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Analogous losses of large animals and trees, socio-ecological consequences, and an integrative framework for rewilding-based megabiota restoration

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Abstract

1. Large-sized animals (megafauna) and trees (megatrees) are key ecosystem components with high cultural and economic importance going back millennia. Once common, both groups of megabiota have been massively reduced in pre-historic and historic times, with human-induced downsizing still ongoing.
2. Key ecosystem services provided by megafauna and megatrees include nutrient and seed transfer, carbon allocation, climate regulation and biodiversity facilitation. Socio-cultural services include food and timber provisioning and the 'charisma' of large-sized organisms, with its associated high cultural, recreational and nature conservation values for human societies worldwide.
3. Conservation and restoration of megafauna and—trees in a socio-ecological framework are needed to counteract past and ongoing analogous downsizing of both groups of megabiota and the loss of important ecosystem services in a human-dominated world. Importantly, synergistic megatree–megafauna restoration promotes self-regulating biodiverse ecosystems across the full range of land use intensities ranging from current downsized wildlands to highly human-modified landscapes.
4. We propose an integrative rewilding-based restoration framework applicable across the whole range of human land use intensity. This includes individual-based protection, assisted colonisation and facilitation of urban wildlife. Active management of megafauna and -trees can be economically beneficial and necessary to minimize human–wildlife conflicts in highly human-dominated landscapes. Societal acceptance and adaptation to old big trees and wild megafauna are prerequisites for successful megabiota restoration in human-modified landscapes and elsewhere where human–wildlife conflicts are hard to avoid.
5. The prime goal of such integrative rewilding activities should be a proactive facilitation of the self-regulation potential of natural and novel ecosystems for which large-sized trees and animals would be some of the most important components for enhancing biodiversity and societal value in the Anthropocene. Such megabiota restoration needs to be done on a wide scale to restore functional effects on the biosphere.

KEYWORDS
adaptive management, downsizing, large-sized trees, megafauna, resilience, restoration, rewilding

1 | INTRODUCTION

Large-sized animals and trees play important, often unique roles in ecosystems and are of extraordinary importance for the natural and cultural heritage of societies worldwide (Enquist, Abraham, Harfoot, Malhi, & Doughty, 2019; Hall, James, & Baird, 2011; Lindenmayer, Laurance, & Franklin, 2012; Svenning et al., 2016). Both groups of megabiota (cf. Enquist et al., 2019) used to be common features of ecosystems across much of the earth, but have experienced massive human-driven declines over the past millennia. These declines are still ongoing in many places (Dirzo et al., 2014) and risk to be exacerbated in the future due to unsustainable human exploitation of natural resources and other global change-induced pressures. Typical scenarios resulting from these losses continuing in the Anthropocene appear as landscapes depauperated in big trees and big animals (Figure 1), with contingent reduced ecosystem functionality (Enquist et al., 2019; Galetti et al., 2018). Active restoration of both groups of megabiota in a socio-ecological framework is therefore a key challenge for the Anthropocene, but a coupled focus on megabiota has been neglected so far (except Enquist et al., 2019). Here, we review the patterns and drivers of downsizing along with the key ecological, cultural, and socio-economic services provided by megafauna and trees. Additionally, we outline a framework for integrative restoration of both groups in a socio-ecological context, applicable across the whole range of human land use intensities. Here, we adhere to the minimum size definitions of Malhi et al. (2009) defining megafauna in continental settings as large herbivores (45–999 kg), megaherbivores (≥1,000 kg), large carnivores (21.5–99 kg) and megacarnivores (≥100 kg). However, we allow deviations from this definition for specific settings (e.g. island faunas) where we define megafauna as the largest animal species in a given ecological community or guild in the absence of anthropogenic defaunation (Hansen & Galetti, 2009). Accordingly, we define megatrees as trees with a with a minimum stem height of 20 m (cf. Lindenmayer & Laurance, 2016) and representing the largest 1% of trees (cf. Ali et al., 2019; Lutz et al., 2018) in a given ecosystem in the absence of strong past downsizing. Knowledge about past downsizing can be obtained from the collective memory of local communities or other sources of historical or pre-historic information. The latter can include e.g. paleoecological records, historic pictures or literature, or direct methods of historic reconstruction (e.g. using tree ring and decay stage analysis of tree stumps; Storaunet, Rolstad, & Groven, 2000).

2 | LOSING THE GIANTS–ANALOGOUS ANTHROPOGENIC DOWNSIZING OF ANIMALS AND TREES

Downsizing of global faunas is a well-recognized fact; however, a similar effect on trees is less widely realized, especially in its historical context (but see Lindenmayer et al., 2012). Nevertheless, recent and historical downsizing of trees caused by losses of megatrees is repeatedly reported across all latitudes (Jönsson, Fraver, & Jonsson, 2009; Laurance, Delamônica, Laurance, Vasconcelos, & Lovejoy, 2000; McIntyre et al., 2015). The reasons for the ongoing analogous downsizing of animals and trees are multifaceted, but ultimately human-driven. Size-selective hunting and logging as well as habitat destruction are the main recognised historical and current drivers (Dirzo et al., 2014; Lindenmayer & Laurance, 2016). Hunting-linked megafauna losses started at least some 50,000 years ago (Sandom, Faurby, Sandel, & Svenning, 2014). Logging has been the major driver of tree downsizing for at least 8,300 years (Yasuda, Kitagawa, & Nakagawa, 2000) and is still dominant in much of the world today (Lindenmayer et al., 2012). Today, these long-term drivers of megatree losses are complemented by novel stressors such as modern forestry, aiming for economic optimization of timber production by cutting trees well before they reach maximum size (Miklín & Čížek, 2014). Furthermore, global climate change is driving drought—and/or heat-induced tree mortality, often with particularly strong effects on large trees, causing their selective loss (McIntyre et al., 2015).

3 | THE SOCIO-CULTURAL AND ECONOMIC CONSEQUENCES OF THE ANALOGOUS ANTHROPOGENIC DOWNSIZING

Megafauna and trees have been of high socio-economic value for humanity for millennia. Traditional indigenous as well as modern societies have strong spiritual and cultural connections to large-sized trees, reflected in their predominance in mythology, prehistoric and historical art, but also in modern blockbuster movies (e.g., Grandmother Willow in Pocahontas 1995, Treebeard in Lord of the Rings: The Two Towers 2002, Tree of Souls in Avatar 2009, Sacred Tree of Jedi in The Last Jedi 2017, Alligator juniper in Only the Brave 2017). Megafauna is a prominent subject of pictorial art since the emergence of art in human societies, with the rock and cave paintings of Bradshaw (Australia), Chauvet or Lascaux (France) and Altamira (Spain) as famous examples dating back at least 35,000 years (Chauvet, Deschamps, & Hillaire, 1996; Pike et al., 2012). Elephants and other proboscideans played an important role in pre-historic times not only as a major food source and for the production of tools (e.g. axes), but also in symbolic imagery (figurines and statuettes) with high cosmological importance (Lev & Barkai, 2016). Large-sized herbivores, predators, and trees are popular motifs in our modern societies where they serve as emblems on currencies, stamps, seals, and flags of numerous institutions (Farmer,

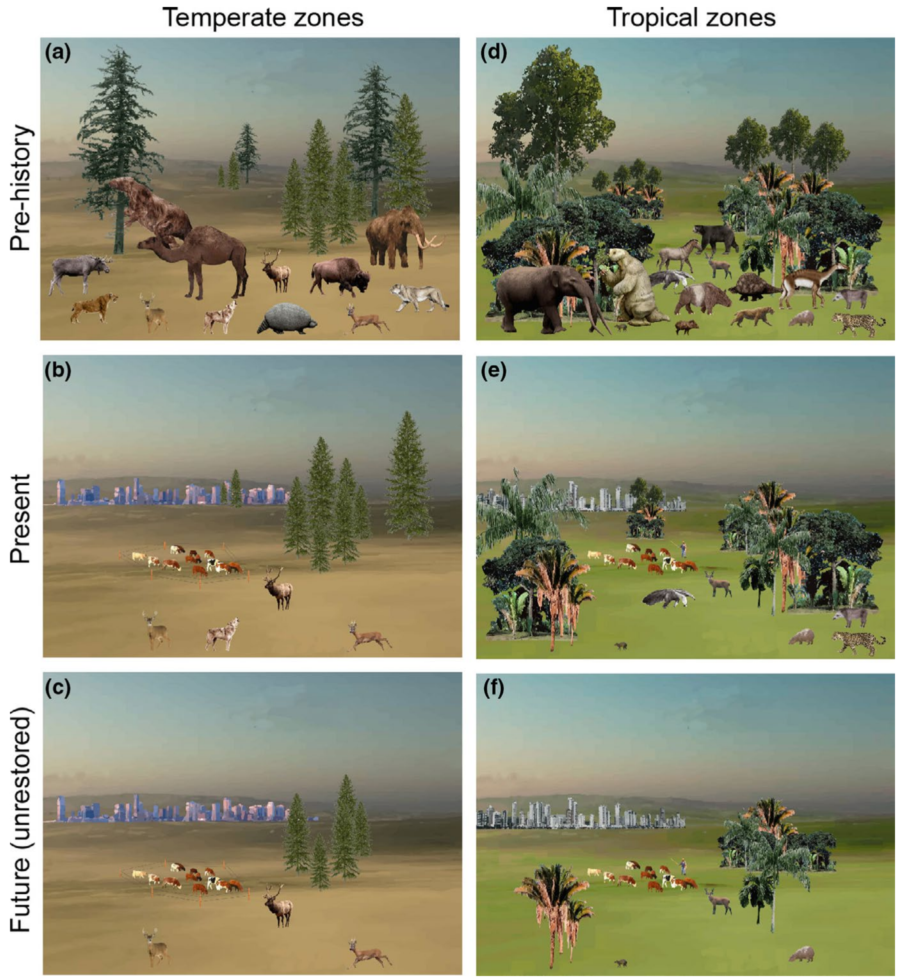

FIGURE 1 Megatree-megafauna landscapes through time. Megafauna and megatrees have coexisted over long periods of pre-historic time in major parts of the world (e.g. temperate zone: a-c or tropical regions: d-f). (a, d) Massive losses of megafauna and megatrees during the Late Pleistocene to historic times have resulted in the downsized tree and animal communities currently predominating our landscapes (b, e). Without active protection and restoration of megafauna and megatrees, ongoing defaunation and deforestation in combination with the current and expected climate changes and other anthropogenic disturbances will reinforce this downsizing (c, f)

2010) or are utilized in magazines, television and the advertisement of consumer products like, e.g. beer and cider (Feldhamer, Whittaker, Monty, & Weickert, 2002). Megafauna and—trees represent 'charismatic' organisms many people sympathise with and comprise an essential part of the modern world's cultural and natural heritage (Hall et al., 2011). Both are major tourist attractions drawing millions of people to e.g. national parks, representing a source of income not only for the parks but also for the surrounding economy (Lindenmayer & Laurance, 2017; Ripple et al., 2014).

Megatrees were and still are of high economic importance by providing important resources like food or construction materials. Timber use of megatrees for construction dates back millennia. Lebanon cedar (*Cedrus libani*), for example, was already used in ancient Egypt to build sarcophagi and other burial appurtenances and was heavily exploited in the Middle East and Mediterranean regions until the early 20th century (Liphshitz & Biger, 1991). Nowadays, populations of this species are severely fragmented, likely downsized and in decline due to historic overexploitation and ongoing land use change (Gardner, 2013). Baobab trees (*Adansonia digitata*) are in daily use by local communities in Africa to produce a variety of products with international economic importance (Chadare, Hounhouigan, Linnemann, Nout, & Boekel, 2008). Brazil nut (*Bertholletia excelsa*) is one of the most economically important non-timber forest products in South America (Wadt, Kainer, & Gomes-Silva, 2005), but strongly threatened by deforestation (IUCN, 1998).

The domestication of megafauna like horses, cattle and sheep is one of the most important developments in human history in the past 13,000 years and a prerequisite to the rise of civilization (Diamond, 2002). Nowadays, a large portion of human diet originates from intensive livestock farming with adverse effects on global ecosystems, climate as well as animal welfare (Garnier et al., 2019; Tilman, Cassman, Matson, Naylor, & Polasky, 2002). Climate change is expected to strongly limit this conventional livestock production (Rojas-Downing, Nejadhashemi, Harrigan, & Woznicki, 2017). Meat of wild and semi-wild megafauna managed in sustainable production systems (e.g. herding, semi-intensive domestication), extensive livestock management of cattle or other domesticated megafauna or integrated, crop-livestock or forest-livestock systems provides an alternative. Although still of minor importance, this alternative source of meat is globally gaining economic importance due to the increasing concern of modern societies about healthy and sustainable resource use (e.g. Bussoni, Alvarez, Cubbage, Ferreira, & Picasso, 2017; Hoffman & Wiklund, 2006; Lemaire, Giroud, Bathily, Lecomte, & Corniaux, 2019). Replacing ruminants (such as bovids) with other herbivores (hind gut fermenters such as horses) can furthermore strongly reduce greenhouse gas emissions (Cromsigt et al., 2018). This could be especially relevant from a climate change perspective because ruminants are intensively used in livestock farming which contributes currently about 18% to the global warming effect (Steinfeld & Wassenaar, 2007).

Based on their popularity, large-sized trees and animals often play an important role in the marketing of nature conversation where they are frequently used as 'flagship' or 'umbrella' species to garner public support for the protection of whole ecosystems including the numerous less visible and less charismatic species (Hall et al., 2011). Losing the megabiota will have significant socio-cultural and socio-economic consequences, hereunder potentially reducing public support for nature protection.

4 | THE ECOLOGICAL CONSEQUENCES OF ANALOGOUS DOWNSIZING

4.1 | Large-sized trees and water fluxes, carbon allocation, and habitat provisioning

The main evolutionary reason for trees to become tall is to outcompete co-occurring species for light, maximizing photosynthetic gain of energy (carbon) to maximise reproductive output and, in turn, evolutionary fitness (Larjavaara, 2014). With increasing plant height, trees increase competitive ability. Furthermore, morphologically based, positive relations exist between plant height and photosynthesis-related traits like leaf mass, nitrogen per area, and canopy area. Because of this, plant height is a key trait for carbon gain (Falster & Westoby, 2003).

Taller trees are reported to show higher metabolic and growth rates and, thus, higher rates of carbon storage than smaller trees (Stephenson et al., 2014). Trees allocate proportionally more carbon to structural above-ground tissue when they grow taller, potentially due to increased light availability and total leaf area—both compensating for size (age)-related declines in photosynthetic efficiency (Reich, 2001). This positive relationship between growth rate and height is reported to be a general phenomenon, consistent across species, continents, ecosystems and competitive strength. This makes fast growth of megatrees a global norm rather than a local or species-specific peculiarity (Stephenson et al., 2014). However, growth slows with increasing age/height and is limited to a certain maximum size (currently reported to be 115 m) most likely due to hydraulic limitations of photosynthetic carbon gain (Koch, Sillett, Jennings, & Davis, 2004; Larjavaara, 2014). Even in the downsized setting of our modern world, megatrees play a major role in global carbon storage (Ali et al., 2019; Moles et al., 2009), with large-sized trees accounting for up to 50% of above-ground live biomass in current forests (Lutz et al., 2018).

Megatrees also play a key role in the global water cycle. Large trees often have higher transpiration rates than smaller trees (Wullschleger, Hanson, & Todd, 2001). This can increase water evapotranspiration from forested watersheds, altering water cycling between atmosphere and vegetation with an effect on local and regional climate. Stands of old-growth, big trees can have markedly higher water yields than younger stands (Watson, Vertessy, & Grayson, 1999). This can increase flood risk (e.g. Watson et al., 1999), but also soil moisture and water availability in the upper soil layers, facilitating smaller trees and other understorey vegetation (Dawson, 1996).

Large and especially old trees constitute living diversity hotspots by providing microenvironments, nesting sites and shelter for a plethora of organisms (Cockle, Martin, & Wesołowski, 2011; Lindenmayer & Laurance, 2016; Lindenmayer et al., 2012). Megatree species dispersed by large-sized animals like the baobab and oaks (*Quercus* spp.) can provide megafauna with habitats, food and water (Kelly, 2000; Mysterud et al., 2007). Continuing loss of megatrees will therefore have important effects not just on carbon storage and the rate and magnitude of water movement through vegetation and the regional and global water cycles, but also on the rest of biodiversity. Downsizing of trees must be expected to decrease habitat heterogeneity, forest surface roughness, evapotranspiration and latent and sensible heat transfer considering the disproportional importance of large-sized trees on water and carbon cycles, habitat structure and biodiversity. Near-surface soil moisture and streamflow will also decrease instigating potentially adverse effects on water availability for ecosystems and humans and affecting poorly understood feedbacks on the local, regional and global climate.

4.2 | Large-sized animals and the turnover of organic matter, nutrient translocation, seed dispersal and habitat modification

Positive relationships between body size, metabolism, and locomotion qualify megafauna as particularly important for the sequestration, remobilization and translocation of organic material including nutrients (Doughty, Roman, et al., 2016). Increasing the net metabolic rate in combination with increasing gut capacity and increasing rate of food intake result in substantially higher amounts of organic material (food) being consumed by large compared to small animals (Pires, Guimarães, Galetti, & Jordano, 2018). Larger animals have larger home ranges (Jetz, Carbone, Fulford, & Brown, 2004) and travel longer distances (Bunney, Bond, & Henley, 2017), spreading more nutrients and other labile organic substances per individual over larger areas (Müller et al., 2013).

Large carnivores are reported to enhance carbon storage in tropical and boreal forest stands by regulating browsing pressure of large-sized herbivores (Schmitz et al., 2014; Terborgh et al., 2001). Additionally, large-sized predators are reported to have beneficial effects on ecosystem functioning and services including disease control in wild ungulates and domestic livestock (Packer, Holt, Hudson, Lafferty, & Dobson, 2003) as well as reduction of crop damage by mammal herbivores (Ripple et al., 2014). Disproportionately long gut retention times and travel distances, large home ranges and increased rate of food intake in combination with low gape limitation qualify large-sized frugivorous mammals as important agents for long-distance seed dispersal, notably for large seeded tree species (Bunney et al., 2017; Pires et al., 2018). Furthermore, some light-demanding megatree species like many oaks (*Quercus* spp.) depend on semi-open, savanna-like landscapes, generated at least partly by large-sized herbivores (Vera, 2000) or fire (Nowacki & Abrams, 2008). Large herbivores and carnivores increase diversity of plants, invertebrates and birds by increasing habitat heterogeneity or by decreasing competition between co-occurring plant species (Berger, Stacey, Bellis, & Johnson, 2001; Bump, Peterson, & Vucetich, 2009; Rambo & Faeth, 1999). Furthermore, large-sized herbivores and carnivores can have disproportionately strong regulatory effects on trophic interactions, affecting the structure of trophic webs in terrestrial ecosystems (Estes et al., 2011; Ripple et al., 2014).

Considering the disproportional importance of megafauna for biodiversity, trophic networks and nutrient fluxes, the globally ongoing downsizing of faunas must be expected to have strong effects on biodiversity and ecosystem functioning, continuing and reinforcing the effects of pre-historic megafauna extinction (Doughty, Roman, et al., 2016). A global loss of megafauna will strongly diminish long-distance seed dispersal of trees, which are often megafauna-dispersed (Galetti et al., 2018). Reduced dispersal caused by ongoing defaunation will result in range contractions for megafauna-related trees with significant effects on carbon storage capacity of forest ecosystems (Doughty, Wolf, et al., 2016). Lost seed dispersal interactions between large trees and animals due to the extirpation of the latter can significantly decrease tree height and woody biomass production, further reducing carbon storage in tropical rain forests (Bello et al., 2015). In summary, restoring global megafaunas is likely to have beneficial effects on ecosystem functionality and human wellbeing. However, this only holds true if human–wildlife conflicts potentially emerging from restoration activities are actively minimised by active prevention, protection and mitigation strategies (see e.g. Lamarque et al., 2009 for a comprehensive overview of strategies).

5 | AN INTEGRATIVE REWILDING FRAMEWORK FOR MEGABIOTA IN THE ANTHROPOCENE

The analogous pre-historic and current losses of megafauna and—trees call for new, integrative restoration schemes considering the importance of both groups for ecosystem functioning and biodiversity, but also for human culture and economy. We argue that the (re-)introduction of large-sized animals combined with conservation and restoration activities targeting megatrees will in many cases be beneficial to foster the self-regulation and biodiversity and, thus, functionality of ecosystems. Our proposed framework refers to the definition of trophic rewilding as an ecological restoration strategy that uses megafauna introduction to restore trophic and other ecological interactions to promote self-regulating biodiverse ecosystems (cf. Svenning, Munk, & Schweiger, 2019; Svenning et al., 2016). Here, we go beyond this concept to also include the effects of a key functional group of primary producers, namely megatrees. More generally, we define rewilding according to Perino et al. (2019) as activities restoring trophic complexity, natural disturbances and dispersal as key components of the complexity and resilience of many ecosystems. The integrative restoration of megafauna and—trees will strongly promote these key components. Both definitions call for minimum human management in the long term. However, rewilding activities can encompass initial human interventions. Furthermore, ongoing minimized management might be needed where the degraded ecosystems are not expected to otherwise recover due to anthropogenic constraints or ecosystem management is inevitable to ensure human safety (cf. Perino et al., 2019). This might lead to situations of partial rewilding (see Pedersen, Ejrnæs, Sandel, & Svenning, 2020).

We furthermore argue that megabiota fulfil similar ecological functions (including megatree–megafauna interactions) and ecosystem services in human-modified, semi-open landscapes and forested landscapes. Our proposed megabiota rewilding framework (Figure 2) is therefore generally applicable under different landscape settings and across the full range of human land use intensities.

Extensive, semi-open landscapes are increasingly recognized as a natural-type landscape with high levels of biodiversity (Parr, Lehmann, Bond, Hoffmann, & Andersen, 2014; Veldman et al., 2015). Large herbivores often play a key role in generating these ecosystems (Bond, 2005). Such landscapes are well recognized as dominant in tropical savanna regions and temperate forest-steppe ecotones, but emerging evidence also point to their natural presence within forest biomes e.g., in Europe (Feurdean, Ruprecht, Molnár, Hutchinson, & Hickler, 2018; Fyfe, Woodbridge, & Roberts, 2015; Miklín & Čížek, 2014; Sandom, Ejrnæs, Hansen, & Svenning, 2014). Numerous megatree-forming species depend on or thrive in semi-open environments (Figure 3). Examples include giant sequoia (*Sequoiadendron giganteum*) and several *Quercus* species inhabiting North America and Eurasia as well as acacias and baobabs inhabiting Australia, Africa and the Arab Peninsula. However, this is not the case for several other, shade-tolerant megatree species like coastal redwood (*Sequoia sempervirens*, North America) or tropical tree species like, e.g., *Duguetia surinamensis* (South America) or Murray's Laurel (*Cryptocarya murrayi*, Australia). We therefore do not argue for semi-open, mosaic-like landscapes being a global restoration goal, but rather being a rewilding option for human-dominated, deforested, rural and urban landscapes as well as naturally semi-open, but downsized settings.

A mosaic-like assemblage of tree islands (groves) with different spatial extents can increase heterogeneity and foster regional biodiversity, but can also increase regional carbon uptake and water fluxes, dampening climatic fluctuations. Such a setting will be beneficial in naturally semi-open, but downsized as well as in anthropogenically deforested landscapes. Such megatree islands can serve high cultural and societal values, bearing in mind the long cultural affinity of humanity for megatrees. The high cultural importance

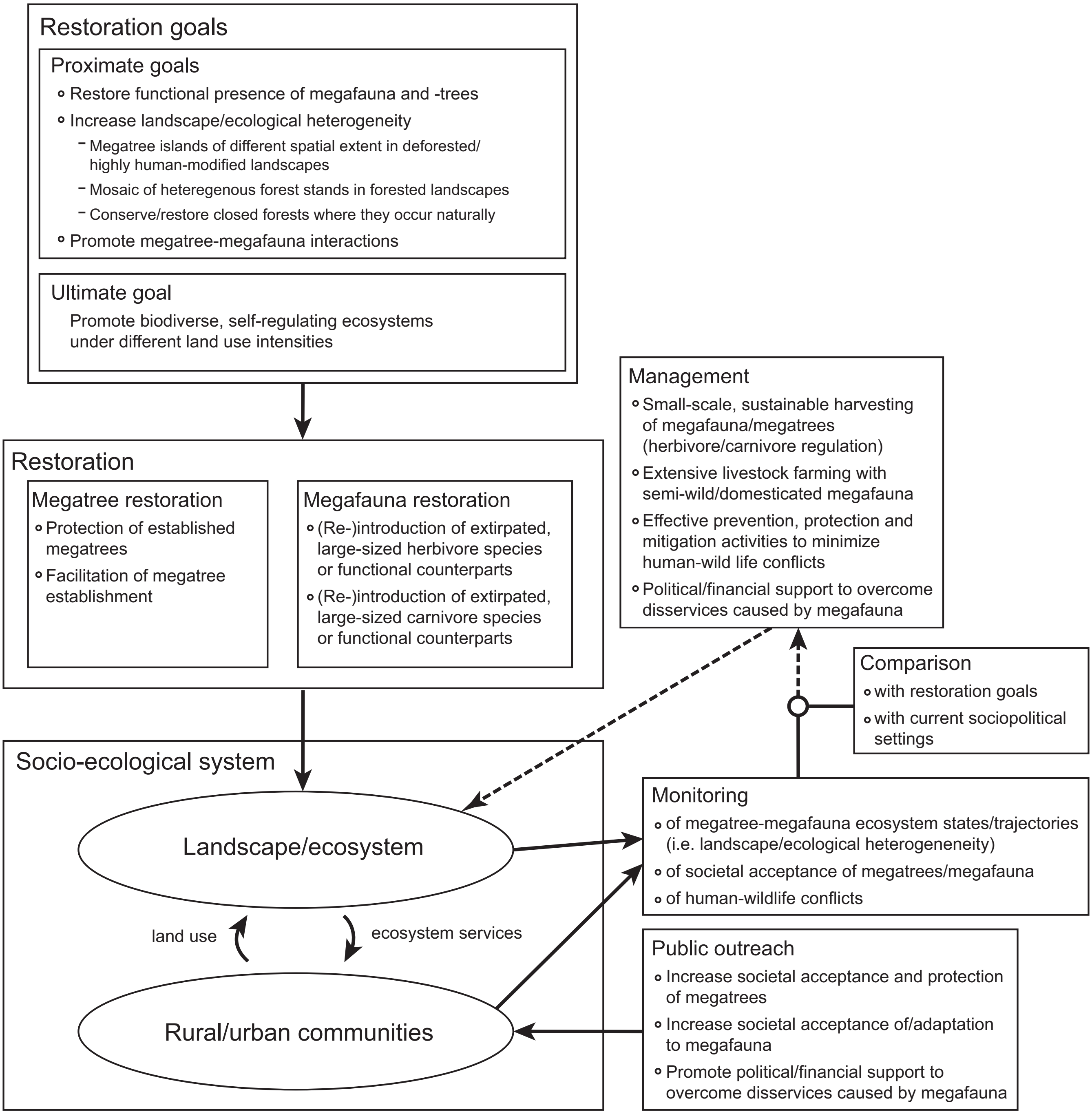

FIGURE 2 Roadmap for rewilding-aimed megabiota restoration in a socio-ecological context. Conservation and restoration of megafauna and -trees will help to foster landscape and ecological heterogeneity and, thus, biodiverse, self-sustainable ecosystems under different land use intensities. Solid arrows visualize direct effects or flows of information between different entities of this framework. Dashed arrows depict optional actions/effects, which will be taken/become operative case specifically. Active management of megabiota with minimal intensity can contribute restoration activities to meet restoration goals and to minimize human–wildlife conflicts. Continuous monitoring of ecosystem state and human–wildlife interactions and comparison with predefined restoration goals and current socio-political settings is needed to evaluate the need of additional management activities. A detailed list of prevention, protection and mitigation strategies/activities to minimize human–wildlife conflicts is provided e.g. by Lamarque et al. (2009)

of such megatree islands is exemplified by sacred forests like the Sacred Mijikenda Kaya Forests in Kenya (UNESCO World Heritage, 2019) or the sacred forests and single individuals of megatrees in Japan, India and Nepal (Omura, 2004), which continue to exist in often deforested landscapes and are closely linked to religious beliefs or infrastructures (e.g. shrines in Japan). The establishment of groves arranged in a mosaic-like setting can therefore be especially beneficial in human-dominated, homogenized, and urbanized landscapes, which currently predominate large parts of the world. Stands of trees should be preferred over single trees whenever possible

FIGURE 3 Still existing and restored megatree-megafauna landscapes. (a) Baobab (*Adansonia digitata*) and African elephant (*Loxodonta africana*). (b) Old pedunculated oaks (*Quercus robur*) and English Longhorn cattle (*Bos primigenius*) at the Knepp Estate rewilding site, England. (c) Douglas fir (*Pseudotsuga menziesii*) and American bison (*Bison bison*) in Yellowstone National Park, USA. (d) Asiatic elephants (*Elephas maximus*) in the Kaziranga National Park, Assam, India. (e) Rewilding site with semi-wild megafauna (water buffalos *Bubalus bubalis* and konik horses *Equus ferus*) in the urbanized landscape around Aarhus, Denmark. (f) University of California Santa Cruz campus located in a costal red wood (*Sequoia sempervirens*) forest inhabited by mountain lions (*Puma concolor*), USA. Photos: Wikipedia, Ferdinand Reus, CC BY-SA 2.0 (a); Wikipedia, Himadri Sen, CC BY-SA 4.0 (d); J.-C. Svenning (b,c,e,f)

and beneficial for local communities. However, even single megatrees growing in highly urbanized landscapes can be of high ecological benefit by providing e.g. crucial habitat resources for wildlife (Stagoll, Lindenmayer, Knight, Fischer, & Manning, 2012).

Locations favouring the growth of megatrees, for example, microclimatically suitable (mesic) refugia, should be preferred for megatree establishment (cf. Lindenmayer & Laurance, 2016). Although originally suitable sites might get lost because of ongoing global climatic changes, new microclimatic suitable refugia might emerge at other locations/in other regions—a fact which emphasizes the importance of assisted migration/colonization for megatree restoration. Semi-wild or domesticated megafauna may in some cases substitute fully wild megafauna in their ecological role in human-dominated landscapes, e.g. to maintain semi-open landscapes as well as nutrient and seed dispersal, if managed in ways to facilitate natural megafauna functions (Pedersen et al. 2020; Svenning et al., 2019).

The long development times and life cycles of large-sized tree species constrain a fast re-establishment of megatree landscapes. The restoration of very large trees will generally require significant spaces and time to achieve their full ecological potential and, thus, will compete (like many other conservation or restoration activities) against alternative land uses with shorter time frames and likely more direct economic benefits. The protection of veteran megatrees still occurring even in human-dominated landscapes is therefore paramount (Lindenmayer & Laurance, 2016). In landscapes with still-reproducing megatree populations, the protection and facilitation of seedlings and saplings is a key approach for megatree restoration. Going beyond this, the establishment of faster—and slower-growing megatree-forming species in combination might be one way to shorten the generally long temporal extent for the implementation of such kind of rewilding activities. Active planting of fast-growing, megatree-forming species—such as giant sequoia (*S. giganteum*), poplar/cottonwood species (*Populus* spp.) and ceiba (*Ceiba pentandra*)—in mixed stands with other tree species might be an additional solution to initialize restoration in megatree-depauperate landscapes. In addition, assisted colonisation offers one way to overcome tree losses where climate change would allow the target tree species to occur outside their current range. When initial nuclei of tree islands are established or still existent, large-sized animals known for their disproportionate importance for long-distance seed and nutrient dispersal can facilitate the spread and establishment of trees on a landscape scale (Catterall, 2018).

Browsing of large-bodied herbivores can also sometimes impede tree recruitment and the establishment of groves, especially when herbivore population sizes become very high, e.g., by overstocking in fenced areas. Local prevention strategies like the fencing of individual trees or tree stands could be a solution for landscapes where herbivores, for one reason or the other, become so abundant that they have a diversity-reducing impact (cf. Lindenmayer & Laurance, 2016). This can happen e.g. through anthropogenic constraints on population dynamics like water source provisioning or carnivore exclusion (Levy, 2006). However, from a rewilding perspective, it is important to have patience and give space for natural dynamics to establish. Reductions in tree recruitment or survival are not necessarily negative and may lead to heterogeneous landscapes with high diversity capacity, and tree recruitment may in some cases occur as part of cyclic dynamics following established patches of browsing-resistant shrubs (Vera, 2000). Top-down control of herbivores by large-sized carnivores can further regulate herbivore pressure to a certain degree (Ripple & Beschta, 2012). When herbivore regulation by large carnivores is not effective (e.g. because mega herbivores are too big for top-down regulation) or not feasible (e.g. in heavily populated urban environments), active regulation of herbivores e.g. by contraception (as done e.g. in feral horse populations; Garrot, Siniff, Tester, & Plotka, 1992) might be considered. Carefully designed hunting may offer an alternative solution, also capable of providing positive economic benefits. However, numerous big herbivores like the mentioned megaherbivores are not top-down regulated under natural conditions. Thus, active regulation of such herbivores might not be beneficial or not necessary to restore functional ecosystems and, thus, should be not seen as an optimal, but rather a sometimes and mainly societally necessary strategy for those species.

Besides creative solutions for a sustainable reintroduction of native megabiota under varying human land use settings, the potential role of non-native species—already established (typically for other, historical reasons) or to be introduced—as functional analogue for extirpated native megafauna has to be carefully considered and assessed (cf. Svenning et al., 2016). Numerous non-native megafauna, thus, species with populations outside their native ranges have globally increased modern-day megafauna species richness and can sometimes have positive effects on the functioning of modern ecosystems (Lundgren, Ramp, Ripple, & Wallach, 2018). Hence, non-native megafauna may contribute to the restoration of functional megatree–megafauna ecosystems, e.g., in highly human-modified landscapes predominated by novel ecosystems (cf. Hobbs, Higgs, & Harris, 2009).

The (re-)introduction of locally extinct megafauna or functional analogues can, however, bear the risk of triggering unpredictable and unwanted changes in ecosystem functionality especially when long time has passed between extirpation and (re-)introduction (Delibez-Mateos et al., 2019). This calls for creative solutions when planning rewilding projects. This includes the consideration of the target landscape's ecological history, which may affect ecological and societal responses to rewilding activities (e.g. Schweiger, Boulangeat, Conradi, Davis, & Svenning, 2019). The integration of different knowledge systems like modern, scientific knowledge and traditional ecological knowledge of the local population can help to find such creative solutions to account for the ecological history of the rewilding site and at the same time meet the needs of the local community. Traditional ecological knowledge represents a cumulative body of knowledge and beliefs based on observations of natural dynamics and patterns, which is handed down through generations by cultural transmission (Gadgil, Berkes, & Folke, 1993). Such knowledge is mostly geographically restricted, but can be detailed including knowledge about habitat preferences, life histories and behaviour patterns of animal species (Gadgil et al., 1993). Further, landscape management based on such traditional knowledge systems is often holistic and adaptive and, thus, contribute to dealing with the complex and dynamic character of ecosystems (Berkes, Colding, & Folke, 2000). Hereby, insights from traditional knowledge systems can help develop the adaptive management approaches that are needed for implementing rewilding (Perino et al., 2019; Svenning et al., 2019). Such an integration of modern science-based knowledge and traditional knowledge has already been empirically shown to provide a successful strategy for the sustainable management of old-growth forests (Becker & Ghimire, 2003). Nevertheless, traditional knowledge referring to already downsized, human-affected ecosystems also carries a risk of providing a misleading baseline for rewilding. Approaches on how to obtain and more efficiently integrate traditional knowledge into modern knowledge systems are summarized e.g. by Huntington (2000) and Barnhardt and Kawagley (2005).

6 | FACILITATING HUMAN–MEGABIOTA COEXISTENCE

We think that the presented rewilding concept can be applied even in human-dominated landscapes, if done in a pragmatic manner (cf. Pedersen et al., 2020). First of all, there are societal benefits of megabiota even in these settings. Urban megatrees provide keystone structures by favouring species diversity, ameliorating microclimatic conditions and providing high cultural value even in densely populated cities (Lindenmayer & Laurance, 2016; Stagoll et al., 2012). Tree-dominated, urban greenspace helps to regulate microclimatic conditions (Streiling & Matzarakis, 2003) and decreases the risk of mental disease in highly urbanized landscapes (Engemann et al., 2019; Nutsford, Pearson, & Kingham, 2013). Urban trees also contribute to various habitats for maintaining and conserving urban biodiversity including large-sized animals (Gallo, Fidino, Lehrer, & Magle, 2017; Stagoll et al., 2012). The presence of megafauna can likewise provide beneficial services for human societies even in highly populated, urban environments, e.g., leopards (*Panthera pardus*) controlling populations of feral dogs and associated risks to people (Braczkowski et al., 2018).

Despite these benefits, megafauna do represent a risk for people and conflicts between megafauna and humans are inevitable. Examples range from elephants raiding crops in Africa and wolves and bears attacking live stock in Europe and North America to tigers and leopards killing people in rural and urban areas of India. Such conflicts are predominantly caused by increasing competition between growing human populations and wildlife for the same declining habitats and resources. Furthermore, rural communities appear to more often have little sympathy for wild megafauna and see them as threat for their safety and food security, increasing the potential of conflicts (Lamarque et al., 2009). Restoration approaches promoting the reintroduction of megafauna even in highly human-dominated landscapes—like the ones we propose—have to involve efficient prevention, protection and mitigation strategies to minimize human–wildlife conflicts (cf. Ceauşu, Graves, Killion, Svenning, & Carter, 2018). Restoration approaches including such strategies have to be culturally acceptable as well as financially and ecologically sustainable (Lamarque et al., 2009). A non-exclusive list of potential strategies includes children and adult education to prevent conflicts, guard animals (i.e. dogs), fences or other (acoustic or olfactory) deterrents to protect livestock, and adapted landscape management (e.g. creating of wildlife corridors linking wildlife areas in otherwise intensively used landscapes) (see, Lamarque et al., 2009 for more detailed information). Hunting for trophies and wild meat can also contribute as nature conservation tool benefitting biodiversity and local economy when implemented carefully (Di Minin, Leader-Williams, & Bradshaw, 2016). Furthermore, fencing can reduce the risk of human–wildlife conflicts especially in highly populated areas as well as sometimes promote more natural ecosystem functioning within protected areas (Bull, Ejrnæs, Macdonald, Svenning, & Sandom, 2018). Nevertheless, hunting and fencing should not be seen as panaceas, but rather as options to consider to allow and promote human–megafauna coexistence.

The size-selective loss of megafauna started much earlier (at least 50,000 years ago; Sandom, Faurby, et al., 2014) than size-selective logging of megatrees (at least 8,300 years ago; Yasuda et al., 2000). Furthermore, most megatrees show much longer lifespans than megafauna species, reinforcing the different time scales over which megafauna versus megatree rewilding will have to act. Megatrees might therefore be still of high cultural relevance for local communities whereas megafauna and their importance might have been lost from the collective memory and, thus, acceptance for megafauna reintroduction might be lower. Nevertheless, megafauna can effectively be established faster than megatrees simply because of their shorter generation times. These differences in temporal scales has to be accounted for a successful implementation of an integrative restoration of megatree–megafauna ecosystems, highlighting the importance of effective public outreach as part of the proposed framework (see Figure 2).

7 | CONCLUSIONS

Ecosystems have across millennia experienced a selected loss of megafauna and megatrees, a loss that is still ongoing or being maintained in most settings despite the ecological and societal importance of these megabiota. Here, we propose an integrative rewilding-based concept for the restoration of megabiota across contemporary landscapes, from the remaining but downsized wilderness areas to highly urban landscapes. In this concept, the restoration of megatree–megafauna ecosystems differs between close-to-natural and human-dominated landscapes (cf. Pedersen et al., 2020). This goes along with the current land sharing versus land sparing debate (Phalan, Onial, Balmford, & Green, 2011). Land sparing means that a division between areas of intense human land use and exclusive nature conservation areas is the preferred option for close-to-natural, yet downsized settings or when conflicts between humans and megafauna (large predators) seem to be inevitable. Land sharing, where megafauna and megatrees are co-occurring with people and are sustainably controlled (or even harvested) to minimise human–wildlife conflicts, might be a suitable option for the more human-dominated, urbanised landscapes. Exemplifying a land sharing scenario, the University of California Santa Cruz campus is located in a megatree forest of coastal redwood (*S. sempervirens*), populated by large carnivores, mountain lions (*Puma concolor*, Figure 3f), which are permanently monitored for scientific purposes but not actively controlled (santacruzpumas.org). The main goal of such rewilding activities—irrespective of land-use intensity—should be a proactive facilitation of the self-regulation potential of natural and novel ecosystems to the benefit of biodiversity, but also with many positive effects for society. We further see this megabiota rewilding concept as providing a good basis for facilitating wildness (cf. Ridder, 2007) in a socio-ecologically sustainable way even in urbanized landscapes (Müller, Bøcher, Fischer, & Svenning, 2018). The range of approaches considered all facilitate wild and semi-wild megatree–megafauna ecosystems in contemporary settings and include interventions such as assisted colonization and use of non-native species as functional analogues for extinct species alongside flexible implementation according to the socio-ecological setting, adaptive management and inclusion of insights from traditional knowledge. Notably, adaptive management strategies where management decisions and actions are iteratively recalibrated based on restoration goals and societal and ecological dynamics will be crucial for minimizing human–megabiota conflicts as well as ecological risks. Further, societal adaptation to the presence of megabiota will be a prerequisite and, at the same time, one of the most important challenges (Le Roux, Ikin, Lindenmayer, Manning, & Gibbons, 2014; Ripple et al., 2014). Generally, megabiota restoration need to be done on a wide scale to restore functional effects on the biosphere—otherwise effects will remain local and, thus, of limited effectiveness.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

AUTHORS’ CONTRIBUTIONS

A.H.S. and J.-C.S. jointly developed the idea and concept. A.H.S. did the literature review and led the writing of the paper with major input from J.-C.S.

DATA AVAILABILITY STATEMENT

No data were collected for this paper.

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