# The importance of ecological memory for trophic rewilding as an ecosystem restoration approach

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ABSTRACT

Increasing human pressure on strongly defaunated ecosystems is characteristic of the Anthropocene and calls for proactive restoration approaches that promote self-sustaining, functioning ecosystems. However, the suitability of novel restoration concepts such as trophic rewilding is still under discussion given fragmentary empirical data and limited theory development. Here, we develop a theoretical framework that integrates the concept of 'ecological memory' into trophic rewilding. The ecological memory of an ecosystem is defined as an ecosystem's accumulated abiotic and biotic material and information legacies from past dynamics. By summarising existing knowledge about the ecological effects of megafauna extinction and rewilding across a large range of spatial and temporal scales, we identify two key drivers of ecosystem responses to trophic rewilding: (*i*) impact potential of (re)introduced megafauna, and (*ii*) ecological memory characterising the focal ecosystem. The impact potential of (re)introduced megafauna species can be estimated from species properties such as lifetime *per capita* engineering capacity, population density, home range size and niche overlap with resident species. The importance of ecological memory characterising the focal ecosystem depends on (*i*) the absolute time since megafauna loss, (*ii*) the speed of abiotic and biotic turnover, (*iii*) the strength of species interactions characterising the focal ecosystem, and (*iv*) the compensatory capacity of surrounding source ecosystems. These properties related to the focal and surrounding ecosystems mediate material and information legacies (its ecological memory) and modulate the net ecosystem impact of (re)introduced megafauna species. We provide practical advice about how to quantify all these properties while highlighting the strong link between ecological memory and historically contingent ecosystem trajectories. With this newly established ecological memory–rewilding framework, we hope to guide future empirical studies that investigate the ecological effects of trophic rewilding and other ecosystem-restoration approaches. The proposed integrated conceptual framework should also assist managers and decision makers to anticipate the possible trajectories of ecosystem dynamics after restoration actions and to weigh plausible alternatives. This will help practitioners to develop adaptive management strategies for trophic rewilding that could facilitate sustainable management of functioning ecosystems in an increasingly human-dominated world.

*Key words*: adaptive management, alternative stable states, anachronism, ecological memory, ecosystem assembly, extinction debt, megafauna, restoration ecology, rewilding, resilience.

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# I. INTRODUCTION

Facing globally pervasive human impacts on ecosystems, nature managers are increasingly moving their focus away from traditional attitudes of preservation towards proactive restoration of biodiversity and ecosystem services (Suding, Gross & Houseman, 2004; Sandom *et al.*, 2013a; Kollmann *et al.*, 2016). Rewilding is one of these alternative approaches that has gained strong scientific and public interest in recent years (Jepson, 2016; Svenning *et al.*, 2016; Fernández, Navarro & Pereira, 2017). Although the term rewilding has a complex history and is related to a variety of different concepts and land-management practices [see Lorimer *et al.*, 2015 and Jørgensen, 2016 for further details], it can be generally defined as an ecological restoration approach that aims to promote self-sustaining ecosystem functioning (Sandom *et al.*, 2013a; Svenning *et al.*, 2016; Fernández *et al.*, 2017). Rewilding concentrates on restoring natural processes (Sandom *et al.*, 2013a; Smit *et al.*, 2015) in contrast to most conventional approaches of nature management, which often focus on the conservation of single species or specific ecosystem states. Rewilding also tries to reach the predetermined restoration goal of self-sustaining ecosystems by keeping human intervention to a minimum (Svenning *et al.*, 2016; Fernández *et al.*, 2017), a clear difference from the majority of classical nature restoration approaches that are characterised by a high degree of ongoing management.

Ecosystems are often at least partially shaped by top-down trophic effects provided by animals. These top-down trophic interactions have to be rehabilitated in order to facilitate self-sustaining, biodiverse ecosystems. The (re-)establishment of missing, often large-bodied, herbivores and carnivores can achieve this. This is a key aspect of trophic rewilding, defined as species introductions to restore top-down trophic interactions and associated trophic cascades to promote self-regulating biodiverse ecosystems (Svenning *et al.*, 2016). The (re-)establishment of large-sized animals may thus occur by active (re)introduction (as a form of active rewilding), but can also occur by species spontaneously recolonising regions from which they have been formerly extirpated, e.g. wolves and beavers in Central Europe. The latter falls under the wider concept of passive rewilding (Navarro & Pereira, 2012;

Svenning *et al.*, 2016), and could be referred to as passive trophic rewilding. There may also be intermediate cases where re-establishment is actively promoted without direct translocation of animals. In all cases, large-bodied animals (megafauna) are assumed to have disproportionally large and beneficial effects on the biodiversity and functioning of ecosystems (Malhi *et al.*, 2016; Smith *et al.*, 2016; Fernández *et al.*, 2017), and all are considered in our discussion of trophic rewilding below. If necessary, rewilding of large-bodied herbivores can be complemented with the (re)introduction of predators when potential negative effects of herbivore (re)introduction (e.g. high herbivore pressure) are likely to occur without effective top-down control. When herbivore regulation is necessary, but control by large carnivores is not effective (e.g. for herbivores that are too big for top-down regulation) or not feasible (e.g. in heavily populated urban environments or when rewilding sites are too small to sustain carnivores), active regulation of herbivore densities might be a necessary management strategy complementing rewilding.

Traditionally, megafauna refers to animals with a body mass of $\geq 45$ kg (Martin, 1973) although this threshold in absolute size is arbitrary. Herein, we use a more flexible, relative definition of megafauna as the largest animal species in a given ecological community or guild (Hansen & Galetti, 2009). This is likely more ecologically meaningful, especially when comparing ecosystems with different degrees of isolation (e.g. mainland *versus* islands).

Rewilding, especially active rewilding, is the subject of active scientific and public debate, which sometimes moves beyond our current scientific understanding and is often based more on opinion than facts (Sandom, Hughes & Macdonald, 2013b). There is much discussion about the potential socio-economic consequences and conflicts emerging from rewilding [for further details see e.g. Bauer, Wallner & Hunziker, 2009], but the ecological consequences of (re)introducing large animals are also controversial, especially relating to when and where the introduction of megafauna might be beneficial or practical (Malhi *et al.*, 2016). The absence of scientific monitoring for most existing rewilding projects (a general problem for conservation and restoration) leads to ambiguous conclusions about the effects of rewilding on the functioning and service provisioning of

ecosystems. This engenders criticism over the generalisation of positive effects and widespread implementation of trophic rewilding. The lack of practical experience as well as theoretical and empirical understanding about ecosystem responses to megafauna (re)introduction (Svenning *et al.,* 2016) may increase negative views of rewilding.

To maximise the benefits and reduce potential ecological risks linked to trophic rewilding, we need a thorough understanding of the complex role of megafauna in ecosystem functioning (Smith *et al.,* 2016). Case studies (e.g. Yellowstone National Park) are often highly debated in the scientific literature and reveal complex responses to the reintroduction of megafauna due to the multitude of interactions and feedbacks that characterise ecosystems (Beschta & Ripple, 2012; Dobson, 2014). Here, we argue that for trophic rewilding as well as for any other restoration approach, the history of an ecosystem is a key factor to consider for planning and implementation [see Chazdon, 2008 and Crouzeilles *et al.,* 2016 for forest restoration]. The importance of ecosystem history for rewilding projects is rarely recognised and insufficiently conceptualised in the current literature (Navarro & Pereira, 2012; Sherkow & Greely, 2013; Smit *et al.,* 2015; Nogués-Bravo *et al.,* 2016; Svenning *et al.,* 2016). The benefits, risks and costs of trophic rewilding must be evaluated by integrating our recent understanding of ecosystem dynamics to ensure a scientifically sound implementation of this proactive restoration approach (Fernández *et al.,* 2017). However, empirical research is fragmentary and theoretical frameworks to guide empirical studies on the role of ecosystem history for trophic rewilding are missing (Malhi *et al.,* 2016; Svenning *et al.,* 2016).

Here, we propose a conceptual framework that could be used to establish a scientifically sound basis for future management and decision-making about trophic rewilding. It furthermore can provide guidelines for future studies on the ecological effects of nature restoration practices like trophic rewilding. We frame current perspectives on trophic rewilding into existing theoretical concepts related to ecological memory. The ecological memory of a specific ecosystem is here defined as an ecosystem's accumulated abiotic and biotic material and information legacies from past dynamics (Nystroem & Folke, 2001; Folke, 2006). Detailed specifications of these legacies are discussed below. We first provide a summary of the current theoretical understanding of ecological memory and integrate these concepts into the framework of trophic rewilding. We then relate existing observations about the ecological effects of megafauna extinction and rewilding to ecological memory. These illustrative examples aim at covering a large range of spatial and temporal scales. Although our considerations and examples are focused on practices related to trophic rewilding of large-bodied, extant animals, our theoretical framework is general enough to be easily adapted to other forms of rewilding (e.g. passive rewilding: Gillson, Laddle & Araújo, 2011) or ecosystem restoration.

## II. CURRENT UNDERSTANDING OF ECOLOGICAL MEMORY AND ITS RELEVANCE TO TROPHIC REWILDING

Understanding the history of ecosystems is a prerequisite when planning restoration activities like trophic rewilding that aims for sustainable maintenance of biodiverse, functional ecosystems (Landres, Morgan & Swanson, 1999; Smith *et al.,* 2016; Svenning *et al.,* 2016). Most attributes observable in current ecosystems (e.g. landscape and vegetation structure, species composition and diversity, food-web topography) are contingent on historical influences just as future system attributes will be contingent on current conditions affected by current land use and restoration activities (Landres *et al.,* 1999). This contingency is conceptualised in the idea of 'ecological memory', which focusses on abiotic and biotic material and information legacies within ecosystems (Fig. 1 and Table 1). These legacies are represented by observable attributes of current ecosystems such as remnant populations or diaspores of locally extinct species, behavioural or morphological adaptations to lost ecological interactions or even landscape characteristics (e.g. Peterson, 2002; Schäfer, 2011; Johnstone *et al.,* 2016; Blackhall *et al.,* 2017; Genes *et al.,* 2017). Since these observable, quasi-static attributes result from long-term ecosystem dynamics, the ecological memory concept is relevant for investigating the effects of an ecosystem's history on its response to changes such as the (re)introduction of megafauna (Padisák, 1992; Peterson, 2002). Each component of ecological memory affects ecosystem responses at different temporal, spatial and organisational scales (Fig. 1). In the following sections, we distinguish internal components of ecological memory that act within the focal rewilding ecosystem, and external components that are present in the surrounding environment (Table 1; Schäfer, 2009).

### (1) Internal components of ecological memory

The internal components of ecological memory are inherent to the focal rewilding ecosystem. They are either material legacies represented by observable attributes, e.g. wood stems, diaspores, etc., or information legacies represented by attributes such as species' behavioural, morphological, or genetic traits. Many of these legacies result from past biotic dynamics, e.g. species interactions with now extirpated species or past abiotic environmental conditions. The internal components of ecological memory can act on the landscape, community and intraspecific scales (Table 1). Whereas material legacies generally predominate at the landscape scale, information legacies gain in importance at the community scale and dominate at the intraspecific scale. Information legacies acting at the landscape scale are generally underrepresented but can be revealed for instance by the structure (topology) of ecological networks.

Landscape-scale material legacies are represented by structural attributes like terrain complexity, soil properties, etc., which result from past geomorphodynamic and

Attributes of ecological memory components:
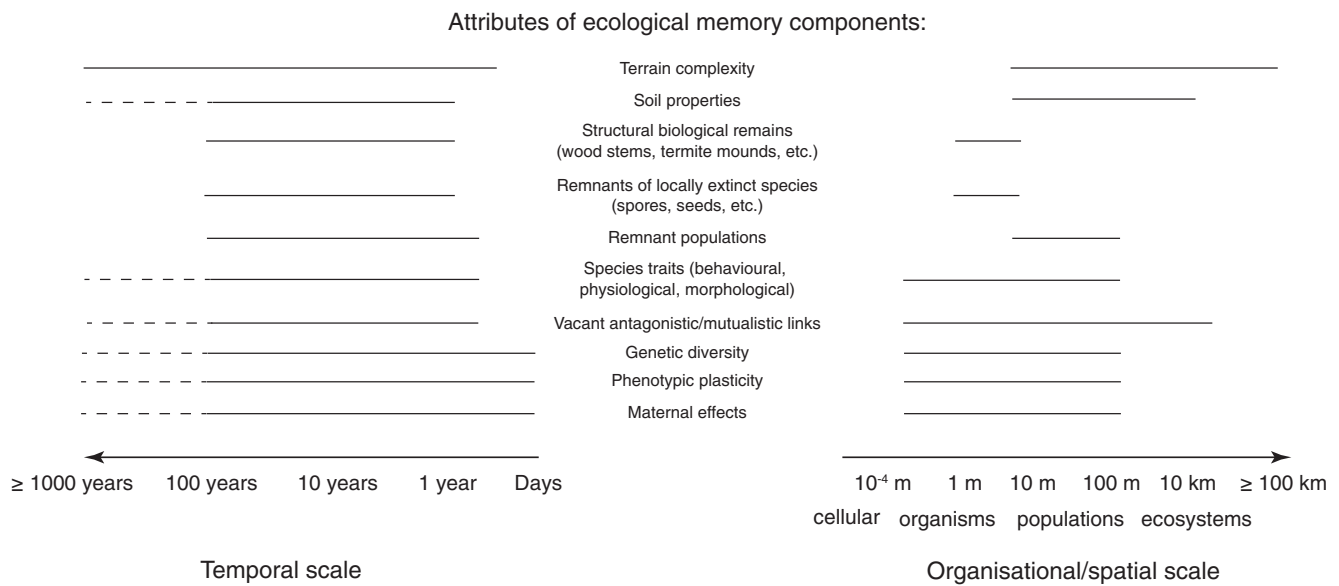


**Fig. 1.** Temporal and organisational/spatial scales on which different material and information legacies as observable attributes of ecological memory components affect ecosystem responses to restoration activities like trophic rewilding. The named legacies represent a non-exhaustive list of observable ecosystem attributes.

biological processes like denudation and biotic weathering, soil formation by soil biota (e.g. humification by arthropods and microbes) and bioturbation. This last process does not need to be limited to arthropods or small mammals. An impressive example of megafaunal bioturbation is the large number (>1500) of burrows scattered across the Brazilian landscape that are tens of meters in length and 1.5–4 m in diameter, probably resulting from the burrowing activity of extinct giant ground sloths and armadillos (Pereira Lopes *et al.,* 2017). Material legacies can also be observed through the structural remains of past biological activities like woody stem fragments, unpopulated termite mounds, or specific vegetation structures resulting from past browsing or grazing activities (Schäfer, 2011; Blackhall *et al.,* 2017). Remnants of historical human land-use such as dumps, mines and habitat fragments (e.g. Müller *et al.,* 2017) must also be considered as material legacies.

All these material legacies are likely to influence the response of ecosystems to megafauna (re)introduction. An example is the topography-related heterogeneous habitat use of red deer (*Cervus elaphus*) recolonising a former brown-coal mining area in Denmark (Müller *et al.,* 2017). In this case, landscape structures are mostly the result of past human land use, i.e. human-generated topography. Additional examples of such anthropogenic components of ecological memory are presented by Moore *et al.* (2015) who showed that the spatial availability of preferred foraging vegetation as a result of human land use affects the overall grazing behaviour of red deer in the landscape. Another example is provided by Schippers *et al.* (2014) who report that anthropogenic forest fragmentation can affect the habitat use and browsing pressure of large herbivores in landscapes. Such anthropogenic components of ecological memory are

of particular relevance in ecosystems with a long history of human land use (e.g. Normand *et al.,* 2017).

Internal ecological memory components at the community scale result from past species distributions, compositions and interactions across space (Nystroem & Folke, 2001). Material legacies can be represented by viable remnants of locally extinct species (e.g. tests, spores, seeds) or remnant populations of long-lived species (Schäfer, 2009; Johnstone *et al.,* 2016). Lost populations can be re-established from such viable remnants like soil seedbanks for plants if conditions become suitable again (Navarro & Pereira, 2012).

Compared to material legacies, information legacies are probably the dominant component of ecological memory at the community scale (Table 1). These information legacies can be represented by species' behavioural, physiological or morphological traits affecting the responses of resident species to the (re)introduction of large-bodied animals in trophic rewilding. Examples of such observable attributes are anachronistic fruit characteristics as a result of historical co-evolution with currently extinct, frugivorous mammals (Janzen & Martin, 1982), or defensive traits (e.g. spinescence) and resprouting behaviour of woody plants reflecting adaptations to now extinct native herbivores (Göldel *et al.,* 2016; Blackhall *et al.,* 2017). All these legacies can strongly interact with the (re)introduction of megafauna. Empirical evidence is provided by e.g. Milchunas & Lauenroth (1993) who report the effect of introduced grazers on plant community composition to be strongly affected by the ecosystems' evolutionary history of grazing, with changes in species composition increasing with a longer history of more intense co-evolution.

Historically established interaction links which are currently lost can be reactivated by restoration activities and

Table 1. Examples of internal and external components of ecological memory represented by material and information legacies, and the corresponding attributes observable at landscape, community and intraspecific scales. Internal components of ecological memory act within a focal ecosystem, whereas external components usually refer to the surrounding environment of the studied ecosystem

| | Material legacies | Information legacies |
|---|---|---|
| **Internal components** | | |
| Landscape scale | Terrain complexity, soil properties (type, texture, carbon and nutrient content), structural biological remains (wood stems, unpopulated termite mounds, etc.), vegetation formations | Structure/physiognomy of ecological networks |
| Community scale | Living remnants of locally extinct species (e.g. tests, spores, seeds), remnant populations of long-lived species | Species traits (behavioural, physiological, or morphological), currently lost antagonistic and/or mutualistic links between present and (re)introduced species |
| Intraspecific scale | — | Genetic diversity, phenotypic plasticity, maternal effects |
| **External components** | Individuals, diaspores or propagules for species recolonisation, fluxes of energy/material ('meta-ecosystems'), spatial configuration of dispersal (habitat structure, soil properties of the surrounding ecosystems) | Metapopulation genetic diversity ('landscape genetics') |

are of major importance when planning rewilding activities (Genes *et al.*, 2017). These include antagonistic links, e.g. consumer–resource relationships, as well as mutualistic links. Conversely, legacies that imply the absence of interactions in the past can also strongly interact with faunal introduction. For example, naïve prey on islands have not evolved fear because of a history without predators. Ecological networks involving such naïve prey species show strong changes after the introduction of predators like weasels, martens or rats (Traveset & Richardson, 2006). All these information legacies acting at the community scale are nevertheless dependent on the species present to rewire the lost interactions and thus

cannot be seen as independent from the material legacies acting at the community scale.

Ecological memory on an intraspecific scale results from species' genetic adaptations to the past abiotic environment and past biotic interactions. It is predominated by information legacies within one species or even within a single organism. Genetic diversity, phenotypic plasticity and local adaptations within species or populations might be examples of observable attributes, revealing these intraspecific information legacies and affecting the response of individuals within one species to rewilding. Additional intraspecific information legacies might result from maternal effects, i.e. the causal influence of the maternal genotype or phenotype on the offspring phenotype, that mediate offspring response to environmental change (Galloway, 2005; Wolf & Wade, 2009; Dyer *et al.*, 2010; Heger, 2016; Ren *et al.*, 2017). These legacies are potentially relevant for mediating the response of resident species or populations to trophic rewilding.

### (2) External components of ecological memory

Besides the above-mentioned internal components, we must also consider the spatial context of a focal ecosystem to anticipate its response to rewilding. The ecosystems surrounding the focal ecosystem form external components of ecological memory that act as potential sources for compensatory processes after disturbance such as the (re)introduction of megafauna (Nystroem & Folke, 2001; Golinski, Bauch & Arland, 2008; Schäfer, 2009, 2011). These external components predominate at the community scale as they provide genes as well as individuals or propagules for species recolonisation. Without the availability of source pools in the surrounding landscape, it is often not possible to re-establish extirpated species or to rewire lost interactions in the focal ecosystem (Suding *et al.*, 2004; Halffter *et al.*, 2008; Schäfer, 2011), and re-introductions might then have little effect. For instance, Janzen (1983) demonstrated a long-lasting lag in the recolonisation of Costa Rican ecosystems by dung beetles that co-evolved with Pleistocene megafauna, due to missing source pools in the surrounding areas. This occurred despite introductions of large-bodied herbivores (livestock cattle and horses) that provided functionally similar dung compared to extinct megafauna. Halffter *et al.* (2008) drew similar conclusions for the Mexican dung beetle fauna. They found that livestock brought by the Spanish conquistadors partly compensated for the vacuum of suitable resources (dung) for the dung beetles that had co-evolved with the extinct Pleistocene megafauna. However, the authors argue that the Mexican dung beetle communities are far from being saturated because of insufficient compensation from surrounding source areas.

Faunal elements missing in the focal ecosystem, additionally to the (re)introduced megafauna, typically must be re-established from source areas outside the target ecosystem, thus relying on the external component of ecological memory. Besides species, energy and material that flow between the focal and surrounding ecosystems

must be considered as external components of ecological memory [*cf.* the meta-ecosystem concept of Loreau, Mouquet & Holt, 2003]. For instance, the spatial configuration of habitat patches and soil properties of surrounding landscapes will influence the amount and type of matter that reaches a focal ecosystem, where it interacts with the introduced fauna (Hansson, 1991; Dunning, Danielson & Pulliam, 1992; Table 1). Although material legacies seem to predominate, information legacies can play an important role in forming the external components of ecological memory. Information legacies can be represented, for example by the genetic diversity of metapopulations within a landscape (e.g. Pannell & Charlesworth, 1999). For example, DiLeo *et al.* (2017) evaluated how the functional re-connection of formerly isolated grassland fragments by rotational sheep herding influenced the metapopulation genetic structure of a rare grassland plant species in south Germany. They demonstrated that well-connected plant populations had higher within-population genetic diversity, showed higher genetic similarity among different populations and had higher reproductive output compared to ungrazed or more isolated grazed populations. This change in the genetic structure of local populations was only possible because genetic information was still 'stored' in other habitat patches in the landscape.

### (3) Ecological memory and resilience in the context of trophic rewilding

Ecological memory is usually considered in the context of disturbances that disrupt ecosystem integrity (e.g. Schäfer, 2009; Blackhall *et al.*, 2017). Strong ecological memory is expected to enhance ecosystem capacity for reorganization after disturbances and environmental changes and prevents ecosystem shifts to alternative states by offering resources to recover ecosystem integrity (Gunderson, 2000; Carpenter *et al.*, 2001; Nystroem & Folke, 2001; Power *et al.*, 2015; Johnstone *et al.*, 2016). This capability of ecosystems to absorb disturbances and avoid shifts to alternative states by system reorganisation is defined as ecological resilience (Gunderson & Holling, 2002; Carpenter & Folke, 2006; Folke, 2006). In this context, resilience can be seen as an emergent property of ecological memory.

High resilience, however, as a result of strong ecological memory, can also impede restoration action such as trophic rewilding, which aims at shifting an ecosystem from a less-desirable current state to a new, more desirable state (Folke, 2006; Gibbs *et al.*, 2014). This Janus-faced effect of ecological memory on ecosystem resilience from a restoration ecology point of view has strong links to concepts of positive and negative resilience (Lake, 2013). This is important to consider because megafauna, especially herbivores, can actively induce state shifts, which might be desired under some circumstances (e.g. to reduce fire risk; Bowman, 2012). An empirical example is provided by Blackhall *et al.* (2017) who showed that the introduction of large-bodied herbivores to fire-dominated systems changed the dominance relations between pyrophytic and pyrophobic woody plants,

altering the material legacy component of the systems' resilience to fires. However, whether shifts to alternative states occur in response to megafauna (re)introduction strongly depends on the ecological memory related to the reintroduced megafauna or its functional counterparts, with higher megafauna-related memory (e.g. longer evolutionary history of grazing) reducing the probability of state shifts as a consequence of megafauna (re)introduction (Cingolani, Noy-Meir & Díaz, 2005).

Generally, the capacity of ecosystems to adapt to environmental changes seems to be especially relevant in a human-dominated, dynamic world. This is in line with the principle goal of trophic rewilding to build self-sustaining, biodiverse, and functional ecosystems in changing environments (Svenning *et al.*, 2016). By contrast, a static reproduction of past ecosystem settings, a common goal of classical ecological restoration, will often not be desirable or feasible (Landres *et al.*, 1999; Suding *et al.*, 2004; Higgs *et al.*, 2014).

### (4) Ecological memory, species interactions and disequilibrium dynamics in relation to megafauna extinctions and trophic rewilding

Past interactions among species or between species and the environment play a crucial role in forming ecological memory. The degree to which interactions evolved in the past between currently extinct megafauna and other species of plants or animals will influence the success of trophic rewilding projects. Empirical evidence for this argument is provided by Favila (2012) who argues that dung beetles' low dung-processing efficiency of the dung of introduced, large herbivores in Australia compared to the relatively high efficiency of dung beetles in Central and South America is caused by differences in the biogeography/ecological history of the dung beetle assemblages on both continents. Australian native dung beetles are not able to process dung of the new megafauna (cattle, horses, and goats) introduced by humans due to missing co-evolution with functionally similar megafauna (i.e. missing information legacies) probably in combination with massive losses of dung beetles around 40000 years ago in response to the near-complete megafauna extinction. By contrast, native dung beetle assemblages of the Americas closely co-evolved during the Neogene and Pleistocene with Palaearctic, Nearctic and Neotropical megafauna (horses, camels, bison) that are functionally similar to present-day, human-introduced livestock. This scenario of megafauna species, but also partly its interacting species, going extinct, gives rise to anachronisms (Janzen & Martin, 1982) as well as extinction debts (Tilman *et al.*, 1994) and credits of ecological interactions (Genes *et al.*, 2017). Such lagged responses to environmental changes (e.g. extinction of megafauna) result in disequilibria between species' abundance (or absence) in the focal ecosystem and current environmental conditions (e.g. absence of the particular megafauna species). The presence of a disequilibrium or lag is an information legacy thus directly related to the ecological memory of a focal ecosystem.

A pronounced disequilibrium after megafauna extinction therefore represents a strong ecological memory. In other words, trophic rewilding projects are expected to be most successful and ecological interactions to stand the greatest chance of rewiring where large disequilibria or response lags to a past loss of megafauna are observed (*cf.* Pires, 2017).

Pronounced temporal lags in ecological responses are commonly found in remnant adaptations to prehistorical extinct megafauna. These remnant adaptations are generally defined as ecological anachronisms (Galetti *et al.,* 2018) and are assumed still to be prevalent, e.g. in temperate plant communities showing adaptations to extinct, large-bodied grazers (Bakker *et al.,* 2004), in the foraging behaviour (prey choice) of neotropical large-bodied predators (jaguars) still adapted to behavioural and morphological traits of extinct prey species (Hayward *et al.,* 2016), and in overbuilt neotropical fruits still showing morphological adaptations to dispersal by extinct megafaunal frugivores (Janzen & Martin, 1982; Donatti *et al.,* 2007; Guimarães, Galetti & Jordano, 2008). All these long-lasting anachronisms illustrate that the underlying ecosystem responses are generally very slow and often result in large temporal lags and pronounced disequilibrium conditions. Such a slowly vanishing ecological memory is shown empirically by Doughty *et al.* (2016), who report reduced current range sizes of historically megafauna-dispersed plants compared to other animal- but not megafauna-dispersed plant species in the Neotropics.

The speed of response to megafauna extinction and therefore the emergence of disequilibrium conditions should be determined by the speed of abiotic and biotic turnover (e.g. longevity of species; Hubbell, 1980) and the strength of biotic interactions characterising the ecosystem (Donatti *et al.,* 2007). This clearly links the concept of ecological memory to temporal lags and non-equilibrium dynamics in ecosystems.

## III. THE ECOLOGICAL MEMORY–REWILDING FRAMEWORK

In the ecological memory–rewilding framework, we propose that the impact potential of (re)introduced megafauna is mediated by the strength of ecological memory to affect rewilding outcomes (Fig. 2). The impact potential of (re)introduced megafauna is defined as an ensemble of the animal's behavioural, morphological, population and distributional properties that can have an impact on the focal ecosystem. Four different properties of the focal and surrounding ecosystems determine the strength of ecological memory, which affects the focal ecosystem's net response to rewilding by modulating the impact potential of the (re)introduced megafauna (Fig. 2). Three of these properties, the absolute time since megafauna loss, the speed of the turnover of abiotic and biotic components and the strength of species interactions, are aspects of the focal ecosystem's dynamics. Turnover is here defined as a continuous process of loss and replacement of energy, matter or species,
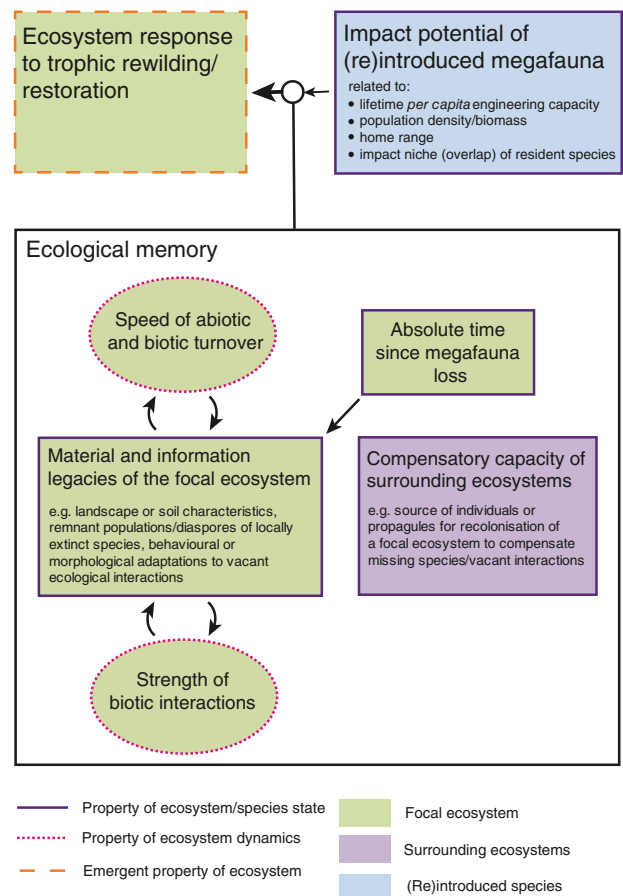


**Fig. 2.** The ecological memory–rewilding framework. The ecological memory of the focal ecosystem mediates the impact potential and, thus, the net impact of (re)introduced megafauna on ecosystem response dynamics. The impact potential of the (re)introduced species is related to its lifetime *per capita* engineering capacity, its population density/biomass, its home range size, and its niche overlap with resident species. The longevity and strength, and thus the importance of ecological memory, is shaped by the speed of abiotic and biotic turnover and the strength of species interactions characterizing the focal ecosystem, the absolute time since the megafauna loss, and the compensatory capacity of surrounding source ecosystems.

which can decrease, stabilise, or increase energy, matter, or species composition in the focal ecosystem. The fourth property determining the strength of ecological memory is the compensatory capacity of surrounding source ecosystems (Fig. 2).

### (1) Properties of the megafauna considered for trophic rewilding

The central element of the ecological memory–rewilding framework is the impact potential of megafauna species considered for rewilding (Fig. 2). To assess this impact potential, one must carefully consider the potential role of the considered megafauna species in the focal ecosystem (Barnosky *et al.,* 2016). The idea of the ecological role of a

species is found in the keystone species (Paine, 1969; Krebs, 1985) and the ecosystem engineer concepts (Jones, Lawton & Shachak, 1994). Species are defined as ecosystem engineers when they actively modify abiotic environmental conditions (resource availability, ecosystem structure), consequently modifying biotic interactions among co-occurring species. This differentiates ecosystem engineers from keystone species, which are defined as species which have a disproportionately large effect on the ecological community relative to their abundance (Paine, 1995) purely by biotic (trophic) interactions, e.g. predation (Coggan, Hayward & Gibb, 2018). These two concepts are particularly relevant in the context of trophic rewilding when (re)introduced species are expected to have a strong impact on the ecosystem (Byers *et al.*, 2006; Svenning *et al.*, 2016). The introduction of ecosystem engineering or keystone species is also important to promoting species diversity as both groups of species increase abiotic and biotic structural heterogeneity of ecosystems (Brunbjerg *et al.*, 2017), a key driver of species diversity (Stein, Gerstner & Kreft, 2014). The high relevance of ecosystem engineers to the restoration of ecosystems is already realised in the literature and by local managers. Ecosystem engineers can be seen as an efficient and comparably cheap management strategy to restore degraded ecosystems (Byers *et al.*, 2006).

Large-bodied animals are defined within the ecosystem engineering concept as allogenic engineers, i.e. species that change the environment by transforming living or non-living materials from one physical state into another. More generally, the impact potential of this type of ecosystem engineer can be quantified as the magnitude to which they change the quality, quantity and temporal and spatial distribution of abiotic and biotic resources available for other co-occurring organisms (Jones *et al.*, 1994). The greater the influence of ecosystem engineering megafauna on abiotic resources like the availability of water, light, nutrients etc., or on biotic resources like trees providing habitat or food, the higher the impact potential of these ecosystem engineers on the biotic interactions in the focal ecosystem (Byers *et al.*, 2006). The impact potential of a species reintroduced in the focal ecosystem is thereby affected by characteristics of the resident species, such as the extent to which resident species can potentially exploit resources and modify the environment prior to the arrival of newcomers (*cf.* Vannette & Fukami, 2014). If resident species already have a strong impact on the resources and the environment (large impact niche) and use similar resources to the (re)introduced megafauna (high niche overlap), the impact potential of this added megafauna species is expected to be small.

Two of the best-recognised megafauna ecosystem engineers are elephants and beavers, which may transform closed, tree-dominated systems to open (grass-dominated) systems, strongly modifying the abiotic and biotic resources available to co-occurring species. Both elephants and beavers have high *per capita* engineering capacity and act over large spatial scales, making their impact on ecosystem structure and functioning quite substantial. Furthermore,

both ecosystem engineers have long-lasting effects on the structure and thus function of ecosystems as they are both long-lived species compared to the slow regrowth of the trees they impact. Although such single megafauna species might sufficiently affect ecosystem structure, the introduction of different species of megafauna affecting different resources to varying degrees provides a preferable management strategy for tackling complex restoration goals (van der Plas *et al.*, 2016).

The higher the impact potential of the (re)introduced megafauna on a target ecosystem, the more carefully one has to understand its role in the focal system and the properties defining this role. Furthermore, the strength of interaction between a species of megafauna considered for rewilding and the other resident species in the target ecosystem is related to the abundance of the (re)introduced species (Genes *et al.*, 2017). Thus, species abundance is an important factor to consider when planning trophic rewilding projects. Following the ideas of the keystone species and ecosystem engineering concept, we propose that four key properties need to be known in order to estimate the impact potential of candidate rewilding reintroduction species: (*i*) the lifetime *per capita* engineering capacity, (*ii*) the population density, (*iii*) the home range size, and (*iv*) the impact niche overlap between resident and introduced species (Figs 2 and 3). A species' lifetime *per capita* engineering capacity depends on its longevity and its per-individual activity. Information about the species' life expectancy can be obtained relatively easily from demographic studies or proxies (e.g. tooth annuli) found in the literature, but per-individual activity might be more difficult to quantify. Some examples of studies providing empirical estimates are the estimation of browsing activity of elephants, the bioturbation activity of wild boars using high-resolution imaging techniques (LIDAR or multispectral cameras), and plot-based investigations to detect structural or compositional changes in vegetation (Fig. 3). Furthermore, manipulative experiments varying the presence/absence or density of the rewilding candidate species might provide helpful insights regarding the potential ecosystem effects of rewilding (Coggan *et al.*, 2018). This kind of experimental implementation of restoration activities seems to be especially suitable for rewilding projects, which are generally planned to be open-ended (Biggs & Rogers, 2003). Information about natural population densities are more challenging to acquire, but can be obtained from field investigations or management literature or can be inferred from body-size scaling relationships (e.g. Pedersen, Faurby & Svenning, 2017). Finally, information on home range size and impact niche overlap between the rewilding candidates and resident species can be obtained from field investigations or literature or can be estimated from body-size scaling relationships (e.g. Jetz *et al.*, 2004; Gravel *et al.*, 2013).

## (2) The speed of abiotic and biotic turnover in the focal ecosystem

The time since extinction of a lost megafauna species is a key element affecting the strength of ecological memory
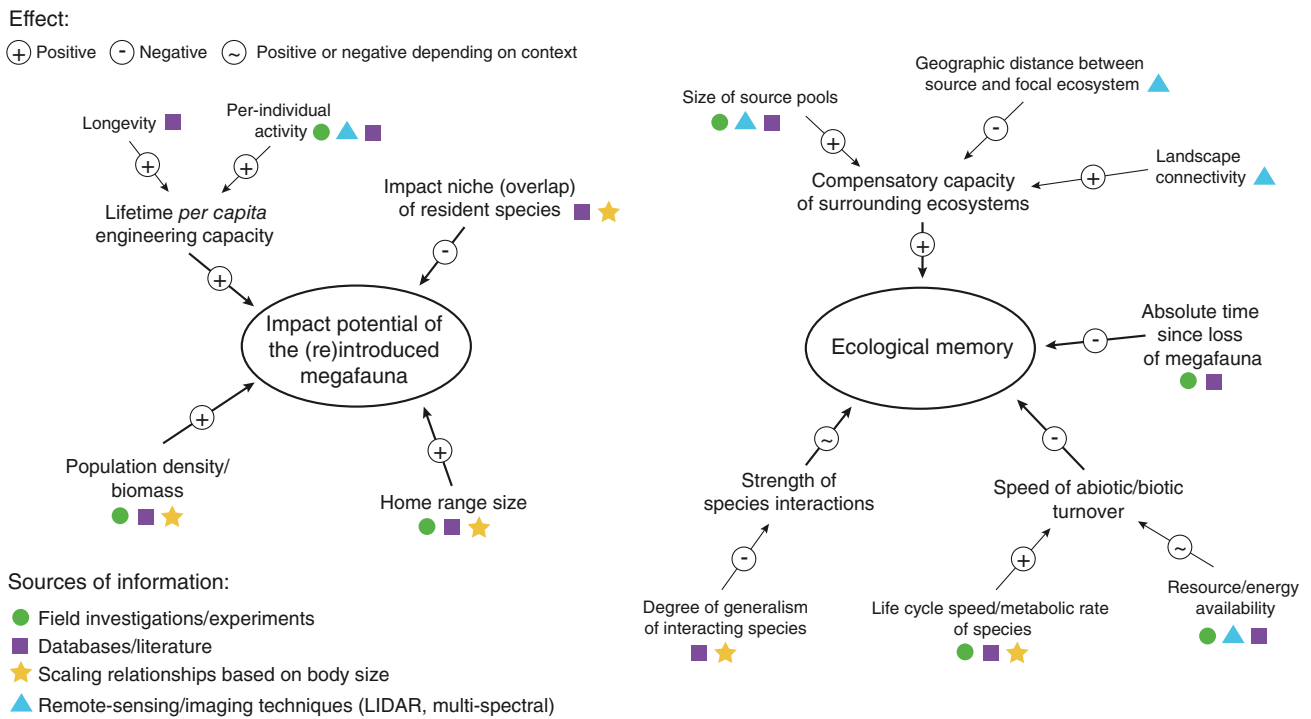
**Fig. 3.** Key determinants of ecosystem responses to trophic rewilding. An increase in each element has the shown effect (positive, negative, or context dependent) on the strength of the drivers of ecosystem responses. For example, an increase in the time since the loss of megafauna will decrease the strength of ecological memory of the focal ecosystem. Potential information sources for each element are also provided. See text for further details.

related to this lost species in a focal ecosystem (Figs 2 and 3). With increasing time since extinction, ecological memory related to the extinct megafauna species increasingly fades away (see Section II.4). The fact that thousands of years have passed since the extinction of Pleistocene megafauna is often used as a major argument against Pleistocene rewilding (e.g. Lorimer *et al.,* 2015). It is however rarely valid due to the pronounced disequilibrium conditions and temporal response lags that characterise ecosystems (see Section II.4; Bakker *et al.,* 2004; Donatti *et al.,* 2007; Hayward *et al.,* 2016) or because certain ecosystem states initially created by megafauna were maintained by traditional human land-use activities for centuries after the loss of this megafauna (Bocherens, 2018). Species recently extirpated from the focal ecosystem are still proposed to be better candidates for reintroduction as the ecological memory (information legacies) related to these species is less likely to be lost and should potentially buffer against unwanted ecosystem responses (Sandom *et al.,* 2013*a*).

We argue that the speed at which ecosystems developed in structure and dynamics is at least as important as the absolute time since extinction to determine the strength of ecological memory. Ecosystems must be seen as ephemeral, open systems that are the outcome of broad-scale dynamics in species ranges interacting with local environmental conditions and co-occurring species (Ricklefs, 2008). The assembly of ecosystems is thus determined by the adaptive interaction between dynamically changing pools of local

and immigrating (or introduced) species and their abiotic environment (Higgins, 2017; Schweiger, 2017). Both are cumulatively reflected in the material and information legacies, thus, the ecological memory of an ecosystem. We argue that the speed at which ecosystems assemble based on species–environment interactions is determined by abiotic and biotic turnover rates. The slower the turnover rates are, the more pronounced will be the temporal lags in species responses to megafauna extinction, i.e. the more likely the system will be in disequilibrium (e.g. by showing a high prevalence of anachronisms). The slower the abiotic and biotic turnover characterising a focal ecosystem through its assembly is, the greater the strength (longevity) of the ecological memory (Johnson *et al.,* 2015; Barnosky *et al.,* 2016).

The speed of abiotic and biotic turnover is strongly modulated by resource and energy availability. The effects of megafauna extirpation on vegetation and related abiotic environmental conditions (e.g. microclimatic conditions, carbon and nutrient cycling and pools, etc.) have been reported by several studies to be mitigated under limiting environmental conditions like low rainfall, low water availability (Barnosky *et al.,* 2016), low temperature, and low atmospheric $CO_2$ concentration (Johnson *et al.,* 2015). The speed of abiotic and biotic turnover thus modulates the impact potential and consequently the net ecosystem impact of the (re)introduced megafauna. This relationship between resource/energy availability and megafauna impacts can be

positive or negative depending on the characteristics of the introduced species and the property of the ecosystem that is impacted. For instance, plant species richness is reported by several studies to be decreased by grazing at low productivity, but enhanced in high-productivity systems (Proulx & Mazumder, 1998; Bakker *et al.*, 2006). Furthermore, the magnitude of grazing effects on the composition, richness, and dominant species cover of plant communities was shown to increase significantly with productivity in South American steppes and grasslands (Lezama *et al.*, 2014). Based on a global data set, Milchunas & Lauenroth (1993) report a similar increase of grazing effects on plant species composition with increasing productivity, but stress that an evolutionary history of grazing can diminish current grazing effects. Although effects of herbivorous megafauna on vegetation generally seem to decrease with decreasing resource and energy availability, and thus productivity, large-sized herbivores can still have strong impacts on ecosystem functioning even in arctic ecosystems (Cahoon *et al.*, 2012). A different picture seems to emerge if one looks at the effects of large mammal herbivores on the abundance of other consumers. Based on a meta-analysis, Daskin & Pringle (2016) show that large mammal herbivores reduce the abundance of other consumers and that this effect is stronger in low-productivity ecosystems, probably due to slower plant re-growth and higher relative uptake of forage vegetation by large herbivores.

Ecological responses to megafauna reintroductions are thus linked to resource or energy availability (productivity), but with different responses at different trophic levels or response variables. They can furthermore cascade down through numerous trophic levels of an ecosystem depending on the speed of turnover characterising the different interacting species. We argue that the speed of such cascading responses depends on the speed of turnover characterising the consumer and resource species involved in an effect cascade. This proposed mechanism is similar to the idea of how temporal lags in ecosystems accumulate (Essl *et al.*, 2015). An example supporting this assumption is the extinction of the Steller's sea cow (*Hydrodamalis gigas*) in the Commander Islands in the mid-1700s provided by Estes, Burdin & Doak (2016) who argued that the extinction of this large-bodied, marine mammal was the result of an effect cascade triggered by a population crash of sea otters (*Enhydra lutris*) due to overhunting. This reduction in sea otter numbers reduced the predation pressure on sea urchins, which are major consumers of kelp. As a result, the population size of sea urchins, and consequently herbivore pressure on kelp, increased dramatically. This resulted in a collapse of kelp forests, the main food source for Steller's sea cow, and led to the complete extinction of this marine megafaunal species after its prehistoric range had been strongly reduced by pre-European hunting. We argue that the speed at which the extinction of this large-bodied animal took place is related to a cascade effect. The negative feedback between rapid impacts and slow compensatory responses (i.e. responses tending towards a quasi-equilibrium under given conditions)

and positive feedback between rapid impacts and fast responses led to an ecological chain reaction. The human overhunting of otters represents a negative feedback between rapid impacts and slow responses as the relatively slowly reproducing otters were not able to compensate for culling by humans. The rapidly increasing population size of sea urchins as a response to the decreasing otter population size represents a positive feedback between a rapid impact and a fast response. The next two stages in the presented effect chain, namely the rapid increase in herbivore pressure by increasing sea urchin populations on the kelp forests with slow compensatory regrowth as well as the subsequent potential negative effects on Steller's sea cow (large-bodied mammals with low reproductive rates highly specialized on kelp unable to switch to a new food source or increase their reproductive rates) characterise negative feedbacks between a rapid impact and a slow response.

The reintroduction of large-bodied animals can also induce effect chains cascading through the trophic levels of an ecosystem. One popular example is the reintroduction of wolves (*Canis lupus*) in Yellowstone National Park which have been reported to reduce herbivore pressure of American elk (*Cervus elaphus*) on riparian woody vegetation, subsequently changing river dynamics and related geomorphological processes at a landscape scale (Beschta & Ripple, 2012; Dobson, 2014). The effect of the reintroduction of wolves on herbivore pressure is mainly indirect by affecting herbivore behaviour rather than directly killing herbivores, creating a 'landscape of fear' (Laundré, Hernández & Altendorf, 2001). This represents another positive feedback between a rapid impact (introduction of 20 wolves in the winter of 1994–1995) and fast direct and subsequent responses, i.e. a rapid decrease in browsing pressure on riparian woody vegetation by changing herbivore behaviour, in combination with fast-growing plant species (*Populus* spp. and *Salix* spp.). However, this direct link between wolf reintroduction, herbivore pressure and recovery of riparian vegetation has been questioned by several studies and additional drivers interacting with the wolf reintroduction have been proposed (i.e. climate, topography, and human activities; Mech, 2012; Marshall, Cooper & Hobbs, 2014).

In general, the diminished negative feedbacks caused by slow responses and the accelerated positive feedbacks caused by fast responses in effect cascades, will lead to a smaller compensatory power of ecosystems and faster changes in ecosystem structure in response to the extirpation or (re)introduction of large animals. Depending on the specific goals of a restoration project, this could be helpful or a hindrance for nature restoration.

These relationships between resource availability, the speed of abiotic and biotic turnover and their effects on ecosystem responses to megafauna extinction or (re)introduction are key for trophic rewilding.

The biotic turnover in an ecosystem depends on the life-cycle speed of the inhabiting organisms (Fig. 3). Ecosystems dominated by species with short life cycles (e.g. insects or annual plant species) will generally respond faster

to changing conditions (i.e. the introduction of large-bodied animals) than ecosystems dominated by species with long life cycles (e.g. long-living trees or mammals). Life-cycle speed depends on metabolic rate, which scales strongly with body size (West, Brown & Enquist, 1997; Reich, 2001; Brown *et al.*, 2002). Because we lack life-history data for many (especially smaller) species, body size (biomass) distributions can be used to assess the speed of biotic turnover within an ecosystem, showing how ecological memory will modulate the impact of (re)introduced megafauna (Fig. 3).

Generally, we expect the speed of abiotic and biotic turnover to modulate the impact of the (re)introduced megafauna on the focal ecosystem, by determining the longevity of ecological memory and consequently its strength. The speed of abiotic and biotic turnover is therefore a key determinant of the focal ecosystem's response to trophic rewilding.

## (3) Strength of species interactions in the target ecosystem

The strength of ecological memory and, thus, the impact potential of the (re)introduced megafauna species should also be modified by the strength of interactions between different species in the focal ecosystem as another key determinant of the ecosystem's response to trophic rewilding (Figs 2 and 3). The strength of interactions between two or more species (e.g. consumer–resource interactions) is strongly determined by the degree of generalism of the interacting species (e.g. diet generalism) as shown in several theoretical and empirical studies on ecological networks (e.g. May, 1972; Montoya, Pimm & Solé, 2006; Nichols *et al.*, 2009; Coggan, 2012). Generalist species can easily switch to alternative pathways like alternative food sources or alternative mutualistic partners when one or several interaction links are disrupted. A negative relationship exists between the number of interactions per species (degree of generalism) and the mean strength of these interactions (May, 1972; Montoya *et al.*, 2006). In other words, generalist species tend to have more, but weaker, interactions whereas specialist species have fewer, but stronger, interactions with other species. Thus, cascading effects induced by the loss of megafauna and their associated interactions will have less pronounced and shorter duration effects in ecosystems dominated by generalist species compared to ecosystems dominated by specialist species (Nichols *et al.*, 2009; García *et al.*, 2013). Empirical evidence for this is provided by Coggan (2012) who reports diet specialisation of dung beetles to be the main driver of the strong relationship observed between megafauna extinctions and changes in dung beetle assemblages/extirpation of dung beetle species. Furthermore, the higher the proportion of generalist species, the more rapidly can lost interactions (i.e. information legacies in the target ecosystem) be rewired after species (re)introduction (Devictor *et al.*, 2010; Genes *et al.*, 2017). The more specialised are past interactions between extinct megafauna and extant resident species, the more difficult will be the rewiring of these lost, but memorised interactions, by megafauna reintroduction. The

degree of functional similarity between the lost species and the functional counterpart planned for (re)introduction is therefore especially important when the specificity of interactions characterising the target ecosystem is high. Furthermore, generalist rather than specialist species should be preferred for initial co-introductions when interaction partners for the (re)introduced megafauna are heavily impoverished due to co-extinction (Genes *et al.*, 2017). Nevertheless, (re)introduced megafauna should generally create environmental heterogeneity, which is a key driver of species diversity (Stein *et al.*, 2014). This is a key effect of rewilding beyond megafauna-specific memory effects and regardless of the megafaunas' degree of generalism but should still relate to species pools in the landscape, and thus to ecological memory.

Information about the spectrum of generalism occurring amongst the resident species of the focal ecosystem can provide a quantitative measure of the strength of species interactions and the resulting strength of ecological memory (Fig. 3). Simple measures like the mean degree of generalism in combination with standardised measures of variation (like the coefficient of variation) of species generalism could already provide meaningful quantities. Species-specific information about the degree of generalism is available for a large number of mammal species from databases (Jones *et al.*, 2009; Kissling *et al.*, 2014; Wilman *et al.*, 2014) or from the ecological literature (Fig. 3). Databases with observational data on food webs or other mutualistic interaction networks (e.g. plant–pollinator or seed dispersal networks) can also help determine the degree of species generalism. However, assessing the degree of generalism across a broad taxonomic range will be challenging due to the large proportion of species that lack diet or interaction data (Penone *et al.*, 2014) and the varied ways in which data are collected for different groups of species (Davis & Pineda-Munoz, 2016). Mechanistic models that can infer potential species interactions based on body-size relations between potential predators and prey (Gravel *et al.*, 2013) or based on functional traits (Laigle *et al.*, 2017) might provide an additional source of information when observational data about the degree of generalism for individual species are lacking (Fig. 3).

## (4) Compensatory capacity of the surrounding ecosystems

The compensatory capacity of the surrounding ecosystems is another modulator of the strength of ecological memory and consequently for the net ecosystem impact of the (re)introduced megafauna species (Figs 2 and 3). In general, the compensatory capacity of surrounding source ecosystems is related to the amount of resources (e.g. species) available in the surrounding ecosystems and the landscape connectivity allowing the transfer of species or other resources from surrounding ecosystems to the focal ecosystem (Conradi & Kollmann, 2016; Conradi, Temperton & Kollmann, 2017). The latter is strongly related to the geographic distance and biogeographic barriers between the source and the sink ecosystems (*cf.* Brunbjerg *et al.*, 2017), conditions

which also affect the spread of megafauna from surrounding ecosystems into defaunated areas (Ziółkowska *et al.*, 2016). When geographic barriers are insuperable or external source ecosystems are lacking, a targeted introduction of missing species parallel to the (re)introduction of megafauna could help to overcome missing material and information legacies actively in the focal ecosystem. However, such interregional or even intercontinental co-introductions are riskier than the megafauna introductions themselves. Species like dung beetles or other insects may actually be harder or even impossible to control after introduction (e.g. Lovett *et al.*, 2016). Nevertheless, active translocations of smaller species are already common practice in biological control (Manchester & Bullock, 2001) or restoration, like the reintroduction of locally extirpated plant species *via* seed addition or planting as a form of active restoration [e.g. see Donath *et al.*, 2007 and Török *et al.*, 2011 for grasslands].

## IV. IMPLEMENTATION OF THE ECOLOGICAL MEMORY–REWILDING FRAMEWORK

The fundamental challenge we have in restoration/trophic rewilding is that we want (or do not want) to change the state of the focal ecosystem to follow a certain restoration goal. Depending on this decision, we must actively decrease or increase the resilience, and thus attempt to erode or preserve the ecological memory maintaining the ecosystem in its current (desirable or undesirable) state. The focal ecosystem will respond differently to megafauna (re)introduction based on the difference between its current state and the desired state, its ecological memory, and the impact potential of the chosen megafauna species. Restoration as well as management and monitoring strategies have to be adapted correspondingly. The information we provide about the key determinants of ecosystem responses to tropic rewilding within the ecological memory–rewilding framework (Figs 2 and 3) can help to anticipate possible trajectories of ecosystem dynamics after rewilding and to adapt restoration, management, and monitoring strategies in order to maximise the success and to minimise the risk of unwanted, negative outcomes of trophic rewilding or other restoration projects.

To facilitate the success of rewilding projects, the overall goal of a restoration activity must be clearly defined *a priori* and the success of the implemented restoration/rewilding action in achieving this goal should be scientifically monitored for a sufficient time afterwards. A clear definition of the specific goals of a restoration project (e.g. maintenance of biodiversity or persistence of a focal species, increasing water retention or carbon storage, decreasing soil erosion, etc.) will also help to answer the fundamentally important question in adaptive nature management: 'resilience of what to what?' This is crucial to identify the relevant ecosystem properties and processes that are necessary to keep or bring the focal ecosystem onto a desirable trajectory for reaching the restoration goal (Carpenter *et al.*, 2001; Folke, 2006; Higgs *et al.*, 2014). Monitoring conducted

for a sufficiently long period after the initial restoration action [e.g. megafauna (re)introduction] will be needed to understand the response trajectories of the restored ecosystem and to prevent the ecosystem from following unwanted response trajectories towards undesirable states. Adaptive management as a strategy where management decisions and actions are permanently recalibrated based on the *a-priori* defined goals and the knowledge obtained from continuous monitoring of the current response trajectory of the focal ecosystem (Biggs & Rogers, 2003) can be a helpful or even necessary management approach to ensure the success of any restoration project. Specific restoration goals can sometimes change over time when knowledge obtained about the response trajectory of the focal ecosystem or drastic changes in ecological, socio-economic or political boundary conditions reduce their desirability. This adaptive way of managing restored ecosystems seems to be especially important when the focal ecosystem is far from its desired state and ecological memory is low.

As rewilding projects are generally planned to be open-ended, their key goals are: (*i*) the promotion of dynamic landscapes, natural processes, and, in some cases, concomitant ecosystem services, and (*ii*) the general maintenance of high levels of biodiversity rather than fixed reference states in species composition or habitat characteristics (Hughes *et al.*, 2011; Svenning *et al.*, 2016). Adaptive management as described above is particularly suitable for the monitoring and evaluation of programs with such dynamic goals.

## V. CONCLUSIONS

(1) Trophic rewilding is a novel and promising restoration approach to promote self-sustaining, biodiverse ecosystems, but ambiguity still exists about the ecological outcomes of megafauna (re)introduction. This mainly results from fragmentary empirical data and missing theoretical frameworks.

(2) We provide a novel conceptual framework to help anticipate ecosystem responses to trophic rewilding based on two interacting factors: (*i*) the impact potential of (re)introduced megafauna and (*ii*) the ecological memory of the focal ecosystem.

(3) The impact potential of (re)introduced megafauna species can be estimated by species' properties: lifetime *per capita* engineering capacity, population density, home range size, and niche overlap with resident species.

(4) The impact potential of (re)introduced megafauna species on a focal ecosystem is expected to be modulated by ecological memory through its four elements: absolute time since megafauna loss, the speed of abiotic and biotic turnover, the strength of species interactions characterising the focal ecosystem, and the compensatory capacity of surrounding source ecosystems. The result of this interaction between the megafauna's impact potential and the elements of ecological

memory will determine the outcome of (trophic) rewilding actions.

(5) Ecological resilience is seen in our framework as an emerging property of ecological memory. The different internal and external components of ecological memory (see Table 1) affect the degree to which an ecosystem is capable of reorganising and adapting to future changes, a crucial part of ecosystem resilience.

(6) We propose a strong link between ecological memory and temporally lagged responses to restoration activities, stemming from disequilibrium dynamics in ecosystem assembly.

(7) We provide practical advice on how to characterise quantitatively the key elements of the ecological memory–rewilding framework to assess likely ecosystem responses to trophic rewilding. This could help managers and practitioners to weigh plausible strategies to maximise the success of rewilding projects and minimize the risk of unwanted ecosystem changes. Monitoring of ecosystem responses to trophic rewilding over an extended period in combination with adaptive management strategies will help to prevent adverse effects of trophic rewilding even under unstable, unpredictable conditions (i.e. far from equilibrium). The framework and the management suggestions, although specifically developed for trophic rewilding, are easily transferable to other restoration projects. We hope this review will help facilitate sustainable management of functioning ecosystems in an increasingly human-dominated world.

## VI. ACKNOWLEDGEMENTS

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