impacts on ecosystem stoichiometry and biogeochemistry. This should include individual-scale processes, dynamic feedbacks, multi-element interactions, and integration with other ecological processes. Emerging viewpoints and technologies offer exciting opportunities to quantify and monitor element distributions and stoichiometries at fine spatiotemporal scales. Together, these advancements can help align wildlife management decisions to support ethical restoration attempts in ways that are more effective, efficient, and natural.

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