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SYNTHESIS

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Feedback loops between 3D vegetation structure and ecological functions of animals

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Abstract

Ecosystem functions in a series of feedback loops that can change or maintain vegetation structure. Vegetation structure influences the ecological niche space available to animals, shaping many aspects of behaviour and reproduction. In turn, animals perform ecological functions that shape vegetation structure. However, most studies concerning three-dimensional vegetation structure and animal ecology consider only a single direction of this relationship. Here, we review these separate lines of research and integrate them into a unified concept that describes a feedback mechanism. We also show how remote sensing and animal tracking technologies are now available at the global scale to describe feedback loops and their consequences for ecosystem functioning. An improved understanding of how animals interact with vegetation structure in feedback loops is needed to conserve ecosystems that face major disruptions in response to climate and land-use change.

KEYWORDS

3D vegetation structure, animal behaviour, ecosystem ecology, feedback, lidar, movement ecology, remote sensing

INTRODUCTION

Global climate change and biodiversity loss have highlighted the need to understand how ecosystems function. Ecosystem functioning is largely driven by feedback loops between biotic and abiotic components, in which plants and animals influence each other and their environment in ways that change or sustain ecosystems (Schmitz, 2010; Schmitz et al., 2018). Feedback processes have been documented in a variety of ecosystems. For example, tropical rainforests can be self-reinforcing in that evapotranspiration from vegetation forms clouds that lead to heavy rain, thus reinforcing the climate necessary for rainforests to persist (Wu et al., 2013; Zhu et al., 2023). Severe plant water stress of sufficient frequency and duration has the potential to disrupt this feedback and transform tropical rainforests to savanna-like ecosystems (Saatchi et al., 2021). How ecosystems persist or change can therefore depend on feedback loops among ecosystem functions.

Vegetation structure, defined here as the distribution of leaves, stems and branches in three-dimensional (3D) space, including height, cover and vertical and horizontal complexity (Valbuena et al., 2020), is an essential component of ecosystems that influences animal diversity and behaviour (Burns et al., 2020; MacArthur

& MacArthur, 1961; Zellweger et al., 2013). Vegetation structure affects the distribution of microclimate refugia for animals (Scheffers et al., 2017), energetic costs of movement (Davies et al., 2017; McLean et al., 2016), spatial distribution of predation risk (Yovovich et al., 2021) and availability of preferred nest sites (Davies et al., 2019; Swift et al., 2017). In these ways, the vegetation structure influences how and where animals move to find resources (Wittemyer et al., 2019). In turn, vegetation structure itself is modified by animals, which can browse and trample vegetation, disperse seeds and redistribute nutrients necessary for plant growth (Berzaghi et al., 2018; Davies et al., 2018; Doughty, Roman, et al., 2016). In terrestrial ecosystems, a feedback loop forms whereby vegetation structure influences the behaviours of animals, whose ecological functions, in turn, shape vegetation structure. Research typically investigates one or the other of these relationships without integrating them into a framework that describes the feedback explicitly.

Ecological functions of animals are often recognized in conservation strategies for their ability to sustain ecosystems or restore them to an earlier state of structure and functioning (Enquist et al., 2020; Gordon et al., 2023; Malhi et al., 2022). Some conservation strategies have benefited from acknowledging components of a feedback loop between vegetation structure and animal ecological roles, such as how landscapes can change after reintroducing animals (Gordon et al., 2023). Tools and methods now exist to describe animal–vegetation feedback loops and their importance for ecosystem functioning, with broad applications for conservation. Remote sensing has become central to research on animal–vegetation structure interactions, especially Light Detection and Ranging (lidar), which characterizes 3D landscape structure at local and global scales (Davies & Asner, 2014; Dubayah et al., 2020). Similar advances in animal tracking, biologging and big data processing (Jetz et al., 2022; Ripperger et al., 2020) will enable widespread evaluation of how animals respond to and shape vegetation structure.

Describing feedback loops between vegetation structure and animal ecological roles may reveal important aspects of ecosystem function as climate change, land-use change, and other stressors that threaten ecosystem productivity and stability. The primary goal of this review is to investigate the lines of research that form feedback loop components and synthesize results to describe such feedback loops in detail (Figure 1). Because an animal–vegetation feedback loop will consist of different components and processes across ecosystems, a secondary goal is to review methods that can be used to better describe feedback loops in ecosystems and their potential applications. We first describe the essential functions of vegetation structure for habitat selection, movement and other behaviours of animals, with a focus on terrestrial vertebrates. Next, we provide examples of how animals modify vegetation structure, both directly and indirectly. Drawing on remote sensing and animal tracking research, we then describe ways to measure the components of an animal–vegetation

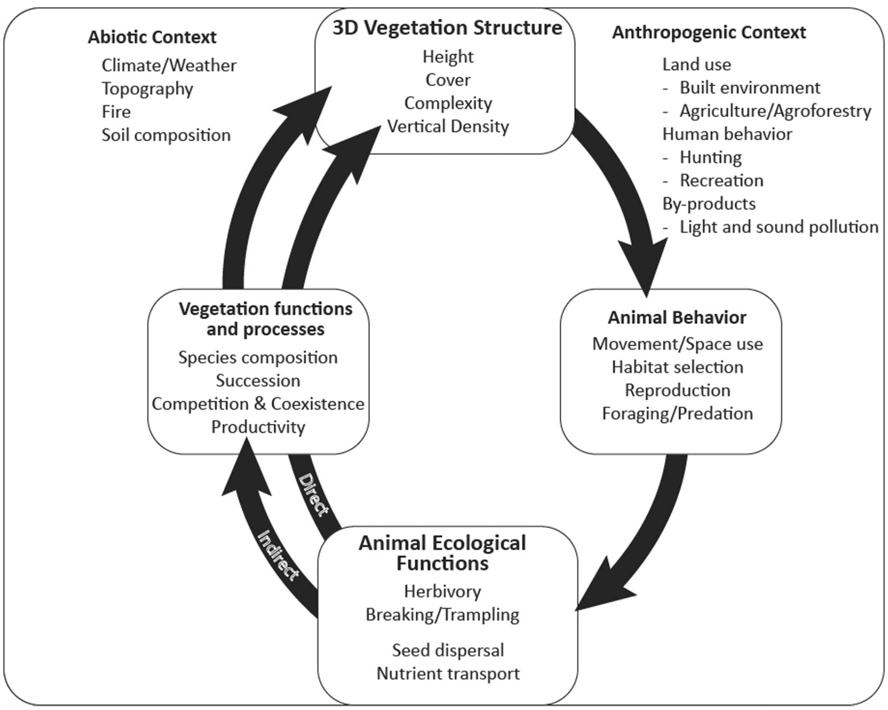

FIGURE 1 3D vegetation structure influences animal ecological functions, which can influence vegetation structure directly (e.g. herbivory, breaking/trampling) or indirectly (e.g. seed dispersal, nutrient transport). The black arrows represent this feedback loop. These feedback loops sit in the broader context of abiotic and anthropogenic factors, which can also influence vegetation structure and animal behaviour.

feedback loop and draw inferences. Finally, we discuss human impacts on animal–vegetation feedback loops and how using the feedback concept could improve conservation strategies. We conclude by outlining topics in need of further research to improve understanding of how animals interact with vegetation structure to shape and sustain terrestrial ecosystems.

HOW VEGETATION STRUCTURE INFLUENCES ANIMAL BEHAVIOUR

The 3D structure of vegetation forms a major component of ecological niche space that species occupy and has led to important adaptations in animal behaviour. Ecoregions with diverse vegetation structure broaden the diversity of movement strategies that are possible for animals to use, especially among arboreal lineages (Scheffers et al., 2017). Structural diversity also promotes functional diversity by increasing trophic niche space (Pawar et al., 2012; Xing et al., 2023), a key factor driving variation in morphological form and ecological function (Pigot et al., 2020). Moreover, the structural complexity of vegetation indicates potential risks and resource availability, albeit in environments where the cognitive load of memorizing the 3D environment is not too high (Fagan et al., 2013). The ways that vegetation structure influences animal behaviour give rise to its ecological value for animals.

Vegetation structural attributes can influence habitat quality and the distribution of resources for animals (Table 1). Animals must weigh the benefits of accessing resources, such as prey or nesting sites, with the risks and energetic costs of moving towards them—a central tenet of Optimal Foraging Theory (Abrahms et al., 2021; MacArthur & Pianka, 1966). Vegetation can decrease the energetic costs of movement by providing a substrate or increase them by cluttering movement paths. Monkeys and other arboreal animals move along canopy paths with high lateral connectivity, an attribute of 3D vegetation structure that aids in running, jumping and brachiation (McLean et al., 2016). Aerial insectivores, however, often rely on open airspace to forage, and their movements may be hindered by vegetation (Sleep & Brigham, 2003). Most research on animal movements in relation to 3D vegetation structure focuses on movement paths (Casalegno et al., 2017; Davies et al., 2017; McLean et al., 2016), but vegetation structure plays many functional roles that give rise to these movement behaviours.

Vegetation can provide shade for animals and create heterogeneity in microclimate within ecosystems. For example, moose seek taller and denser vegetation to avoid high summer temperatures (Melin et al., 2014), and arboreal animals track their thermal niche by moving vertically through vegetation, often seeking out tree cavities or denser vegetation during the hottest hours of the day (Scheffers et al., 2017; Scheffers & Williams, 2018). Microclimates vary by ecosystem type, with open woodlands yielding greater diurnal variation in temperature and tall, closed canopy forests reducing temperature extremes below the canopy (De Frenne et al., 2019, 2021; Jucker et al., 2018; Vinod et al., 2023). Canopy gap openings (e.g. from treefall or crown damage) create additional variation in microclimates across time (De Frenne et al., 2021; Sprugel et al., 2009). Characterizing thermal variation in landscapes can lend insight into how 3D vegetation structure helps animals thermoregulate, especially as climate change necessitates adaptation or movement towards habitats with suitable microclimates (Davis et al., 2019; Zellweger et al., 2019).

As animals balance the energetic and thermal costs of foraging, they must also consider predation risk. An animal's perceived risk is limited partly by its field of view, or viewshed, which is reduced in areas of high vegetation density (Aben et al., 2018). For example, lions (*Panthera leo*) make more kills in dense vegetation, allowing them to approach their prey more stealthily (Davies, Tambling, et al., 2016). In response, African herbivores, on which lion prey, have been shown to flee from predator vocalizations more frequently in dense vegetation than in open habitats (Epperly et al., 2021). However, dense vegetation can also conceal prey. This function is vital for life stages more vulnerable to predation, such as juveniles who move to or are shepherded by parents to areas with greater protective vegetation cover (Davies, Marneweck, et al., 2016; Stillman et al., 2019). Whether vegetation cover lends an advantage to predator or prey may therefore depend on the hunting mode of the predator and defense mechanisms of the prey. Animal behavioural traits, such as ambush versus cursorial predation and running escape versus hiding, influence how risk and reward are perceived in the context of a habitat's vegetation structure (Davies et al., 2021).

The risks and rewards of animal reproduction are linked to all facets of habitat quality. Successful reproduction for animal pairs requires some combination of courtship, mating, defending territory and rearing offspring. Vegetation structure can modulate behaviours of breeding individuals, such as by increasing conspicuousness of displaying males (Biagolini et al., 2021; Morales et al., 2008) or sheltering females (Morales et al., 2008) and indicating territory quality (Broughton et al., 2006). For cavity-excavating birds such as woodpeckers, breeding success depends on the availability of standing deadwood. Canopy height and heterogeneity metrics can indicate the distribution of this critical resource for reproducing birds, mammals and insects (Carrasco et al., 2014; Martinuzzi et al., 2009; Stitt et al., 2021, 2022). In addition, insight from animal habitat selection can help identify minimum ecological requirements for population persistence, such as features of 3D vegetation structure necessary for survival and reproduction (Davies et al., 2017; Deere et al., 2020). Such thresholds in habitat selection related to vegetation structural metrics could help explain population declines and subsequent decreases in the ecological functions of animals.

TABLE 1 Examples of animal behaviours influenced by vegetation structure.

Animal behaviour	Vegetation structural attributes	Example	References
Movement	Distance to canopy gap, canopy height, crown density, canopy shape, canopy thickness	Monkeys seek canopy pathways with high lateral connectivity	McLean et al. (2016)
Resting/roosting	Canopy height, canopy cover, distance to canopy gap, number of canopy layers, max canopy volume:height ratio	Orangutans often build nests near canopy gaps and in forests with tall, uniform canopy	Davies et al. (2019)
Foraging	Stem density, canopy cover, canopy height, canopy density, canopy gap volume	Stem density filters bat communities according to foraging niche	Blakey et al. (2017)
Thermoregulation	Canopy height, density	Moose seek denser vegetation during the hottest hours of the day	Melin et al. (2014)
Predator avoidance	Shrub cover	Ungulates flee more frequently in response to predator vocalizations in open habitat	Epperly et al. (2021)
Territorial display	Vertical vegetation complexity	Display duration of blue-black grassquit increases with seed abundance and shadow intensity of vegetation	Biagolini-Jr et al. (2021)

TABLE 2 Examples of animal ecological functions that influence vegetation structure.

Animal ecological function	Vegetation structural attributes	Example	References
Ecosystem engineering	Canopy height, coefficient of variation, per cent canopy cover <0.5 m	Megafauna in African ecosystems reduce canopy height and increase height variability	Davies et al. (2018)
Herbivory	Canopy height, cover, structural complexity	Savanna herbivores reduce canopy height and woody cover	Levick et al. (2009)
Breaking/trampling vegetation	Branch thickness, branch fracturing	Orangutans break branches to build nests that comply with their weight	Van Casteren et al. (2012)
Seed dispersal	Aboveground biomass	Reduction of seed dispersal by large frugivores is predicted to decrease aboveground biomass	Peres et al. (2016)
Nutrient transport	Tree density	Nutrient-rich termite mounds diversify the spatial distribution of savanna vegetation	Davies, Baldeck, et al. (2016)
Predation	Browsable plant density, bites available per plant, previous browse, per cent browsed, bites taken per deer unit	Intense browsing by deer leads to bushier vegetation in sites where puma predation is less likely	Yovovich et al. (2021)

HOW ANIMALS SHAPE VEGETATION STRUCTURE

Direct effects

Animals can shape vegetation structure directly through their behaviours (Table 2). Perhaps, the most dramatic examples come from ecosystem engineers, which modify entire ecosystems. The sheer size of an animal can lead it to exert a substantial impact on vegetation structure due to its strength and metabolic needs (Enquist et al., 2020)—Asian elephants (*Elephas maximus*), for example, require 150 kg of vegetation per day, removing large swaths of vegetation as they browse (Vancuylenberg, 1977). The loss of prominent ecosystem engineers is thought to account for significant differences in vegetation structure and composition between African and Neotropical humid forests (Doughty, Wolf, et al., 2016). The outsized impact of ecosystem engineers can also facilitate behaviours of other animal species that further shape vegetation structure. Beavers (Castoridae), for example, cut down trees to dam riparian areas in temperate and boreal forests, consequently flooding surrounding forests and creating standing deadwood, or snags, that attract cavity excavators such as woodpeckers and benefit a variety of cavity-nesting species (Brazier et al., 2021; Cockle et al., 2011). While many effects of ecosystem engineers have lasting impacts on 3D vegetation structure, other effects may be more ephemeral, such as collapsing branches or removing leaves (Figure 2). Trampling of vegetation by large herbivores in forests creates well-worn paths that are used repeatedly. These 'stigmergic paths' are used by a variety of animals and likely reduce the energetic costs of movement (Berdahl et al., 2018). The intensity of animal

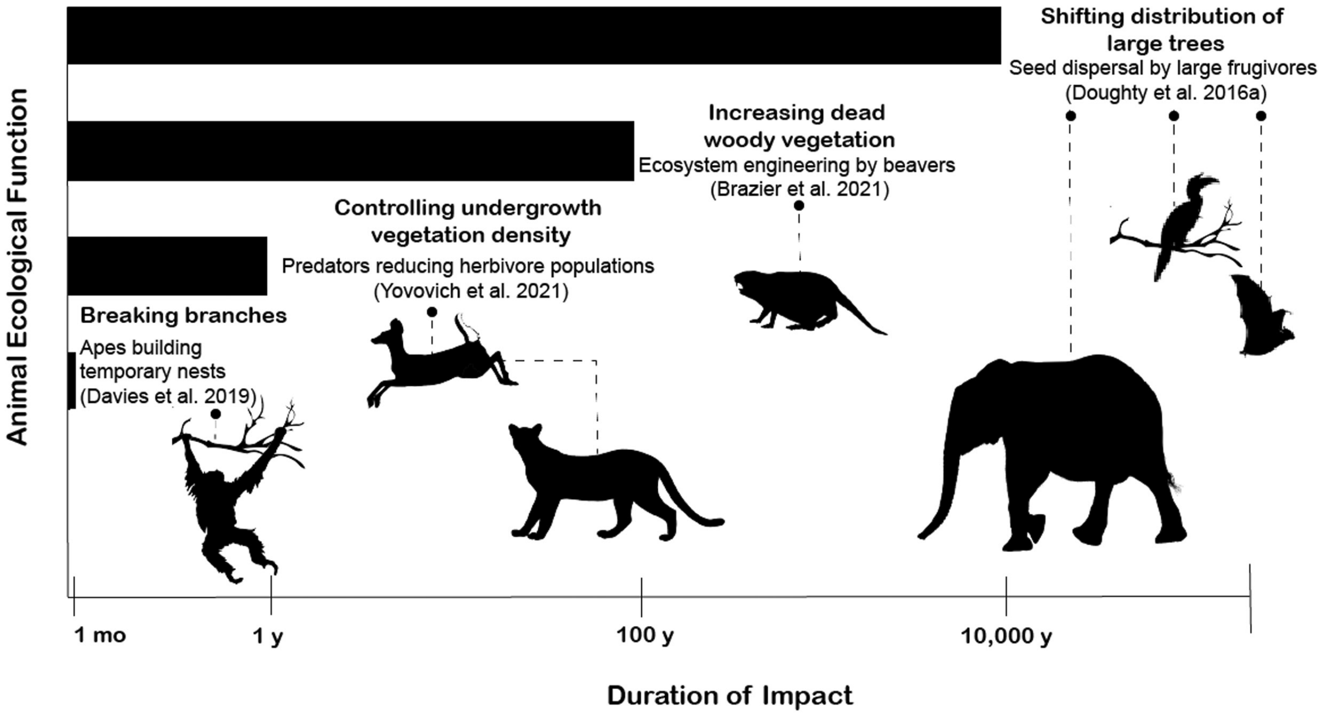

FIGURE 2 Examples of ecological functions of animals that influence vegetation structure and the approximate duration of the impact. Silhouettes downloaded from www.phylopic.org.

behaviours such as herbivory and trampling can dictate whether they have lasting impacts on vegetation structure (Geremia et al., 2019).

Indirect effects

While the direct effects of herbivory and ecosystem engineering by animals are readily visible in landscapes, animal-driven changes to 3D vegetation structure also arise from the indirect effects of actions that influence plant species composition such as seed dispersal. Seed dispersal lays the template for 3D vegetation structure by influencing the floristic species composition of landscapes (Nathan & Muller-Landau, 2000). Without seed arrival, there can be no woody plants. Seed dispersers have been shown to impact the distribution of aboveground biomass and carbon storage in landscapes through models that simulate their extirpation (Bello et al., 2015; Osuri et al., 2016), but their impact on 3D vegetation structure through seed dispersal has not been explored empirically. Animals move with respect to vegetation structure for reasons outlined in the previous section, and about 50% of all plants rely on animals to disperse their seeds (Fricke et al., 2022). Controlled experiments or simulations that use standardized metrics of 3D vegetation structure (Valbuena et al., 2020) could reveal the effects of this widespread ecosystem service on vegetation structure.

Animals also promote plant growth and shape plant species composition by distributing nutrients (Bauer & Hoye, 2014). Nutrient transport by animals often occurs through the distribution of excreta, egesta or carcasses (Bump et al., 2009; Doughty, Roman, et al., 2016; Ellis-Soto et al., 2021) and can serve as a critical link between aquatic and terrestrial ecosystems. Animal behaviours that alter the distribution of water and nutrients in nutrient-scarce environments can have a strong effect on plant communities. In African savannas, termite mounds create focal areas of soil that are rich in water and nutrients, enabling the growth of riparian tree species in drier habitats away from rivers (Davies, Baldeck, et al., 2016). Animals also modulate nutrient cycles in ecosystems through behaviours such as foraging and trampling soil (Schmitz et al., 2018). Carbon, nitrogen, phosphorus and other nutrients released into the soil by live or dead animals can modulate primary production by plants (Schmitz et al., 2018), with potential cascading effects on vegetation structure.

Some animals play multiple roles in shaping vegetation structure. For example, African forest elephants (*Loxodonta cyclotis*) are both herbivores and seed dispersers, although they usually avoid browsing late-successional, slow-growing trees, which are unpalatable due to large amounts of defense compounds used to deter herbivory (Poorter & Bongers, 2006). If these slow-growing saplings reach maturity, however, many will provide fruits for elephants. Elephants then sow the seeds of these late-successional trees in their nutrient-rich dung (Berzaghi et al., 2019; Campos-Arceiz & Blake, 2011). In some cases, an animal species' ecological roles can have counteracting effects on vegetation structure. For example, seed-caching rodents limit seedling recruitment by predating on seeds but may also facilitate recruitment if seeds are left to germinate within their caches. Instances of seed predators neglecting their caches—by death or otherwise—are thought to allow large-seeded tree species to persist in the absence of seed dispersal by larger animals (Hirsch et al., 2012; Jansen et al., 2012). This interaction will need to be incorporated into models that predict changes in vegetation structure due to the loss of large frugivores that disperse the same trees (Gómez et al., 2019).

Predators also modulate vegetation structure indirectly by regulating the population size and behaviours of herbivores. This effect has been detected in a variety of ecosystems, often following the loss or reintroduction of a key predator that changes herbivore foraging pressure (Beschta et al., 2018; Leo et al., 2019). Apart from the top-down effects of predation on vegetation structure, the very presence of predators imposes a 'landscape of fear' response from prey, which alters their behaviour to avoid predation risk. For example, pumas (*Puma concolor*) in California, USA kill deer away from human settlements, thereby creating refuge for deer near humans. In response, deer in human-dominated landscapes quadrupled their vegetation consumption (Yovovich et al., 2021).

Interactions between animals and abiotic and plant processes that shape vegetation structure

While animals play a pivotal role in shaping vegetation structure in many ecosystems, broader-scale patterns in vegetation structure are constrained by additional factors such as climate, fire, soil and plant competition. Moreover, vegetation structure is shaped by plant growth patterns adapted for sunlight capture, so that narrower, more conical trees are more abundant in temperate and boreal forests. In contrast, deeper and wider crowns are more common in tropical forests where sunlight is directly overhead year-round (Terborgh, 1985). Crown architecture has important implications for dispersal mode—taller trees with small crown diameters are more conducive to wind dispersal, whereas trees with large, spreading crowns are more conducive to drop- or animal dispersal (Panzou et al., 2020). Accordingly, animals disperse an estimated 60–90% of trees in tropical rainforests, whereas wind is the dominant dispersal mechanism in most temperate and boreal forests (Howe & Smallwood, 1982; Jordano, 2013; Rogers et al., 2021). Animals are therefore expected to have an outsized impact on tropical tree composition—and hence vegetation structure—relative to wind. Asian tropical forests are a notable exception, however, because many are dominated by wind-dispersed Dipterocarps (Osuri et al., 2016). Still, the stature of Asian tropical forests is hypothesized to be driven by tall individuals in a diverse group of families, including those dispersed by animals (Banin et al., 2012).

Quantifying the relative role of animals in shaping vegetation structure will require reliable measurements of additional factors whose intensity varies by ecosystem type. Fire, for example, plays a dominant role in many dry ecosystems by transforming vegetation structure and releasing nutrients into the soil (Levick et al., 2009). Animals can influence fire regimes by modifying the amount, structure and condition of fuels in the landscape (Foster et al., 2020; Holdo et al., 2009). Megaherbivores (>1000 kg) such as white rhinoceros (*Ceratotherium simum*) create grazing lawns of short grass that influence the behaviours of other grazers and lead to smaller, more heterogeneous fires (Waldram et al., 2008). African forest elephants browse paths along forest edges that limit wildfire spread (Cardoso et al., 2020). Capturing the complex interactions among plants, vegetation structure and additional factors in a feedback loop will require drawing information from a variety of sources.

CHARACTERIZING FEEDBACK LOOPS BETWEEN ANIMALS AND VEGETATION

Considering vegetation structure and animal ecological roles in a feedback loop can increase understanding of processes that influence ecosystem functioning. Feedback in ecosystems can induce change or be self-reinforcing (Figure 3). For example, outbreaks of spruce budworm in boreal forests defoliate spruce stands, thereby allowing broadleaf trees to establish under increased light conditions. These saplings are preferred by moose, whose browsing pressure transforms communities back to being spruce-dominant (Leroux et al., 2020). Feedbacks that maintain structure are more difficult to detect and may be evidenced by a perturbation or the loss of a species. Carnivores, for example, can control herbivore populations, which helps maintain vegetation structural diversity. This role often only becomes apparent after carnivores are extirpated from a system (Gable et al., 2020; Hoeks et al., 2020; Yovovich et al., 2021). Change-inducing feedback loops resulting from the functional extinction of animals can have important implications for carbon storage, nutrient cycling and biodiversity. Still, they may not be detected for tens to hundreds of years, especially within forested environments, due to the slow growth of trees (Berzaghi et al., 2019; Osuri et al., 2016; Peres et al., 2016; Poulsen et al., 2013). Determining the timescale over which a feedback loop operates may present unique challenges. However, the processes that form a feedback loop may already be described for an ecosystem and simply need to

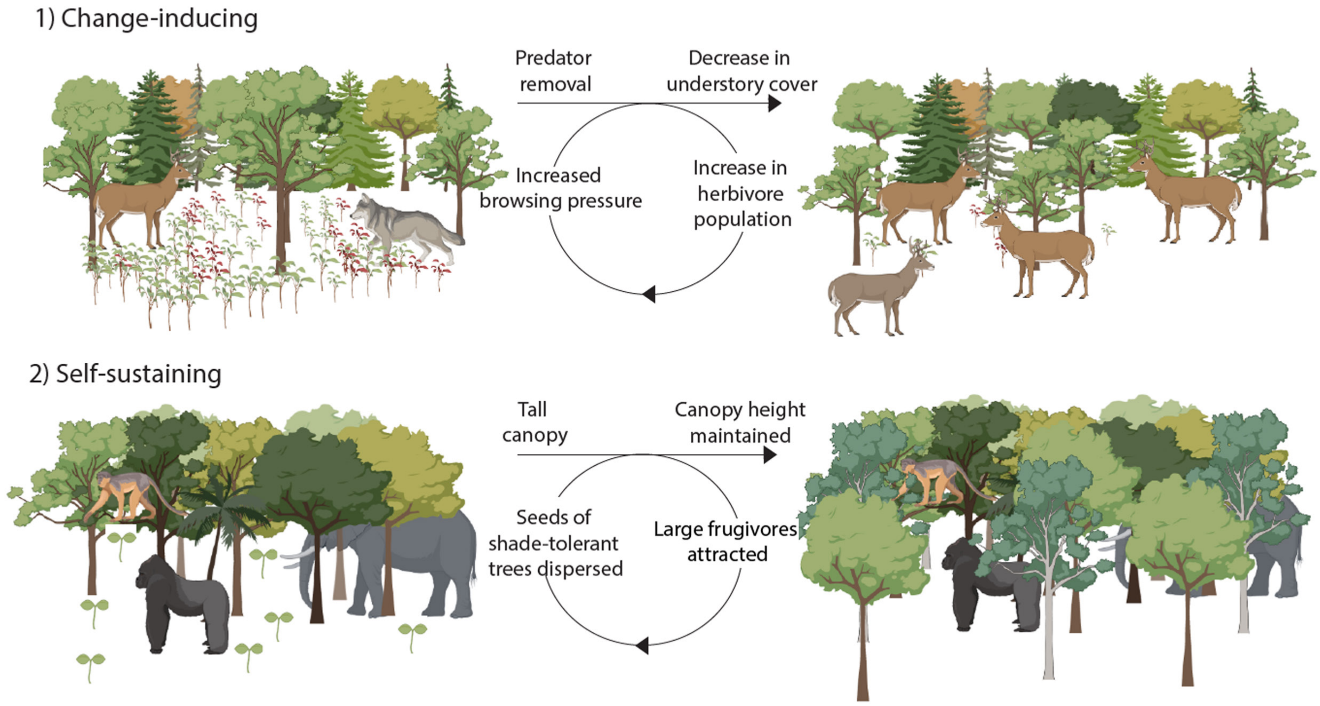

FIGURE 3 Change-inducing vs. self-sustaining feedback. (1) Change-inducing feedback loop in which a top predator (grey wolf; *Canis lupus*) is extirpated from a boreal forest and the ensuing breakdown of a trophic cascade leads to reduced understory cover. (2) Self-sustaining feedback loop in which seed dispersers are attracted to a tropical humid forest with a tall canopy and disperse seeds of trees that become adults and contribute to canopy height. Created with BioRender.com and Adobe Illustrator.

be integrated into a framework that links them together (Borer et al., 2021).

Testing for causal relationships

A feedback loop between animals and vegetation is circular in nature and demands an answer to a fundamental question: what evidence is needed to show that an animal species influences vegetation structure and does not simply choose habitats with favourable structure? Addressing this and other outstanding questions requires appropriate experimental or statistical controls. Large-scale, long-term manipulation or natural experiments are often necessary to establish the direction of effects between animal behaviours and vegetation structure. For example, herbivory by elephants was confirmed as a critical driver of vegetation structure after comparing areas accessible and exclusionary to elephants for more than 60 years in South Africa (Davies et al., 2018). When in situ experiments are not feasible, however, computer simulations can predict changes in vegetation structure resulting from the functional extinction of animals that impact vegetation structure. Simulation approaches have shown that the loss of large frugivores in tropical forests leads to reduced seed dispersal and long-term losses in forest biomass and carbon storage (Bello et al., 2015; Osuri et al., 2016). The processes that influence 3D vegetation structure often do not occur independently, but this problem can be overcome by modelling interrelated factors through an analysis that identifies causal relationships. Structural equation models have proven useful in this regard because they allow researchers to hold statistical variables constant while modelling hypothesized cause-and-effect relationships and to then quantify the magnitude of effects in ecosystem processes with several components (Bernardi et al., 2019; Morante-Filho et al., 2018).

Identifying causal relationships in animal–vegetation feedback loops is critical for modelling tipping points that induce ecosystem change. Alternative ecosystem states are possible when an environment is climatically suitable for more than one ecosystem type (Staver et al., 2011). While climate change, fire and land-use change can accelerate changes to alternative ecosystem states (Saatchi et al., 2021), the influence of animal-driven processes on the frequency of such changes needs further investigation. Ecosystem functioning is driven partly by productivity, stability, vulnerability to invasive species, nutrient dynamics and feedback among these components (Tilman et al., 2014). Interactions between animals and their physical environment can bolster these functions by providing biotic resistance to invasive species (Boelman et al., 2007) or other agents of environmental change, thereby preventing ecosystem degradation and widespread changes to alternative ecosystem states.

Using remote sensing to uncover animal–vegetation structure relationships

A variety of data types are needed to describe feedback between animals and vegetation, and especially its effects on ecosystems. Remote sensing data are particularly useful because they allow researchers to quantify vegetation structure over broader landscapes than field data and with high three-dimensional detail. Many remote sensing techniques exist to measure vegetation structural attributes that influence or are influenced by animal behaviour (Figure 4). Lidar sensors mounted on aircraft or spacecraft can measure attributes of 3D vegetation structure such as vegetation height, fractional vegetation cover and canopy complexity and over scales relevant to habitat selection by wide-ranging animals (e.g. Davies et al., 2017; Davies & Asner, 2014; Evans et al., 2020; McLean et al., 2016; Valbuena et al., 2020). While these metrics are often based on specific hypotheses of how vegetation structure influences animal behaviour, the 3D nature of lidar point clouds can also be preserved in a principal component analysis to show which aspects of 3D structure and heterogeneity are important to animals (Ciuti et al., 2018). Finer-scale interactions between animals and vegetation structure can be described using data from drone-mounted lidar or Terrestrial Laser Scanning (TLS), a lidar mounted on a tripod that scans vegetation below the canopy (Blakey et al., 2017; Orwig et al., 2018). For example, lidar data acquired both above- and below-canopy are useful for quantifying how vegetation structure can aid or impede an animal's line of sight and therefore its ability to detect predators (Aben et al., 2018; Davies et al., 2021; Davies, Tambling, et al., 2016). Lidar data are becoming more common for a variety of ecosystem types, but multiple lidar acquisitions per year are still rare. Such data can reveal how animal behaviours shape vegetation structure over time and how animals shift their behaviour in landscapes where vegetation structure changes seasonally.

Airborne lidar can help reveal drivers of animal behaviours that operate at a scale of several thousand hectares or less, but many phenomena are observable at an ecoregion or global scale. Animal migrations between continents, for example, would require acquisitions of 3D landscape structure data beyond the reasonable operation of airborne lidar. Currently, there is no wall-to-wall global lidar product with regular collections. Therefore, other types of remote sensing data and analytical techniques may be necessary

Remote Sensing Technique	Data Sources	Spatial Resolution	Example Applications
LiDAR	Terrestrial Laser Scanning	<1 cm³	Individual Tree Crown metrics Vegetation structure - Height - Cover - Vertical complexity Vegetation configuration - Connectivity - Edge density
	Airborne/Drone Laser Scanning	<1 m³	
	Spaceborne - GEDI - ICESAT-2	<1 m horizontal 2-3 m vertical	
SAR	Sentinel-1 C-band	10 m	Vegetation presence Vegetation heterogeneity Vegetation biomass
	NISAR L-band	<50 m	
	ALOS PALSAR L-band	10 m	
Optical	Commercial High-Res Imagery - Planet Labs	<5 m	Canopy Height (w/ lidar fusion) Vegetation cover
	Drone Image Photogrammetry - Structure from Motion (SfM)	<1 m³	3D structure mapping of: - Sparsely vegetated habitats - Ultra-fine scale habitat

Example Visualizations

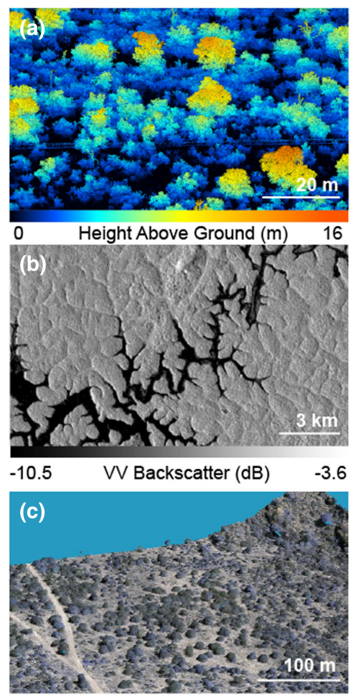

FIGURE 4 Measuring 3D vegetation structure with lidar, synthetic aperture radar (SAR) and optical data. (a) An aerial view of 3D vegetation structure measured with airborne lidar in Kruger National Park, South Africa, coloured according to vegetation height. (b) A map of vertical–vertical (VV) backscatter values for a composite image of the Dja River in eastern Cameroon, using Sentinel-1 C-band SAR. Here it is possible to see the river slicing through a landscape of tropical humid forests and swamps. (c) SfM rendering of 3D habitat structure in Mpala Research Centre, Kenya (data from Strandburg-Peshkin et al., 2017). GEDI: Global Ecosystem Dynamics Investigation; ICESAT-2: Ice, Cloud, and Land Elevation Satellite; NISAR: NASA-ISRO Synthetic Aperture Radar; ALOS PALSAR: Advanced Land Observing Satellite Phased Array type L-band Synthetic Aperture Radar; SfM: structure from motion.

to overcome these limitations. Spaceborne lidar data are freely available for most temperate and tropical ecosystems through the Global Ecosystem Dynamics Investigation (GEDI) mission. While GEDI is contributing to important research in ecology and biodiversity, its spatial sampling regime (25 m diameter shots spaced 60 m apart) leaves gaps in spatial coverage. Machine learning can overcome this problem by fusing data from multiple sources to predict missing values of 3D structural attributes (Qi et al., 2019; Rishmawi et al., 2021). One approach used simulated data from GEDI and another satellite lidar aboard the Ice, Cloud and land Elevation Satellite (ICESAT-2) and Synthetic Aperture Radar data to improve estimates of aboveground biomass compared to any sensor alone (Silva et al., 2021). ICESAT-2 is a spaceborne lidar that measures vegetation height and structure globally, but unlike GEDI, cannot penetrate dense canopies (Silva et al., 2021). Data from this sensor will be especially important for measuring vegetation structure over large scales in polar regions. Synthetic Aperture Radar (SAR) uses backscatter intensity to measure heterogeneity in habitat structure and is often used to map aboveground biomass (Mitchard et al., 2009). Unlike lidar, SAR is not limited by cloud cover, which makes it useful for interpolating vegetation structural metrics where gaps occur in lidar coverage in persistently clouded areas. The National Aeronautics and Space Administration-Indian Space Research Organization SAR (NISAR) is planned to begin collecting L-band SAR data in 2023, providing global coverage of SAR data powerful enough to measure aboveground biomass from ground to canopy (Rosen et al., 2015). In addition, the Earth Explorer-7 Biomass mission is a P-band SAR that is expected to penetrate dense canopies well and contribute to the understanding of 3D vegetation structure (Ustin & Middleton, 2021).

Because airborne lidar scanners can be expensive to operate within a target ecosystem, techniques using optical data to map 3D vegetation structure can sometimes be a substitute. Structure from Motion (SfM) photogrammetry, a technique that maps 3D ecosystem structure from a patchwork of optical photographs collected using a drone has proven useful in ecosystems with few woody plants, such as deserts, grasslands and shrublands (Cunliffe et al., 2016; Forsmoo et al., 2018). In one study, SfM provided structural details for a savanna where an olive baboon troop was GPS-tracked at a high spatiotemporal resolution, helping to show short-term attraction and repulsion to dense vegetation, roads and other features of the landscape (Strandburg-Peshkin et al., 2017). Recent advances in commercial, high-resolution imagery can serve a similar purpose by providing textural details that correspond to canopy height (Csillik et al., 2020). Ultimately, the choice of a remote sensing technique for characterizing animal–vegetation feedback loops will depend on budget and the spatial and temporal scales most appropriate for relating 3D vegetation structure to animal behaviour.

Measuring animal movement and behaviour

Recent advances in animal tracking promise to expand the possibilities for quantifying interactions between animals and 3D vegetation structure. Animals as small as 100 g can now be tracked over their lifetimes with solar-powered GPS tags (Jetz et al., 2022). Tracking the 3D movements of animals will be important for understanding the role of vegetation structure in shaping animal behaviour. While animals moving through airspace have been tracked in 3D using tags that measure changes in air pressure and temperature (Dreelin et al., 2018; Shipley et al., 2017), 3D tracking has not typically been employed for animals moving primarily through vegetation (Belant et al., 2019; Hermans et al., 2023). The use of 2D tracking data to infer habitat selection or ecological functioning of animals is limited because animals often move through 3D space created by vegetation (Gámez & Harris, 2022). Further developments in 3D tracking technology would enhance understanding of many topics discussed here.

Analysing animal tracking data is equally important for understanding animal–vegetation feedback. The family of Habitat Selection Analyses (HSA) are often used to understand how animals move in relation to 3D vegetation structure (Davies et al., 2017; McLean et al., 2016; Northrup et al., 2022; Zeller et al., 2017). This approach compares animal positions, movement steps or full movement paths to randomly generated options considered available habitat. Recent advances have shown how HSAs can be used to generate predictions about animal movements and habitat selection (Potts et al., 2022). This application of HSAs is a promising avenue for inferring ecological functions from GPS data. Population-level estimates are often drawn from HSAs, but the importance of individual variation in movement behaviour has increasingly been recognized as a key factor in ecological functions of animals (Shaw, 2020). Individual personalities (e.g. boldness, exploratory behaviour) can lead to different foraging patterns, space use and reproductive behaviour, all of which can influence their role in shaping vegetation structure (Spiegel et al., 2017; Stuber et al., 2022). Individuals may differ in home range size and the diversity of behaviours they exhibit. Home range, or the space animals use to survive and reproduce, is a useful and widely available metric that can help show how animals interact with vegetation structure through space and time (Jaap et al., 2023). The development of Continuous Time Movement Models has increased the reliability of home range estimates and other characteristics of movement behaviour by reducing the sensitivity of estimates to the sampling regime and treating movement as a continuous process (Calabrese et al., 2016; Noonan et al., 2019). Through an individual movement track, it is also possible to identify a behavioural 'syndrome', such as whether the individual is a central-place forager, nomadic or migratory (Abrahms et al., 2017) and therefore how site fidelity relates to ecological function. The diversity of movement strategies within an animal population is an interesting area of further research with implications for how communities assemble and ecosystems function (Costa-Pereira et al., 2022).

Although GPS locations in themselves cannot capture many important aspects of animal behaviour that might affect vegetation structure, machine learning can be used to infer behavioural states such as foraging or dispersing based on observed distributions of step lengths and turning angles, and where available, body orientation and acceleration (Nathan et al., 2012; Torney et al., 2021; Yu et al., 2021). Hidden Markov Models, for example, estimate unobserved behavioural states using common metrics from GPS or accelerometer data (Klarevas-Irby et al., 2021; McClintock et al., 2020). Continuing to improve analysis methods for animal telemetry data will be important for quantifying the importance of vegetation structure for animal behaviour and how these behaviours in turn shape vegetation structure.

HUMAN IMPACTS THAT ALTER FEEDBACK LOOPS

Human disturbance alters or disrupts feedback between vegetation structure and animals by modifying vegetation structure directly and by influencing animal behaviour (Figure 1). Landscape modification by people is a primary source of change in vegetation structure, often with long-lasting effects (Lenoir et al., 2022). Direct human disturbance encompasses both human footprint and human presence; the former describes the transformation of landscapes through urbanization, natural resource extraction, agriculture, and hunting, whereas the latter describes how humans influence animal behaviour simply by sharing space (Nickel et al., 2020). Both classes of human disturbance have been shown to impact the movement behaviour of a variety of animal taxa, with activities such as recreation and hunting imposing the most substantial effects (Doherty et al., 2021). Animals either reduce their range in response to shrinking habitats (Hirt et al., 2021; Tucker et al., 2018) or move long distances to find suitable habitats in disturbed landscapes (Doherty et al., 2021). Such effects on animal movements alter patterns of nutrient transport, seed dispersal and other ecosystem services that maintain and regenerate vegetation (Bauer & Hoye, 2014). While humans in many contexts have hunted wildlife sustainably for millennia, overhunting in fragmented landscapes has significant effects on animal populations and behaviours and diminishes ecosystem services. For example, in seed dispersal networks of tropical forests, the largest frugivores are most at risk of being hunted by humans, yet they disperse the greatest proportion of large-seeded trees, which typically grow to the greatest sizes. Reduced recruitment of large trees not only disrupts interactions with the animals that depend on and disperse them but can also initiate long-term consequences for regional and global climate because these trees hold the greatest capacity for carbon storage (Enquist et al., 2020; Peres et al., 2016; Rogers et al., 2021). The fruits of these trees may also balance the diets and economy of local people that ensure seed dispersal and cultivation (Van Zonneveld et al., 2018).

Downstream effects of human alterations to landscapes, such as climate change and wildfires, also significantly alter feedback between vegetation structure and ecosystem function. Fire-adapted and fire-naïve ecosystems alike are burning hotter, more extensively, and more frequently due to prolonged droughts and changes in human land use and management (Nimmo et al., 2021). These changes in fire regimes limit the ability of vegetation to recover and wildlife to recolonize habitats (Kelly et al., 2020), thereby disrupting feedback. Many animal species benefit from early successional habitat maintained by regular fires, but if fires are too frequent, characteristic plant species will not have time to mature and provision these species with food or shelter (Kelly et al., 2020). In contrast, ecosystems that depend on natural fires, such as savannas, may not burn if they are overgrazed by livestock (Veldhuis et al., 2019)—another human practice that disrupts vegetation–animal feedback. The consequent reduction or loss of fires and extirpation of wild herbivores leads to woody encroachment in savannas (Stevens et al., 2017). Changes in fire regimes can initiate a feedback loop whereby increases in woody encroachment reduce suitable habitat for herbivores that would otherwise prevent both woody plant recruitment and severe fires by creating heterogeneity in grassy fuel (Foster et al., 2020). Increased frequency and severity of fires imposed by human disturbance thereby threaten the balance between animals and vegetation structure.

Anthropogenic changes to landscapes can shut wildlife out of preferred habitats and force them closer to human settlements, which increases the risk of human–wildlife conflict and disease spillover. Such conflicts can emerge due to deforestation, which dramatically impacts vegetation structure across landscapes and may drive wildlife to alter the structure of other habitat types. For example, grey-headed flying foxes (*Pteropus poliocephalus*) have entered a change-inducing feedback loop in Australia after deforestation caused large roosting colonies ('camps') to form in urban areas where populations are sustained by fruiting and flowering trees (Boardman et al., 2021; Williams et al., 2006). In turn, burgeoning flying fox camps defoliate and break branches of urban trees, which—alongside perceived disease risk—prompts humans to move urban flying fox populations, a practice that merely spreads the problem (Hall, 2002). In this way, the interactions between humans and flying foxes, precipitated by the ways this bat species modifies vegetation structure, could shift flying foxes from providing ecosystem services including seed dispersal and pollination of economically valuable trees to being responsible for ecosystem disservices, such as disease spillover (Eby et al., 2023).

USING FEEDBACK LOOPS IN CONSERVATION

Identifying critical links in the feedback between vegetation structure and animal behaviour can improve biodiversity-focused conservation and restoration strategies, which often place a premium on habitat heterogeneity and the structural complexity of vegetation (e.g. Erdős et al., 2018; Martins et al., 2017; Tuanmu & Jetz, 2015; Zellweger et al., 2013). Structural complexity is a strong driver of both biodiversity and ecosystem functioning, as it creates variation in both vertical and horizontal space for niche partitioning (Coverdale & Davies, 2023; Gámez & Harris, 2022; Larue et al., 2019; Oliveira & Scheffers, 2019; Pawar et al., 2012). Accordingly, attributes of 3D vegetation structure such as height and complexity—both vertical and horizontal—have informed biodiversity-focused conservation of birds (Weisberg et al., 2014), mammals (Deere et al., 2020) and arthropod communities (Müller et al., 2014). Some studies have extended this approach to identify 3D structural attributes important for landscape connectivity and animal movement (Casalegno et al., 2017; Guo et al., 2018; Zeller et al., 2016) as well as species interactions (Sovie et al., 2020).

Managing land to encourage beneficial change-inducing feedback offers a process-oriented approach to restoring degraded ecosystems (Figure 5). However, it is important to note that recent studies have challenged what is meant by 'degraded', highlighting that logged forests can still harbour diverse plant and animal communities with heightened flows of energy and nutrients (Malhi et al., 2022; Sullivan et al., 2022). These findings suggest that plant and animal ecological roles can be harnessed to restore degraded ecosystems.

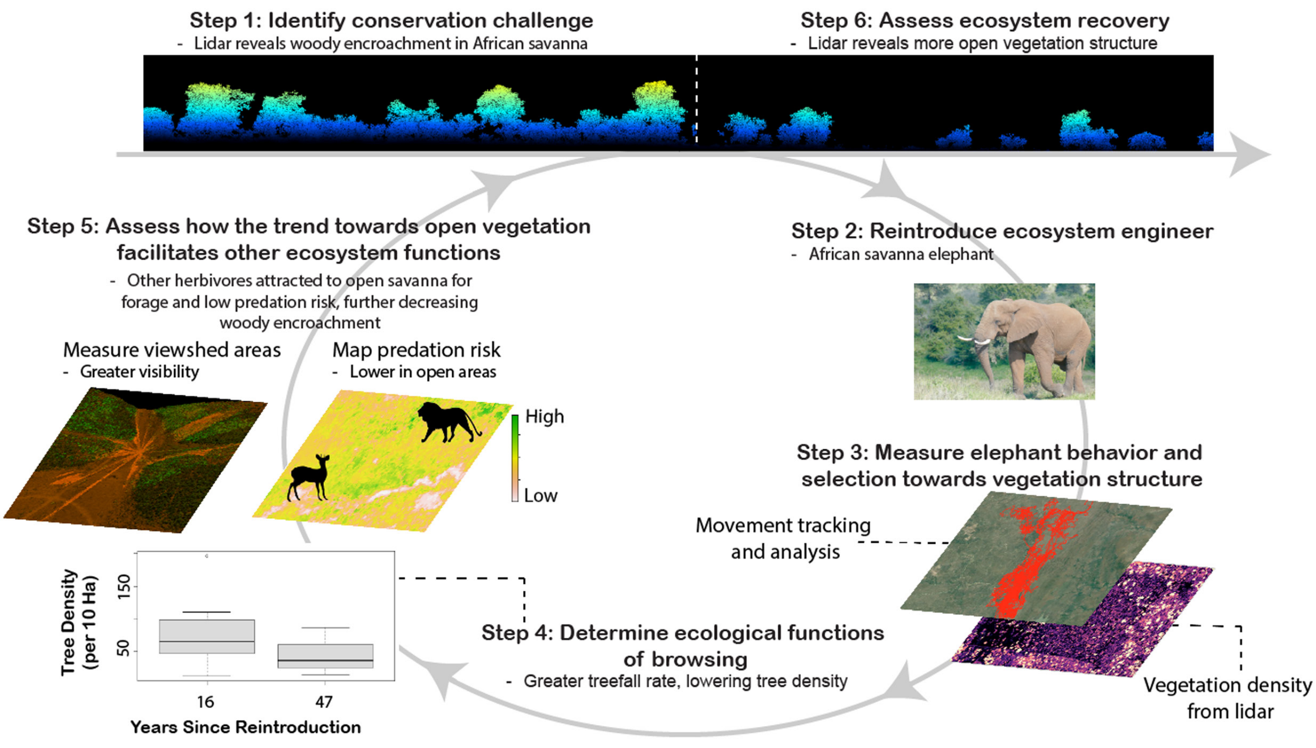

FIGURE 5 Using the feedback loop approach to inform the conservation of an African savanna. In this worked example, we demonstrate the components of a feedback loop between the 3D vegetation structure and ecological functions of animals. This example demonstrates a way to address the challenge of woody encroachment in a savanna by initiating a change-inducing feedback loop, including examples of patterns and processes that can be measured to describe the feedback. In this example, reintroduced African savanna elephants are attracted to dense vegetation, where they browse and knock down trees, creating more open vegetation structure and attracting other herbivores, which contribute to further increases in vegetation openness by browsing and grazing in areas where they can easily find forage and detect predators. This figure draws from many examples in African savannas, with the examples in Steps 1 and 6 from inside and outside the Nkuhlu herbivore exclosure in Kruger National Park, South Africa; the example in Step 2 of rewilding in South Africa from Gordon et al. (2023). Photo: Bernard Dupont, CC BY-SA 2.0 via Wikimedia Commons; elephant tracking data in South Africa in Step 3 from Thaker et al. (2019); tree density data in Step 4 from Gordon et al. (2023) and viewshed in Step 5 from (Davies, Tambling, et al., 2016).

Structural attributes of vegetation promote the ecological roles of animals that rebuild or shape important aspects of an ecosystem's vegetation structure. For example, perches and nest cavities can attract seed rain from birds and aid in the assisted restoration of tropical forests (González-Castro et al., 2018). In addition, planting fruiting trees in disturbed landscapes attracts a variety of frugivores that disperse seeds and accelerate reforestation (Camargo et al., 2020; Carlo & Morales, 2016; Corbin et al., 2016). The lateral connectivity of tropical canopies promotes the movement of arboreal animals such as primates, which disperse seeds and consume foliage (McLean et al., 2016). Accordingly, artificial canopy bridges may support primate populations that contribute to forest recovery (Chan et al., 2020). Assisted reintroductions of species to landscapes can also promote change-inducing feedback that recovers past vegetation structure. One example from a South African savanna showed how elephant browsing behaviour in densely vegetated areas contributed to an eventual increase in landscape openness through a change-inducing feedback loop (Gordon et al., 2023).

Conservation frameworks that show how animals contribute to all stages of plant community succession, such as through changes in the tempo, quantity, and diversity of seed dispersal, highlight the importance of feedback in restoring terrestrial ecosystems (Dent & Estrada-Villegas, 2021). Findings from this review indicate that conservation efforts will benefit from considering all relationships in a feedback loop between vegetation structure and the ecological roles of animals. Such efforts have the potential to enhance strategies to protect or restore ecosystems by piecing together strategies that may have limited effects on their own.

Considering feedback between vegetation structure and animal behaviour is particularly important in forecasting the effects of global change, which can induce shifts to alternative ecosystem states. Ecosystem tipping points are typically brought about by a perturbation, such as extreme weather, land-use change, pollution or introduced species (Dakos et al., 2019; Staver et al., 2011). Such changes are already occurring in humid tropical forests—especially in the Amazon Basin—where a feedback cycle of drought, fire and tree death transforms humid forests into more open woodlands (Saatchi et al., 2021). The feedback that sends these ecosystems into an alternative state will incur high costs for the planet because humid tropical forests harbour over half the world's carbon stocks and two-thirds of its biodiversity (Giam, 2017; Pan et al., 2011). Similar change-inducing feedback may be occurring undetected in other ecosystems; a better understanding of how ecosystems function as a network of feedback loops can improve estimations of ecosystem tipping points and how additional factors, such as trait adaptation of plants and animals, can delay shifts among ecosystem states (Dakos et al., 2019). Priorities for future research include describing the nature of feedback loops between animals and vegetation structure, and how they behave in response to disturbance or assistance (Box 1). A primary goal of this line of thinking is improving how we monitor ecosystem health by estimating whether ecosystems are in a state of self-sustaining or change-inducing feedback. In this way, incorporating the animal–vegetation structure feedback loop concept into conservation decisions can help preserve the ecological processes that keep ecosystems intact.

BOX 1 Outstanding questions

1. How can a feedback loop be identified as self-reinforcing or change-inducing?
2. When do feedback loops switch from self-reinforcing to change-inducing or vice versa?
3. Do animal functions render vegetation structure more resilient to perturbations?
4. What is the influence of animals on vegetation structure relative to other factors at different spatial and temporal scales?
5. Is vegetation structure shaped primarily by many weak interactions or a few strong ones?
6. Which ecosystem types are shaped most strongly by animal influences on vegetation structure?
7. How has coevolution shaped interactions between animals and vegetation structures?
8. How can animal–vegetation structure interactions contribute to the biological and functional diversity of ecosystems?
9. Animals can homogenize or diversify vegetation structure—how should each type of role be prioritized in conservation efforts?
10. Can feedback loops be leveraged to increase the delivery of ecosystem services, for example increased agricultural yields or decreased risk of zoonotic spillover?
11. How do dynamics in human presence (e.g. recreation or poaching) influence feedback loops between animals and vegetation structure?

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NJR wrote the first draft with substantial input from all authors. All authors contributed to the final version.

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DATA AVAILABILITY STATEMENT

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