

# **Biodiversity-enhancing approaches to landscape abandonment and urbanization**

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## **Can rewilding and urban conservation gardening promote biodiversity in a changing landscape?**

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*One touch of nature makes the whole world kin*

*Who are we doing this for if not for each other?*

*Photo Credit: Daniel Mirlea / Rewilding Europe*





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## Lay summary



*Photo Credit: Rewilding Europe*

General consensus in the scientific, and increasingly in the wider, community is that we are in an unprecedented era of change, the Anthropocene. Anthropogenic climate breakdown, rapacious biodiversity loss and the various social cataclysms that can occur dominate modern ecological thinking. Conservatively, 200 species are thought to go extinct every year, which means that the world has lost 700 species since I started my PhD. Despite the dip in CO<sub>2</sub> emissions during the COVID-19 crisis, the increase in CO<sub>2</sub> levels was at their highest ever in historical terms just the year after. This year there were record-breaking heatwaves, droughts, flooding events, wildfires, hurricanes, glacial retreats, ice breaks, avalanches and with them, many human and other species lives lost or ruined. Furthermore, the major efforts to protect and restore our planet seem to be failing. Protected areas are unable to stem the tide of biodiversity loss and international environmental policies remain unenforceable and politically precarious. In turn, these events and figures are beginning to have a notable effect on people's psychological state. Indeed, studies have recently showed soaring levels of anxiety and depression catalysed by these issues.

Yet, parallel to these catastrophic events are many, underreported, positive trends and human efforts. There has been tremendous wildlife comeback of several species across the world, including species that were until recently extinct in the wild. There have been great leaps forward in terms of global and more local environmental policies and there has been major mobilization in tech, finance and other industries to generate environmentally-positive efforts. There is concurrently a growing articulated desire for nature connection and an appreciation for its effect in making our lives healthier and more beautiful. Health practitioners, for example, are beginning to recommend outdoor conservation work as an alternative to medications in some cases. It is therefore of equal importance that we gain a deeper understanding of these positive trends and the consequences they may have for our world. The following work endeavors to investigate two such positive, proactive paths forward, namely rewilding and urban conservation gardening.

In the second chapter of my PhD, I used a pan-European network of vegetation resurvey data to investigate the long-term, large-scale consequences of ungulate herbivore increases in forests across Europe. Policy restrictions on hunting, human-wildlife coexistence measures and reintroduction efforts have increased these species' populations, however, this event has not happened in isolation, but instead against the backdrop of environmental change and other human pressures. I therefore investigated the interaction effect of ungulate herbivory and a major environmental driver of the last century, nitrogen deposition. Given the intended conservation focus of the PhD, I chose to look at conservation-relevant metrics of vegetation community change: non-native, threatened and nitrogen-loving species. I found that whilst high levels of herbivory and N-deposition together act negatively on biodiversity, increasing non-native and nitrogen-loving species to the detriment of threatened species, herbivory in the absence of N-deposition has the exact opposite effect. This

information may have implications for how and where we may wish to bolster herbivore populations in the future.

Increasing herbivore populations is one central tenant of rewilding and restoration efforts, given their documented functional benefits in a variety of capacities. Yet there are many other components to rewilding. Rewilding, per se, entails reestablishing heterogeneous, functional, self-sustaining ecosystems. In chapter 3, I subsequently explored the holistic progress that is being made in key rewilding areas across Europe, as well as the factors that either enhance or hinder said progress. I found that whilst key rewilding measures are leading to improved ecological integrity in some sites, several factors are preventing the upscaling of rewilding. International and regional policies, e.g., that lead to agricultural intensification, are often at conflict with rewilding progress and poorly addressed human-wildlife conflicts can exacerbate wildlife persecution, undermining reintroduction efforts. In contrast, in sites where there has been a concerted effort to garner local and public support, key steps have been made to increase ecological integrity and improve the rewilding status of the site.

Rewilding can be a controversial topic and one that requires not only large swaths of land, but often the absence or sharp reduction of human intervention in the landscape. This is not possible or even desirable to achieve in all areas of Europe. Consequently, I was interested in exploring possibilities for more participatory and integrated ways to enhance biodiversity in our everyday lives. In chapter 4, I introduce and investigate the potential for urban conservation gardening, namely the widespread planting of declining, native plants in urban areas. This chapter outlines not only the ecological, but also the socio-ecological potential of horticulture for restoration. I centered my focus on Germany to determine the positive relationship between horticulture and species occurrence and found that there is complementarity between current protected and urban green areas. I then worked together with experts from different fields to outline interdisciplinary social, economic and policy mechanisms to promote this approach, as well as creating a tiered framework for selecting appropriate declining native species for this concept. Complementary to rewilding, this approach advocates for ecosystem restoration at the anthropogenic end of the 'restoration continuum', namely reconciliation ecology.

Together, this work presents a deeper understanding of how rewilding and reconciliation efforts can complement more traditional forms of conservation and restoration in the landscape. Rewilding efforts have potential and are making some progress, but will only be successful when they are mindful of the context they work in, be it herbivore reintroductions or project establishment. Urban conservation gardening may be a participatory way for people to engage in conservation activities and enhance declining species, yet the native seed industry remains poorly supported and political backing is required to make it mainstream. There is evidently still a long, yet hopeful road for nature recovery to come.





# General introduction



*Photo Credit: Jeroen Helmer / ARK Nature / Rewilding Europe*

We are currently facing the twin challenges of unprecedented, anthropogenic climate change and biodiversity loss (Barnosky et al. 2011; Pimm et al. 2014). These trends are inextricably intertwined, with biodiversity playing a crucial role in climate change mitigation and climate change greatly exacerbating biodiversity loss (Griscom et al. 2017; Mace et al. 2018). Yet despite high level efforts to stem biodiversity loss and curb climate change, worldwide trends continue to deteriorate. The Living Planet Index, whilst subject to legitimate criticism, reported an average decline of 70% in vertebrate population sizes (Buschke et al. 2021) and species extinction rates are estimated to be between 100-1000 times higher than background rates (Ceballos et al. 2015). Furthermore, there are major global shifts in species community structures, with substantial species turnover over the past century (Dornelas et al. 2014) and large losses in some local species abundance (Jandt et al. 2022). Taking a more historical view, approximately 13% of average local species richness has been lost globally since 1500 (Newbold et al. 2015), and current rates of loss may indicate a sixth mass extinction event (Díaz and Malhi 2022; Malhi et al. 2016). Concurrently, anthropogenic greenhouse gas emissions continue to increase with severe consequences already for adverse, extreme weather conditions, species losses and human lives (Pörtner et al. 2022).

There are several drivers of climate change and biodiversity loss, which can often be linked to the same wide and interlinked set of environmental problems (Reid 2005; Vitousek et al. 1997). One of the most important drivers to date is land use change, or habitat loss (Caro et al. 2022). Human land use has both local effects by altering the structure and functioning of specific habitats, but also broader impacts through its interaction with many other components of global environmental change, such as impacting atmosphere, aquatic systems etc., (Foley et al. 2007). Land transformation is also considered as the primary driving force of biodiversity loss, with climate change predicted to take over in the future (Mazor et al. 2018). Whilst humans have modified the European landscape for millennia, two land use changes that are particularly relevant for the contemporary European landscape are large-scale urbanisation and land abandonment (Kuemmerle et al. 2016). Whilst these trends can present major challenges, they are increasingly viewed as presenting opportunities for biodiversity conservation as well. Both have the potential to negatively and positively affect biodiversity in the landscape, depending on how they are dealt with politically and socially (Aronson et al. 2017; Cousins et al. 2015).

There are many negative consequences associated with land use change, particularly in instances where species are coadapted to the particular set of human actions. Agricultural and land abandonment is a major driver of landscape changes in Europe (Fayet et al. 2022). This is defined by the complete removal of agricultural management of the land (Pointereau 2008). The impact of land abandonment can be positive or negative for biodiversity, depending of the area's characteristics and the land use trajectory that follows, as well as the type of agriculture that preceded abandonment (Benayas et al. 2007; van der Zanden et al. 2017). For example, traditional, low-impact forms of agriculture that created heterogeneous landscapes and mimicked the grazing actions of extinct megafauna are thought to provide suitable habitat for many of Europe's species (Pykälä 2000). Furthermore, abandonment is not necessarily the end-state of the landscape. In the majority of cases, the land transitions towards semi-natural habitats, yet land can also transition to urban, recultivated and afforested landscapes (Fayet et al. 2022). There are concerns that this land abandonment can lead to biodiversity loss of some species, especially if the heterogeneity of the landscape is not maintained by natural processes (Queiroz et al. 2014).

Rewilding has been posited as a hopeful, economically-viable alternative to more traditional, often resource-intensive forms of restoration (Chytrý et al. 2009; Navarro and Pereira 2015; Regos et al. 2016), that aims to capitalize on increasing land availability that follows agricultural abandonment. Whilst rewilding has been defined in many ways (Pettorelli et al. 2018; Sandom et al. 2013) the two major tenants of rewilding are the increase in ecological integrity of a system, alongside an increase in ecological autonomy (Perino et al. 2019). Ecological autonomy can also be understood as the ability for an ecosystem to self-regulate without the need for ongoing human intervention. This does not mean that human actions are necessarily excluded from the system, rather that the ecosystem should function regardless of human presence. Here, ecological integrity may be understood as an ecosystem's capacity to undergo change whilst preserving key components of structure, functioning and identity (Wurtzebach and Schultz 2016). Perhaps what distinguishes rewilding the most from other forms of restoration is the approach to natural disturbance, viewing disturbance events as integral, desirable parts of the ecosystem elicited by natural processes (Pettorelli et al. 2018; du Toit and Pettorelli 2019). In fact, disturbance regimes may be better understood as regulatory regimes. In other forms of conservation or restoration the focus may be on either preventing those regulatory processes to maintain certain species

compositions, or to recreate them through human processes, such as mowing. To illustrate this, whilst more traditional forms of restoration may have particular species targets involving target population numbers and particular species compositions, rewilding focuses on the particular processes that these species may create and focus less attention on which species are used to generate said processes (Jepson 2018). Rewilding is therefore defined less by the individual restoration actions, e.g., species reintroductions, no-hunting zones etc., and rather on the establishment of complex, resilient ecosystems, with emphasis on their functionality.

Perino et al., (2019) devised a framework that provides a more detailed overview of the salient features of rewilding, namely stochastic disturbances, trophic complexity and dispersal. The authors agree that in a rewilded ecosystem, these components should ideally be improved. Biologically, the focus is on ecosystem functionality, landscape scale connectivity and keystone species restoration. Philosophically, it highlights a change in the normative values of nature and our role as humans within it (Drenthen 2018). Through a policy lens, it may be considered as a space for innovation in conservation management, allowing us to experiment with concepts of surprise and uncertainty (Sandom et al. 2013). Rewilding has even been approached from a human wellbeing and social perspective, in which the principles of rewilding are applied in the ways we engage with nature and other species (Bekoff 2014; Monbiot 2014). Yet whilst rewilding has gained some traction due to its public appeal, rewilding faces other challenges and controversies that threaten to hinder its progress (Jørgensen 2015; Nogués-Bravo et al. 2016). One of these is the lack of empirical evidence of rewilding outcomes that we try to address in both chapters 2 and 3.

Yet, even with sufficient knowledge of outcomes and a rigorous, widely accepted definition, rewilding is unlikely to act as a biodiversity panacea. Traditional and complementary forms of conservation and restoration will continue to be needed to address the multifaceted challenges facing biodiversity and humanity. Whilst land abandonment is a major land use change and hence challenge for Europe, another is increasing urbanization of landscapes. Urbanisation, expressed as the proportion of people living in urban spaces, has increased exponentially over the past century with 73.5% of people now living in urban spaces in Europe (Oxford Martin school 2015.). Whilst urban areas occupy a relatively small fraction of the terrestrial surface (11% of land in Europe, increasing by >900km<sup>2</sup> per year), the ecological footprint is disproportionately large, impacting ecological processes heavily

(Goddard et al. 2010). Urbanisation, for example, is considered to be a significant factor in species extinctions (McDonald et al., 2008). Concurrently, there is a growing “extinction of experience”, whereby people feel increasingly disconnected from nature (Miller 2005). This in turn has severe implications for both human wellbeing and conservation efforts. These trends demonstrate that it is no longer viable, both ecologically and ethically, to separate human landscapes from nature.

One of the major challenges for biodiversity and human cities will be to reconcile our urban spaces with other species’ needs (Rosenzweig 2003). In complement to reserves and restoration, reconciliation ecology aims to integrate ecologically-friendly practices into highly human-modified land without compromising the dominant land use (Francis and Lorimer 2011). Whilst rewilding may provide one solution to biodiversity enhancement in more rural, abandoned areas, more management-intensive solutions may be needed within cities. One concept that has gained some traction in recent years is that of wildlife-friendly gardening, otherwise known as conservation, naturescape or pollinator-friendly gardening. These practices advocate for participatory gardening practices explicitly designed to enhance biodiversity in urban spaces (Majewska and Altizer 2020; Mumaw and Mata 2022). The major benefits of this practice are twofold. Firstly, the practice aims to engender a sense of nature stewardship amongst urban dwellers who experience a paucity of daily nature connections, and to promote biodiversity awareness. This may be akin to a modern, urban form of land ethic (Leopold 1989). Secondly, it is to better utilize the abundance of greenspaces in urban areas for conservation and create stepping stones to protected areas. Where reconciliation practices exist, urban areas can host high levels of and act as important refuges for biodiversity, including native and threatened species (Callaghan et al. 2088; Goddard 2010).

In this thesis, the idea was to explore how two distinct approaches might be used to enhance and support biodiversity in light of major landscape changes occurring across Europe, land abandonment and urbanisation. Whilst the many aspects of rewilding and its general premise are based on previous ecological studies and processes, both the scale of rewilding projects and the interactive effects of rewilding with modern society and modern environmental drivers remain poorly understood (Bakker and Svenning 2018). We examine some of the implications and progress of rewilding in chapters 2 and 3. Furthermore, in light of the underused potential of urban green spaces and citizen science, we examine the potential

for participatory conservation gardening measures in chapter 4. This may act as a complement to reserves and restoration (rewilding) efforts that may not always be applicable in human-dominated landscapes.

### **Paper overview**

One of the most important and controversial components of rewilding is the reintroduction or population bolstering of large ungulate herbivores in the landscape. This is controversial for several reasons and we chose to focus on one component of the controversy. Whilst the effects of ungulate herbivory have been well-studied in forest systems, the results vary widely in both their outcomes and the value interpretation that comes with it. Firstly, herbivory is considered to have effects on tree biomass by removing saplings, thereby preventing tree regeneration. For forest managers this has negative implications for forest regrowth and related economic practices, whilst for other interest groups, it can be beneficial for landscape heterogeneity (Holladay 2006; Ramirez et al. 2019; Redick and Jacobs 2020). Secondly, there are mixed reported responses of biodiversity to herbivore pressure. Some studies report that herbivores can bolster non-natives species, whilst reducing threatened species, whereas other find that herbivores have the opposite effect (Boullanger et al. 2018; Simončič et al. 2019).

In my first manuscript, I worked together with a pan-European network that compiles long-term resurvey forest vegetation data to understand the effects of herbivore population changes in natural forest systems. The idea was to fill two important gaps in the literature. The first being a paucity of long-term, large-scale studies on herbivory effects. In this paper our median timescale is 47.5 years and the median site size is 2300 km<sup>2</sup>. The second being the lack of understanding of how herbivory interacts with key environmental drivers that are widely known to affect vegetation communities and forest biodiversity. Nitrogen deposition has been shown to lead to biotic homogenization and negatively affect forest vegetation biodiversity (Heinrichs and Schmidt 2017; Keith et al. 2009). Whilst we have a good understanding of the interactive effects of herbivory and N-deposition in grassy systems, this has thus far been overlooked in forests. Therefore, also from a fundamental ecological perspective, it is important to know how these processes might operate differently in different habitats. Unlike in grassy systems, in forests the effects of N-deposition are thought to be attenuated due to the canopy layer with light being a primary limiting factor (Gilliam 2006, 2016; Gilliam et al. 2016). We wanted to understand

whether this would influence herbivory effects in turn. As herbivore populations are generally increasing across Europe, and as rewilding projects aim to bolster certain threatened species populations in the wild, it is essential that we understand the real-world, long-term implications this could have in novel environments.

In this study, I chose to focus on specific, conservation-motivated metrics of vegetation community change. Although I outline the general herbivory relationships with each vegetation layer, i.e., herb, tree and shrub, I focus the main analysis on four specific groups, namely nitrophilous, non-native, threatened (red-listed species) and small-ranged. The reasons for this are as follows. Nitrophilous species are often large-ranged, non-native and/or competitive species (Dawson, 2012). An increase in their extent and cover may indicate a potential threat to vulnerable, smaller-ranged species that are less able to cope with disturbances or N-deposition (Newbold et al. 2018). Nitrophilous species have also been found to increase significantly in forests and grassland sites over time, particularly as a result of eutrophication (Staude et al. 2020, 2021). Non-native species are not only perceived as a threat factor for biodiversity in forests, but they have also been found to be bolstered by herbivores and N-deposition (Bobbink et al. 2010; Boulanger et al. 2018; Gilliam et al. 2016). They are often disturbance-tolerant species that can be easily transported by herbivores and establish quickly. In contrast, red-listed and small-ranged species may be negatively affected by N-deposition as they are often more nutrient-efficient species and it remains unclear how they are affected by herbivory (Clark et al. 2019; Perring et al. 2018). Here, we could leverage a synthesized European database of red-list plant species that we had previously published (Holz et al. 2022) to analyse country-specific threatened species. Small-ranged species can often also be a proxy measure for the threat status of a species (Staude, 2020). This chapter allowed us to investigate this specific component of rewilding and better understand the potential consequences of rewilding efforts on vegetation communities.

The work of **chapter 2** was published as: Segar, J., Pereira, H. M., Baeten, L., Bernhardt-Römermann, M., De Frenne, P., Fernández, N., ... & Staude, I. R. (2022). Divergent roles of herbivory in eutrophying forests. *Nature Communications*, 13(1), 1-10.

For the second manuscript, we wanted to investigate the ecological consequences of rewilding from an integrative perspective, using criteria



and the rewilding framework from Torres et al., (2018). This framework was predicated on a rewilding framework proposed by Perino et al., (2019). Here, the authors summarized the major components of rewilding into three categories, namely stochastic disturbances, trophic complexity and dispersal in a bid to structure rewilding efforts and provide a clear definition for rewilding. We investigated the holistic rewilding progress being made at seven key rewilding sites across eight European countries over the past ~10 years. We conducted this by using a multi-criteria methodology to monitor and evaluate rewilding site changes over time (Torres et al. 2018). Rewilding aims to be a more process-oriented practice with less focus on ecological “state” than more traditional restoration efforts. The monitoring processes should, in turn, reflect this philosophical underlay (Jepson, 2019). Consequently, the original rewilding monitoring framework aimed at encapsulating the key processes important for rewilding progress and measure them in such a way that encompassed process over state (Torres et al. 2018). The second manuscript not only implements the rewilding framework to assess rewilding progress across these sites, it also sought to improve it by fine-tuning the indicators, as well as dealing with some of the inherent biases associated with the monitoring approach.

**Chapter 3** was published as: Segar, J., Pereira, H. M., Filgueiras, R., Karamanlidis, A. A., Saavedra, D., & Fernández, N. (2022). Expert-based assessment of rewilding indicates progress at site-level, yet challenges for upscaling. *Ecography*, (4).

In the third manuscript, I wanted to investigate a potential approach to improve biodiversity restoration and awareness in urban areas. Therefore, I focused on understanding the socio-political and ecological potential for mainstreaming Urban Conservation Gardening, namely the deliberate and widespread horticulture of native, declining plant species in urban areas. These spaces can also comprise large proportions of cities and hold enormous potential to create wildlife-friendly spaces (Ives et al. 2016), as well as wildlife corridors connecting protected areas surrounding urban areas (MacKinnon et al. 2019). In this paper, we built on previous work that focused on wildlife or pollinator friendly gardening and specifically on declining native plant species that could benefit from horticultural practices (Majewska and Altizer 2020; Mumaw and Mata 2022). In part, this was to maximise the utility of urban green spaces for restoration efforts, but also because the number of native plant species far exceeds that of neophytes. Therefore, a practice that specifically targets these species could reap the

greatest conservation payoff in terms of reducing overall extinction risk. The aim of this paper was to examine not only the ecological mechanisms associated with horticultural practices, as well as the socio-economic and policy mechanisms that might be levied to do so. This paper provides a management-intensive complement to spaces where rewilding practices might not be as appropriate.

**Chapter 4** was published as: Segar, J., Callaghan, C. T., Ladouceur, E., Meya, J. N., Pereira, H. M., Perino, A., & Staude, I. R. (2022). Urban conservation gardening in the decade of restoration. *Nature Sustainability*, 1-8.

### **Methodological features**

In the thesis I worked with a wide range of data sets and methodological approaches to address the three research questions. My approach to chapter two was an ecological community statistical modelling, using observational data and applying Bayesian regression models to understand relationships between variables. Chapter two is the combined result of eight different datasets:

1. Primarily, I utilized the dataset from ForestRePlot (<https://forestreplot.ugent.be/>). This is a long-term temperate forest vegetation resurvey dataset that spans Europe and the USA. The vegetation structure and community of temperate forest exhibit slow dynamics, and therefore require resurveys over long periods of time to understand drivers of change (Verheyen et al. 2012). Furthermore, temperate forests are experiencing several global change drivers, such as nitrogen deposition and climate change, making it essential to sample over large environmental gradients (Gilliam 2016). ForestRePlot also provided me with the associated herbivore and forest management data (further discussed in the methodology of chapter 2).
2. In conjunction with the vegetation layers, I utilized a dataset I coauthored during my PhD that synthesized the most recent plant Red Lists in Europe (Holz et al. 2022). This allowed me to individualise threatened plant status by country during my analysis, as opposed to using coarser, and often older, measures of threat status, such as the European Red List.

3. I additionally used the Global Register of Introduced and Invasive Species (GRIIS; <http://www.griis.org>) for its designations of non-native species per country.
4. I used a combination of two datasets to understand the species' ecological indicator values for the plants' nitrogen values (Chytrý et al. 2018; Ellenberg et al. 2001). Ellenberg values are based on ordinal classifications of plants' positions of their realised ecological niche along an environmental gradient. It allows us to determine which variety of conditions will allow for the optimal growth and production of a species, and can also be used to make community composition assessments. Ellenberg indicator values vary from 1-9. In the case of nitrogen, sometimes referred to as nutrient, values, a value of 1 means that the species requires the least nitrogen/nutrients and is an indicator of extremely infertile soils. A value of 9 means the plant species thrives under high levels of nitrogen and is indicative of very fertilized or polluted soils. In this study, I used this indicator to determine the community composition of nitrophilous vs nutrient-efficient plants, as these are often also indicative of non-native, competitive vs threatened, small-ranged plants respectively.
5. Additionally, I used the EuMedClim database (Fréjaville and Garzón 2018) to determine site productivity. This database provides yearly bioclimatic data from 1901 – 2014 at a 1km resolution grid for Europe. I calculated the annual precipitation to potential evapotranspiration ratio (AP: PET) as a proxy metric (Al-Yaari et al. 2020) measured in the year of the baseline and resurvey.
6. I further used the EMEP database ([https://emep.int/mscw/mscw\\_moddata.html](https://emep.int/mscw/mscw_moddata.html)) to calculate cumulative N-deposition for the sites. The EMEP is a program for measuring the long-term transmission of air pollutants in Europe. I focused on the depositions of nitrogen that have been calculated by a model and gridded on a 0.1° x 0.1° longitude-latitude grid per country (further details are discussed in the methodology section of chapter 2).
7. I also used the Global Biodiversity Information Facility GBIF ([gbif.org](http://gbif.org)) to calculate species' geographic range sizes. GBIF is an international facility that provides open access data about biodiversity, including information on species' point occurrences. This in turn allows us to estimate species range sizes as their area of occupancy (AOO). Although there are sampling biases and data gaps in GBIF, GBIF-related range sizes correlate strongly with expert-drawn range maps for plant species in Europe. Furthermore, I chose to use AOO instead

of extent of occurrence, because AOO is a better representation of species population sizes and species niche than EOO (Gaston and Fuller 2009). In turn, I used the AOO estimates per plant species to determine which plant species could be classified as small-ranged, an indicator that is strongly correlated with important measure of threat status.

My third chapter used a different approach in that I focused on using expert opinion. I collected raw quantitative and qualitative data from rewilding experts from a questionnaire and a series of interviews. The experts were informed by available data in each site; however, this availability was highly variable across sites and therefore an approach had to be used to standardize results. For this reason, we applied the Delphi Technique in order to reduce certain types of bias from this methodological approach. The Delphi Technique is predicated on the well-tested assumption that decisions or predications from a “structured” group as more accurate than those from an “unstructured” group. A group of experts start by making independent evaluations of a topic, and then test those evaluations in a series of systematic, iterative collective sessions (Niederberger and Spranger 2020). The outcome from these iterations should be a consensus decision and a convergence of estimates about the topic. The benefits of this are two-fold. Firstly, this technique allows for deeper reflection among the individual participants themselves, who may be better able to nuance their opinion after hearing from others. Secondly, information gaps can be filled by combining the judgements of experts from different fields, thus leading to better informed results (Mukherjee et al. 2015). This technique was useful for our study as we were working with experts from a variety of backgrounds and perspectives, as well as variable data sources and availability across the sites. By implementing the Delphi technique, we could reduce some of the resulting reporting bias and extreme values that arose in the initial, individual iteration of the interviews. The Delphi technique in turn was used to calibrate a rewilding monitoring approach designed by Torres et al., (2018).

My fourth chapter consisted of data analysis from several datasets, as well as a literature review. The datasets consisted of two ecological datasets and one spatial analysis. Data was taken from (Eichenberg et al. 2021), as well as the same Ellenberg indicator values data from chapter 2. Eichenberg et al., (2021) provide spatiotemporal plant occurrence data for 2136 plant species between 1960 and 2017 over an area of 350,000km<sup>2</sup> on a 5 x 5 km grid cell

basis within Germany. This allowed us to measure species occurrence changes over 57 years with high spatial precision. Furthermore, we could differentiate between the occurrence changes of archaeophytes and neophytes. In addition, we took spatial layers of protected areas and urban green spaces in order to determine complementarity of these two land use types ([protectedplanet.net](http://protectedplanet.net); [land.copernicus.eu/local/urban-atlas](http://land.copernicus.eu/local/urban-atlas)). For the last analysis, we conducted a webscrape of threatened plant species that are available to buy online, for which we used the German Red List. The literature review was conducted to give us a comprehensive overview of the interdisciplinary components of the paper. For this component of the paper, we did not conduct a systematic review of the literature, but relied rather on searches using key terms, as well as literature provided by the specific subject experts on the paper. For example, I worked with an ecological economist and an expert on the native seed industry to elucidate important aspects of the field.

The three papers therefore span different approaches, ranging from data analysis to interviews to literature reviews, as well as different data types.

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## Chapter 2

### Divergent roles of herbivory in eutrophying forests



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*Photo credit: Staffan Widstrand / Rewilding Europe*

## *Divergent roles of herbivory in eutrophying forests*

Josiane Segar, Henrique M. Pereira, Lander Baeten, Markus Bernhardt-Römermann, Pieter De Frenne, Nestor Fernandez, Frank S. Gilliam, Jonathan Lenoir, Adrienne Ortmann-Ajkai, Kris Verheyen, Donald Waller, Teleki Balázs, Jörg Brunet, Markéta Chudomelová, Guillaume Decocq, Thomas Dirnböck, Radim Hédli, Thilo Heinken, Bogdan Jaroszewicz, Martin Kopecký, Martin Macek, František Máliš, Tobias Naaf, Anna Orczewska, Kamila Reczynska, Wolfgang Schmidt, Jan Šebesta, Alina Stachurska-Swakon, Tibor Standovár, Krzysztof Swierkosz, Ondrej Vild, Monika Wulf, Ingmar R. Staude

### **Abstract**

Ungulate populations are increasing across Europe with important implications for forest plant communities. Concurrently, atmospheric nitrogen (N) deposition continues to eutrophicate forests, threatening many rare, often more nutrient-efficient, plant species. These pressures may critically interact to shape biodiversity as in grassland and tundra systems, yet any potential interactions in forests remain poorly understood. Here, we combined vegetation resurveys from 52 sites across 13 European countries to test how changes in ungulate herbivory and eutrophication drive long-term changes in forest understorey communities. Increases in herbivory were associated with elevated temporal species turnover, however, identities of winner and loser species depended on N levels. Under low levels of N-deposition, herbivory favored threatened and small-ranged species while reducing the proportion of non-native and nutrient-demanding species. Yet all these trends were reversed under high levels of N-deposition. Herbivores also reduced shrub cover, likely exacerbating N effects by increasing light levels in the understorey. Eutrophication levels may therefore determine whether herbivory acts as a catalyst for the “N time bomb” or as a conservation tool in temperate forests.

### **Introduction**

Temperate forests represent globally important ecosystems both as habitats supporting a unique set of species and providing essential ecosystem services<sup>1,2,3,4</sup>. These ecosystems are threatened, however, by unprecedented forest dieback and loss of species diversity<sup>5,6,7</sup>. It is critical, therefore, to understand the processes that are beneficial or detrimental to forest

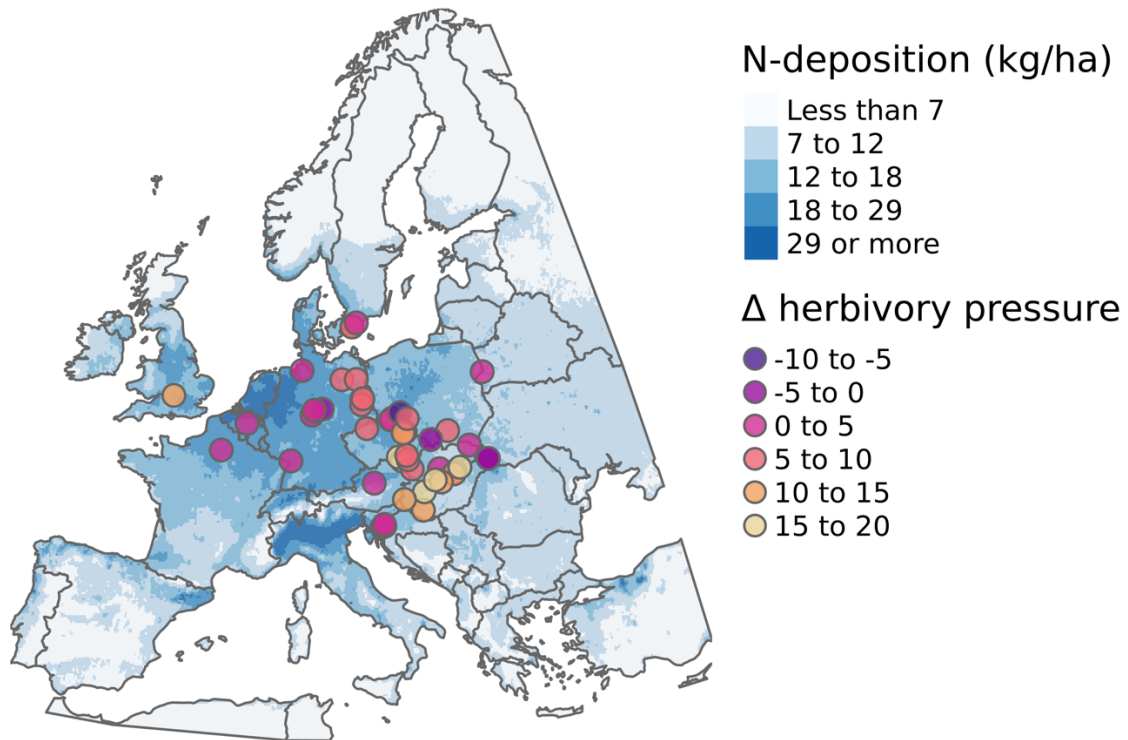
functioning<sup>8</sup>. Herbivory by ungulates is an important driver of ecological change in forests and populations are broadly increasing across Europe. Yet their conservation role remains highly contended<sup>9:10:11:12:13:14:15:16:17</sup>. Effects of herbivory are often varied and highly context-dependent<sup>10</sup>, with studies rarely exploring interactions with other global change drivers. Herbivory and eutrophication have been shown to strongly interact and drive vegetation dynamics in grassland and tundra systems by mitigating light limitations and releasing low-stature, often threatened, species from competition<sup>18:19</sup>. However, this interaction is poorly understood in forests where nitrogen (N) deposition often continues to exceed critical loads<sup>20:21:22</sup>. Examining how herbivory interacts with N-deposition in forest plant communities is, therefore, key to making informed forest management and restoration decisions.

The second half of the 20th century witnessed the resurgence of many populations of wild grazer and browser species, increasing their density and range across European landscapes<sup>23:24</sup>. Several factors contributed to these trends, including restrictions on hunting, hunter desires for higher game densities, land abandonment, reduction of natural predators and deliberate reintroductions<sup>25:26</sup>. Human pressures have also acted to push some of these species from semi-open into closed forest systems<sup>27</sup>. Consequently, the majority of wild herbivory pressure now occurs in forests which can shape forest systems in different ways<sup>23:28:29</sup>. Herbivores can reduce understorey vegetation biomass and tree regeneration, compact soils and alter rates of nutrient cycling<sup>30:31:32</sup>. Through browsing and grazing lawns, herbivores can further create positive consumer-resource cycles that impact vegetation composition, enhance seed dispersal and structural heterogeneity<sup>33:34</sup>. Studies find highly heterogeneous, sometimes non-linear vegetation responses to herbivory<sup>35</sup>. Some plant species benefit, while others decline or disappear, in turn affecting composite indicators like plant cover and diversity<sup>9:10:11:12:13:14:15:16</sup>. The conservation effects of herbivory are yet more contentious. Some evidence suggests that herbivory can reduce threatened species<sup>15</sup> while favouring non-natives<sup>36</sup>. Other studies find that herbivory suppresses competitive species, in turn favouring low-stature and threatened species<sup>37:38:39</sup>. Understanding the varying effects of herbivory is central to policy recommendations for forest and wildlife managers.

Concurrent with herbivore expansions, eutrophication of natural communities greatly increased over the last century largely in response to atmospheric N-deposition and other nutrients, as well as shifts in forest

management<sup>40</sup>. This has led to the reordering of native woodland plant communities<sup>622</sup>. N-demanding species tend to be generalists with larger climatic and geographic ranges that are most competitive in areas with high N-loads<sup>41</sup>. Higher growth rates allow them to outcompete N-efficient species, many of which are of low-stature and/or with more restricted geographic ranges, traits typical of many rare and threatened species<sup>414243</sup>. Nonetheless, experimental evidence of N-additions to forest understories appears less consistent than those observed in grasslands, with forest systems remaining more stable than predicted under increasing eutrophication<sup>20212243444546</sup>. Shifts towards a “high forest” management system over the last century have led to average increases in the biomass of tree and/or shrub layers across many temperate European forests<sup>434748</sup>. The buffering capacity of canopies, accentuated by such a biomass increase, is hypothesized to attenuate the impact of N-deposition by reducing light availability to the understorey, generating time lags in vegetation responses<sup>7495051</sup>. The slow but pervasive effects of N-deposition have led some to label this threat a “N time bomb”<sup>43</sup>.

Given that large herbivores tend to reduce shrub and herb cover and height, they often increase light levels in the understorey (here, the herb layer)<sup>525354</sup>, thereby potentially influencing N-effects and competition among plants<sup>5556</sup>. Here we test three alternative hypotheses: (1) Increases in herbivory could alter the effects of N-deposition by mitigating light limitation and competitive effects on low-stature species as it does in grassland and tundra systems<sup>1819575859</sup>; (2) as light regimes in forests differ greatly from grasslands, herbivory in forests might instead preferentially facilitate the spread of non-native, N-demanding species<sup>6061</sup>, as these proliferate in N-enriched sites when light availability is high<sup>62</sup>; (3) herbivory does not interact with N-deposition as systematic increases in canopy cover<sup>63</sup> attenuate any effect of herbivory on the shrub and understorey layers<sup>56</sup>. Our study leverages long-term vegetation data from 2928 resurveyed plots from 52 sites across seminatural temperate forests in Europe (median: 47.5 yrs between surveys; Fig. [1](#)) to test these hypotheses. By quantifying the interactions between herbivory and N-deposition, we add to the growing debate about whether and under what conditions herbivory plays a role in contemporary forest management at times of unprecedented environmental change.

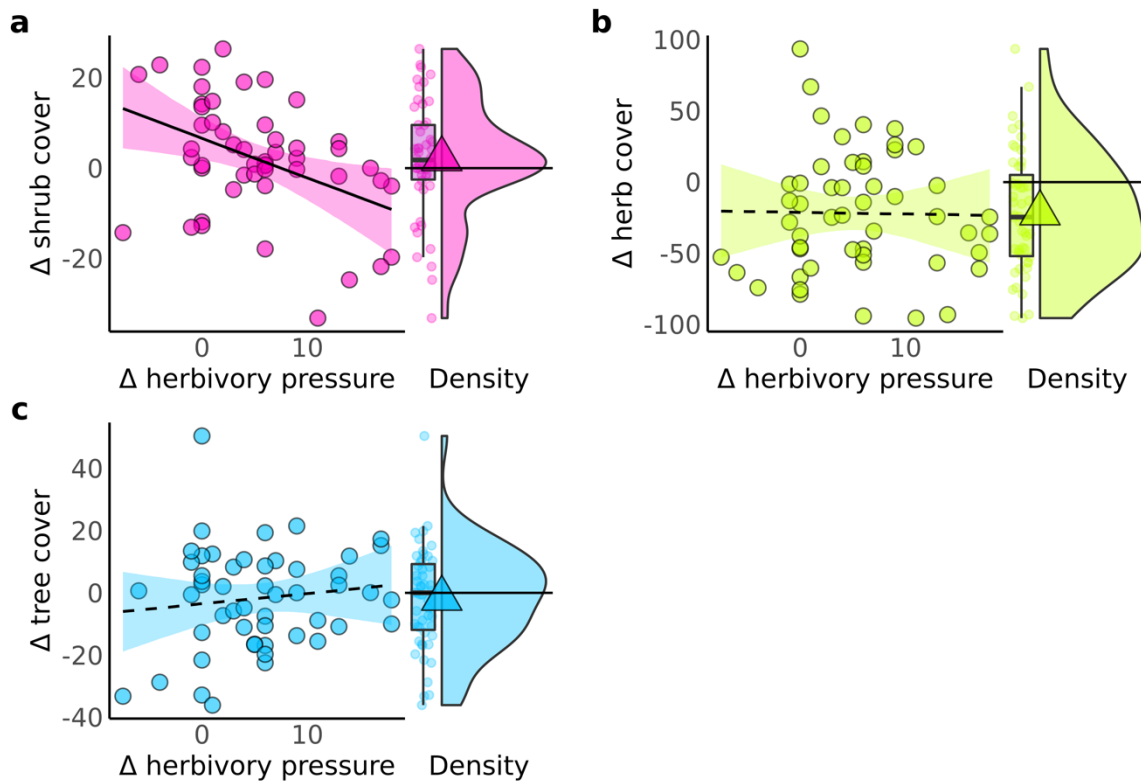


**Figure 1. Spatial distribution of resurvey sites, N-deposition in the year 2000, and changes in ( $\Delta$ ) herbivory pressure across Central Europe.** Our analysis spans 52 resurvey sites with inter-census time spans ranging from 10 to 64 years (median: 47.5 years). Color of points corresponds to the magnitude of change in site herbivore pressure between the baseline survey and resurvey (Supplementary Data file [1](#)). Total nitrogen deposition (wet and dry, reduced and oxidized) is calculated using the EMEP database for the year 2000 and displayed across a color gradient of light to dark blue representing lowest to highest values at a spatial resolution of 10 km.

## Results

We found that, on average, shrub layer cover increased, herb layer cover decreased, and tree layer cover remained mostly constant over time in our forest sites. Increases in herbivory were clearly associated with declines in shrub layer cover ( $\beta = -0.42$ ,  $\sigma = 0.17$ ). However, it was statistically uncertain whether increases in herbivory were associated with changes in the herb and tree layer cover; both associations were neither strong nor very precise ( $\beta = -0.02$ ,  $\sigma = 0.17$ ;  $\beta = 0.13$ ,  $\sigma = 0.18$  respectively; Fig. [2a–c](#) and Supplementary Tables [3–5](#)). Given that prior forest management may initiate different trajectories in these vegetation layers<sup>38,56,64,65</sup>, we tested for the role of historic, and recent changes in management. With the exception of a greater increase in tree cover at sites where management intensity had recently decreased, management did not clearly predict changes in

vegetation cover, and the relationship between herbivory and shrub suppression persisted when management change was accounted for (Supplementary Fig. 1 and Supplementary Tables 6–11).

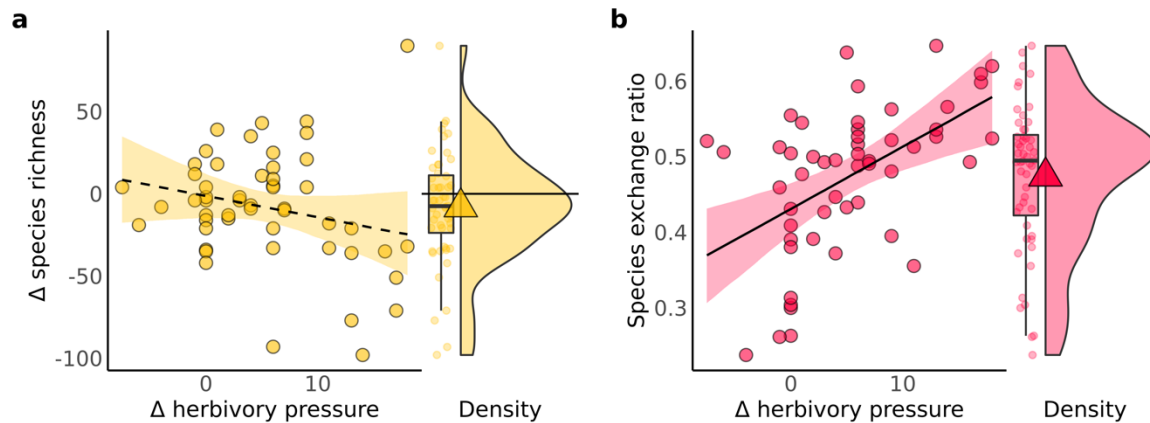


**Figure 2. Higher herbivory decreased shrub layer cover, but not herb and tree layer cover.** Relationships between changes in ( $\Delta$ ) herbivory pressure and **a**  $\Delta$  shrub layer cover, **b**  $\Delta$  herb layer cover, and **c**  $\Delta$  tree layer cover. All models included inter-census time span, site area, and baseline herbivory as covariates. Note two sites lacked shrub and tree cover and one site also lacked herb cover data so that there were  $n = 50$  and  $n = 51$  independent resurvey sites for a, c, and b, respectively. Lines and ribbons represent the posterior mean line and the 95% credible interval. Dashed regression lines represent statistically unclear relationships. Frequency distributions (density, boxplot and points) of the respective response variables are displayed alongside. Boxplots bound the interquartile range (IQR) divided by the median and whiskers extend up to a maximum of  $1.5 \times$  IQR beyond the box. Triangles indicate the mean. Horizontal lines at zero indicate no change. Source data are provided as a Source Data file.

Herb layer species richness tended to decrease over time at the site level, but it was statistically uncertain whether herbivory contributed to this trend; the posterior mean slope for this association was negative, yet the posterior distribution also indicated a 9% chance of a positive slope ( $\beta = -0.23$ ,  $\sigma = 0.17$ ; Fig. 3a and Supplementary Table 12). In contrast, greater increases in herbivory clearly elevated temporal species turnover in the herb layer



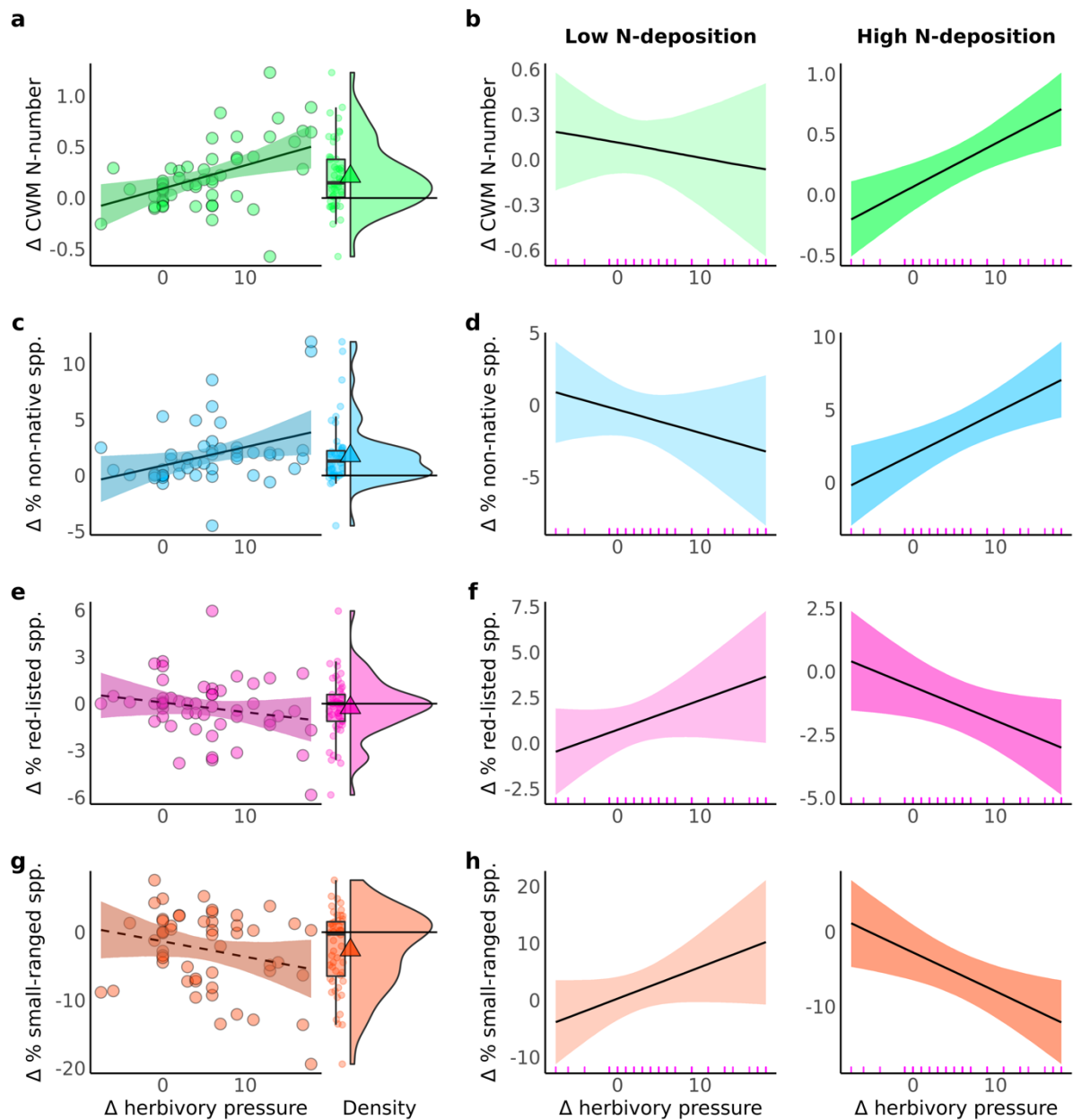
( $\beta = 0.52$ ,  $\sigma = 0.14$ ; Fig. 3b and Supplementary Table 13), accounting for the evident positive effect of inter-census time span on temporal turnover ( $\beta = 0.32$ ,  $\sigma = 0.13$ ; Supplementary Table 13). Moreover, this role of herbivory as a catalyst for community change was not confounded by changes in forest management (Supplementary Tables 14–15).



**Figure 3. Herbivory increased temporal species turnover but was not clearly associated with changes in species richness.** Relationships between change in ( $\Delta$ ) herbivory pressure and **a**  $\Delta$  species richness (number of species) and **b** temporal species turnover (unitless) at a study site. All models included inter-census time span, site area, and baseline herbivory as covariates, with  $n = 52$  independent resurvey sites. Lines and ribbons represent the posterior mean line and the 95% credible interval. Dashed lines represent statistically unclear relationships. Frequency distributions (density, boxplot and points) of the respective response variables are displayed alongside. Boxplots bound the interquartile range (IQR) divided by the median and whiskers extend up to a maximum of  $1.5 \times$  IQR beyond the box. Triangles indicate the mean. Horizontal lines at zero indicate no change. Source data are provided as a Source Data file.

By testing the separate effects of herbivory and N-deposition, we found that increases in herbivory shifted forest plant communities towards species with higher nutrient demands as inferred from increases in the community-weighted mean of species indicator values for nutrients (CWM-N) ( $\beta = 0.43$ ,  $\sigma = 0.15$ , Fig. 4a and Supplementary Table 16). Similarly, greater increases in herbivory were associated with a higher proportion of non-native species ( $\beta = 0.37$ ,  $\sigma = 0.17$ , Fig. 4c and Supplementary Table 17). Per contra, increases in herbivory tended to be negatively associated with the proportion of species classified as threatened in national Red Lists, or small-ranged species; however, these associations were uncertain, with 88 and 92% posterior probabilities for a negative slope, respectively ( $\beta = -0.19$ ,  $\sigma = 0.17$ ;  $\beta = -0.25$ ,  $\sigma = 0.17$ ; Fig. 4e, g and Supplementary Tables 18, 19). These ties between species turnover and herbivory again persisted when

management change was accounted for, except for non-native species whose association became unclear, with a 97% probability of a positive slope (Supplementary Tables [20–23](#)). Forest management itself was not associated with turnover, except for small-ranged species that declined with reductions in management intensity (Supplementary Table [23](#)). To better understand the relationships between herbivory, shrub suppression and community composition, we tested how changes in shrub layer cover related to changes in non-native and N-demanding species. Increases in shrub layer cover reduced the proportion of non-native species ( $\beta = -0.37$ ,  $\sigma = 0.14$ ; Supplementary Fig. [2a](#) and Supplementary Table [24](#)). The association with CWM-N was also negative but, with a 93% posterior probability for a negative slope, statistically unclear ( $\beta = -0.19$ ,  $\sigma = 0.13$ ; Supplementary Fig. [2b](#) and Supplementary Table [25](#)). As expected from previous studies<sup>41</sup>, N-deposition reduced the proportion of threatened species ( $\beta = -0.46$ ,  $\sigma = 0.21$ ), but increased the proportion of non-native species ( $\beta = 0.56$ ,  $\sigma = 0.20$ ; Supplementary Fig. [3a, b](#) and Supplementary Tables [26, 27](#)). Higher cumulative N-deposition also tended to be associated with declines in small-ranged species (96% posterior probability for a negative slope) and increases in nitrophilous species (80% posterior probability for a positive slope), but these associations were uncertain as the 95% credible interval of the posterior mean slope included zero (Supplementary Fig. [3c, d](#) and Supplementary Tables [28, 29](#)).



**Figure 4. Herbivory effects depend on N-deposition levels.** Relationships between change in ( $\Delta$ ) herbivory pressure and **a**  $\Delta$  community-weighted mean N-number (CWM-N), **c** percentage change in ( $\Delta$  %) non-native species, **e**  $\Delta$  % red-listed species, and **g**  $\Delta$  % small-ranged species. Frequency distributions (density, boxplot and points) of the respective response variables are displayed alongside. Boxplots bound the interquartile range (IQR) divided by the median and whiskers extend up to a maximum of  $1.5 \times$  IQR beyond the box. Triangles indicate the mean. Horizontal lines at zero indicate no change. Herbivory effects depend on N-deposition (**b, d, f, h**). Conditional effects of herbivory are depicted at the 10th (348 kg/ha; left) and 90th (1010 kg/ha; right) percentile of cumulative N-deposition in the data. There are  $n = 52$  independent resurvey sites for all models. Lines and ribbons represent the posterior mean line and the 95% credible interval. Dashed lines represent statistically unclear relationships. Rugs in figure bottom in **b, d, f, h** depict the marginal distribution of the predictor. Cumulative N-deposition is calculated between the baseline and resurvey

year per site. See Supplementary Fig. 3 and Supplementary Table 26–29 for model outputs of the effects of N-deposition alone. See Supplementary Fig. 4 for interaction effects on species richness change and exchange ratio. Source data are provided as a Source Data file.

Responses of all four variables to changes in herbivory not only varied but actually reversed direction between sites subject to low vs. high levels of cumulative N-deposition (Fig. 4b–h and Supplementary Tables 30–33). That is, the linear trends reported above masked consistent differences in how vegetation responses to herbivory depended on N-deposition. For example, increased herbivory was associated with higher proportions of threatened and small-ranged species at sites subject to low cumulative N-deposition, whilst reducing them at sites with high N-deposition (interaction:  $\beta = -0.38$ ,  $\sigma = 0.19$  and  $\beta = -0.51$ ,  $\sigma = 0.18$ , respectively; Fig. 4f, h). Increased herbivory further reduced the proportion of non-native species at low N-deposition sites, whereas at high N-deposition sites, herbivory was associated with increases in non-native species (interaction:  $\beta = 0.36$ ,  $\sigma = 0.17$ ; Fig. 4d). Likewise, the association between herbivory and nitrophilous species reversed direction along the N-deposition gradient (Fig. 4b;  $\beta = 0.33$ ,  $\sigma = 0.17$ ). At sites with low cumulative N-deposition, increased herbivory was associated with lower CWM-N, while at sites with high cumulative N-deposition, increased herbivory yielded conspicuous increases in community N-numbers (Fig. 4b). Interaction effects for non-native and small-ranged species remained statistically certain when changes in forest management was accounted for, whereas effects became marginally uncertain for red-listed and nitrophilous species (97% posterior probability for a negative and positive slope respectively; Supplementary Tables 34–37). In sum, the role of herbivory in shaping forest understorey community composition appears to depend on levels of N-deposition.

## Discussion

Long-term data from 52 forest sites across Europe allowed us to assess the separate and combined effects of herbivory and eutrophication on changes in forest understorey composition. Specifically, we were able to test how shifts in herbivory and N-deposition interact to shape community composition. Herbivory did not mitigate the negative effects of eutrophication as found in grasslands<sup>19,57,58</sup>. Instead, it played divergent roles in forests that depended on historical accumulations of nitrogen inputs (Fig. 4). At high cumulative N-deposition, increased herbivory favored nitrophilous and non-native species while diminishing species of

conservation concern. Conversely, at low cumulative N-deposition, herbivory reduced nitrophilous and non-native species while favoring species of conservation concern. These results suggest that herbivory can amplify the deleterious effects of terrestrial eutrophication in forests, despite providing conservation benefits when nutrient inputs are low. These contrasting, context-dependent roles of herbivory echo and may help to account for the reported heterogeneous effects of herbivory on forest community composition<sup>26</sup>. Our findings are further consistent with the hypothesis of a N time bomb in forests that may be triggered by disturbances that increase light availability, such as herbivory.

Herbivory may increase light availability and act on vegetation dynamics in several ways. Although shrub layer cover increased on average across the sites of our study, herbivory reduced it (Fig. [2a](#)). This finding is consistent with other studies showing that herbivory can reduce the density and volume of woody vegetation<sup>36,53,66</sup>. Changes in tree layer cover, however, did not covary with changes in herbivory, and were furthermore not directional (Fig. [2c](#)). While we see that recent declines in management intensity led to increases in canopy cover (Supplementary Fig. [1](#)), thus impacting light availability, the relationships between herbivory and herb layer vegetation dynamics remained largely robust. Whilst herb layer cover and richness were not associated with herbivory, herbivory sharply accelerated species temporal turnover (Figs. [2b](#), [3a, b](#)). As this catalyst role of herbivory persisted even after accounting for changes in management, we suggest this turnover may be partially driven indirectly by increased light availability following the suppression of shrub layer cover from herbivory (Fig. [2a](#) and Supplementary Fig. [1](#)). Turnover rates may further be directly affected by herbivores via browsing, grazing, rooting, fraying and stripping<sup>9,36,67,68</sup> as well as zoochorous seed dispersal<sup>32,69</sup>, reducing some species and enhancing propagule pressure and colonization of others. Precisely which species benefit from these processes likely depends on additional factors, such as available ambient N.

In contrast to grassy systems where light is not a primary limiting factor, and eutrophication effects are fast-acting, N-deposition effects are hypothesized to be attenuated in the low-light conditions of forests<sup>18,19,52,59,70</sup>. This has led previous studies to posit an N time bomb, potentially catalyzed by disturbances, such as herbivory, that release light limitations and exacerbate N-effects<sup>43</sup>. This is different in grassy systems, where herbivory instead mitigates the biotic pressure and light limitation that results from

eutrophication on resource-conservative species<sup>59</sup>. Such species in forests must, however, already be adapted to low-light conditions. Thus, herbivory may encourage resource-conservative, smaller-ranged and threatened species under low N-levels (Fig. 4, Supplementary Fig. 5, and Supplementary Tables 38, 39) by selectively feeding on more palatable species, thereby freeing up physical space. This is consistent with studies showing that herbivory favors low-stature herbs in the absence of eutrophication, many of which have lower N-demands<sup>1571</sup>. Conversely, under elevated N-levels, selective feeding may not suffice to control N-demanding species, as these may be too strongly promoted by the convergent increase in N, light and disturbance. The twin drivers of high herbivory and N-deposition may therefore elicit the colonization and spread of nitrophilous and non-native species, as these often require nutrient-rich, open and disturbed sites<sup>67</sup> (Fig. 4, Supplementary Fig. 5 and Supplementary Tables 38, 39). This is consistent with studies suggesting that herbivory directly promotes N-demanding, palatable species via browsing lawns in systems with elevated N-levels, but not where N-levels are low<sup>34</sup>. Finally, our results highlight that these herbivory-induced changes in species community composition are more often caused by species losses at high N-deposition, whereas species losses were offset by gains under low N-deposition (Supplementary Fig. 4).

Studies of herbivory effects typically rely on short-term comparisons involving artificial herbivore exclosure/enclosure sites, e.g., ref. 67. Our study instead leveraged data across a broad spatiotemporal scale to emphasize ecological realism with wild plant communities and free-roaming herbivores (Supplementary Data file 1). Nevertheless, our observational approach has limitations. Our approach cannot account for all potential confounding variables (or test for higher-order interactions among them). For example, although we did not find a statistically clear effect of site productivity here (Supplementary Tables 40–43), it would be useful to explore whether the interaction effects we observed would hold across larger productivity gradients. Furthermore, our dataset reflected the natural dominance of red, roe and fallow deer and wild boar species in Europe (Supplementary Data file 1). These species can have different feeding preferences, physiologies, and biomass requirements to the larger feeders such as bison and moose<sup>72</sup> that were only present in a few sites. Our results are likely to be driven by these dominant species, making it essential to understand whether the observed relationships would hold should populations of other herbivores increase. Finally, our herbivore densities

reflect expert local knowledge, subject to uncertainty and error, particularly for the baseline surveys. More precise experimental approaches will be essential to substantiate our findings and fully account for potential collinearities of key variables, such as management, N-deposition and herbivory; however, these may realistically not match the spatiotemporal scales of our study.

As ungulate herbivory broadly increases across Europe and N-deposition often continues to exceed critical loads<sup>2441</sup>, our study suggests that herbivory and N-deposition can interact to shape forest ecosystems. The role of herbivory strongly depended on levels of forest eutrophication for all of the key indicators we examined. These interacting effects have important implications for conservation, and especially rewilding efforts that focus on the reintroduction of herbivores in forest settings. Despite recent efforts to curtail N-emissions, rates continue to exceed critical loads in many areas with potential legacy effects on communities in the future<sup>45737475</sup>. The ability of N-demanding and many non-native species to outcompete and displace rarer and more range-limited species of conservation concern are likely to amplify and sustain such legacy effects. Therefore, policies that effectively curtail N-emissions are essential for forest protection in the long run. Depending on our ability to do so, herbivory can act either to trigger the N time bomb or as a tool to bolster species of conservation concern in the future.

## Methods

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### Database

We compiled baseline vegetation survey and resurvey data from 52 sites with associated herbivory data distributed across 13 European countries in the temperate deciduous forest biome (Fig. 1; see [www.forestreplot.ugent.be](http://www.forestreplot.ugent.be) and ref. 43 for inclusion criteria; Supplementary Tables 1, 2). These sites occur in historically continuously forested natural and seminatural forests that have not experienced any substantial change in land use (i.e., no stand-replacing disturbance) either prior to the baseline survey or between the two surveys (sensu ref. 76). Site areas ranged from 5.5 ha to  $2.5 \times 10^6$  ha (median: 2300 ha). At each site, researchers surveyed species in the herb, shrub and tree layer across 10 to 190 permanent or quasi-permanent plots per site (median: 50; total: 2928). Time intervals between the baseline survey and resurvey ranged from 10 to 64 years (median: 47.5 years). We accounted for changes in species taxonomy

between surveys and sites by harmonizing species names following GBIF's backbone taxonomy<sup>77,78</sup>. This prevented double-counting species or inferring inflated estimates of turnover. Altogether, our dataset contains 1257 species across all sites and time periods. Note, because we include new resurveys here and herbivore densities were not available for all surveys in the forestREplot database, our data comprise a different set of sites than previous forestREplot publications (e.g., 50 and 15% overlap with refs. [43,56](#)).

## Explanatory variables

### *Herbivore pressure*

We quantified ungulate herbivore pressure at the level of a study site for the baseline survey and resurvey time period based on expert assessment from each site's dataset custodian in the forestREplot network<sup>18</sup>. Custodians provided density estimates using the best available information alongside expert knowledge of the site. Many of these densities have been used in previously published analyses (see also refs. [8, 15, 37, 43, 79](#)). Density estimates incorporate one or more of the following sources; interviews (e.g., with local foresters, site managers, hunters, and national park administration), published and unpublished local data records, extrapolation of local/regional hunting statistics and/or direct animal count surveys. Herbivore densities were iteratively checked and revised twice by each dataset custodian and internally reviewed by the entire consortium. Custodians provided herbivore densities per species of ungulate as the number of individuals per 100 ha. This was then converted to an ordinal scale from 0 (no herbivores present) to 8 (>500 individuals per 100 ha), to account for a margin of error in the raw herbivory densities (Supplementary Data file [1](#)). In total, there were 13 ungulate species across all sites, ranging from roe deer to European bison. We also considered wild boars as herbivore species: (1) because plant biomass comprises the majority (~90%) of their diet and they substantially impact plant regeneration (e.g., refs. [31, 80](#)); and (2) because their feeding and rooting habits affect plant cover, diversity, height and regeneration and can have ecosystem-level effects<sup>81</sup>. We then summed these ordinal values across species at each site and time period, to reflect the overall herbivore pressure, following a similar approach as in refs. [8, 18, 82](#) (see Supplementary Data file [1](#) for all herbivore data and description of ordinal scale). We then also measured the equivalents of basal metabolic rates by multiplying the mean body mass of a species by its ordinal value, and summing across species per site. Mean body mass per species was taken from the Phylacine database<sup>83</sup>. As this indicator correlated



highly with the above herbivore pressure index (Pearson's  $\rho = 0.82$ ; Supplementary Fig. [6a](#)) and given an extreme outlier of one site ( $\rho = 0.92$  when this outlier was removed, Supplementary Fig. [6b](#)), we used the herbivore pressure index above in all analyses to avoid leverage. Temporal change in this index was calculated as the difference between the last resurvey and the baseline survey values per study site<sup>18</sup>, with change values ranging from  $-8$  to  $18$  (Fig. [1](#) and Supplementary Data file [1](#)).

#### *N-deposition*

We quantified total cumulative N-deposition using the EMEP database ([https://emep.int/mscw/mscw\\_moddata.html](https://emep.int/mscw/mscw_moddata.html)), using cumulative wet and dry deposition of oxidized and reduced nitrogen<sup>84</sup>. We calculated the cumulative N-deposition between the baseline year and the year of the resurvey based on the methods described in ref. [8](#). First, we calculated N deposition between 1900 and the year of the baseline survey ( $N_{t1}$ ); second, we quantified the cumulative N deposition between 1900 and the resurvey ( $N_{t2}$ ); and third, we calculated the difference,  $N_{t2} - N_{t1}$ , to quantify cumulative N deposition between surveys. Therefore, cumulative N-deposition per site will be influenced by the rate of deposition per year, as well as the length of the intercensal intervals (i.e., sites with lower yearly rates but long intervals may have similar values to sites with high yearly rates but shorter intervals). The values of cumulative N-deposition ranged from  $130$  to  $1296 \text{ kg ha}^{-1}$  (Supplementary Table [2](#) and Supplementary Fig. [7b](#)).

#### *Site productivity*

To control for the potentially confounding influence of productivity on vegetation responses to herbivory<sup>85,86</sup>, we obtained local environmental data from the EuMedClim database<sup>87</sup> on both the potential evapotranspiration and annual precipitation for each site averaged across the baseline and resurvey years. We then calculated the annual precipitation to potential evapotranspiration ratio (AP:PET) as a productivity proxy metric<sup>88</sup>. The EuMedClim database ranges from 1901 to 2014, so any sites that had been resurveyed since 2014 were given the 2014 value as their resurvey value. We calculated the average of the two time points. The AP:PET values ranged from  $0.58$  to  $2.1$  across sites.

#### *Forest management*

Changes in forest management during the inter-survey period can lead to changes in light regimes and confound the role of herbivory<sup>38,56,64,65</sup>.

Therefore, we compiled data on recent changes (baseline to resurvey) in the management intensity of our forest sites (Supplementary Table 2). Management intensity has not changed at 79% of the sites and decreased at 21% of the sites between surveys. In addition, as past management practices can lead to legacy effects<sup>56</sup>, we also compiled information on historical management practices in the 1800s and categorized management as either high forest (HF) or coppice with standards (CWS), the two predominant silvicultural systems at the time (following the approach of refs. <sup>56, 89</sup>). Fifty-two percent of sites were managed with HF, 27% with CWS, and 21% with a mixture of both in the 1800s. Management was described using expert testimony and historical site records<sup>56</sup>.

## Response variables

### *Herb, shrub, and tree (canopy) cover*

We classified vegetation layers as follows: herb (all vascular plant species <1 m), shrub (1–7 m) and tree/canopy (>7 m). For each time period and layer, we quantified the total cover value at the site level. To do so, we summed species cover values in each plot per site (where species plot cover was estimated visually as the percent cover within a given plot). Plot totals were summed across plots and then divided by the total number of plots at a site. We quantified temporal changes in layer cover by subtracting the baseline cover from the resurvey cover<sup>890</sup>. Two sites lacked shrub cover data, with one of these sites also lacking herb cover data, leaving 50 and 51 sites available for study for these respective variables. Changes in herb layer cover ranged from –94 to 67%, changes in shrub layer cover ranged from –24 to 22%, and changes in tree layer cover ranged from –50 to 29%.

### *Species richness change and exchange ratio*

Species richness change was calculated as the difference in the number of herb layer species at each site between the resurvey and baseline survey<sup>890</sup>. Herb layer species turnover was estimated using the richness-based species exchange ratio<sup>91</sup> calculated at the site level as  $E = (S_{imm} + S_{ext}) / S_{tot}$ , where  $S_{imm}$  is the number of species gained at resurvey,  $S_{ext}$  is the number of species lost at resurvey and  $S_{tot}$  is the total number of unique species at baseline and resurvey. The range of change values for species richness and exchange ratios were –98 to 90 and 0.24 to 0.65, respectively.

### *Species of conservation concern*

We identified species of conservation concern using two criteria: (1) Species listed as threatened in national Red Lists based on a recent database synthesizing national Red Lists across Europe<sup>92</sup>. That is, we determined the threat status of each species at a given site based on the respective national Red List of the country in which that site was located (based on IUCN threat classifications, see ref. <sup>93</sup>). We then calculated the percentage of threatened species per site per survey period (baseline site mean = 2.2%, resurvey site mean = 1.9%). (2) Species that have small geographic range sizes. Our range size estimates are based on areas of occupancy (AOO, in km<sup>2</sup>) derived from point occurrence records in GBIF by ref. <sup>93</sup>. We determined the lowest quintile of range size, which we classified as small-range. We then calculated the percentage of small-ranged species at each site and survey period and used differences between baseline and resurvey to quantify the temporal change (baseline site mean = 4.1%, resurvey site mean = 3.8%).

### *Non-native and nutrient-demanding species*

We identified the non-native species present at each site using the Global Register of Introduced and Invasive Species (GRIIS; <http://www.griis.org>) and its designations of which species are non-native in each country. We then calculated the percentage of non-native species per site per survey period and the difference over time (baseline site mean = 3.0%, resurvey site mean = 4.8%). We estimated shifts in species' N-demands using ecological indicator values (EIVs) compiled from ref. <sup>94</sup> ([sci.muni.cz/botany/juice/ELLENB.TXT](http://sci.muni.cz/botany/juice/ELLENB.TXT)), filling data gaps with values from ref. <sup>95</sup>. Coverage of N-numbers was 92% of species (1156 out of 1257 species). For each study site and survey period, we quantified the community-weighted mean N-number (CWM-N), weighted by baseline and resurvey occupancy per species per study site (i.e., the number of plots a species occupied during a given time period divided by the total number of plots at that site), and calculated the difference in CWM-N over time. Temporal changes in CWM-N ranged from -0.57 to 1.23 across sites.

### *Data analysis*

We fitted Bayesian linear models using the “brms” package in R for all statistical analyses<sup>96</sup>. Data to reproduce the results of our study are available in the Supplementary Information and Source Data files. For all analyses, we ran four Markov chains. We set the default, weakly regularizing priors for all parameters. Convergence was assessed using the Gelman–Rubin

statistics for each parameter (with values  $<1.01$  taken to indicate adequate convergence) and visually inspecting trace plots<sup>97</sup>. The adequacy with which the models fit the data was examined using graphical posterior predictive checks. For all analyses, we used the 95% credible interval to determine statistical clarity<sup>98</sup>.

Response variables were changes in the shrub, herb, and tree layer cover, changes in species richness, species exchange ratio, and changes in threatened, small-ranged, non-native, and nitrophilous species. Our focal explanatory variable was the change in herbivore pressure over time. We controlled for baseline herbivory, as vegetation change is likely to unfold differently (for the same temporal change in herbivory) when starting herbivory was low vs. high<sup>99-100-101</sup>. We also accounted for total site area and inter-census time span in all models, as time and area affect the magnitude of vegetation change. Moreover, the inter-census time span mildly covaried with herbivory change (Pearson's  $\rho = 0.25$ ), and thus needed to be taken into account. Changes in herbivory, baseline herbivory, inter-census time span, and site area form the main variables for the models in our base results predicting vegetation change from herbivory change alone. We included additional covariates in supplemental models to test whether associations between the response variables and herbivory change held when accounting for forest management, tree cover change or site productivity. All main models held upon inclusion of site productivity (e.g., Supplementary Tables [40–43](#)) and tree cover change (e.g., Supplementary Tables [44–47](#)). Most models held upon inclusion of forest management and the three instances where this differed are reported in the main results. We also tested and confirmed that the effect of herbivory change was robust when baseline herbivory was excluded from the models (e.g., Supplementary Tables [48–51](#)). Consequently, for the models testing the interaction effects between herbivory change and N-deposition on community composition, we only included site area and inter-census time span to reduce the risk of model overfitting (given that we only have 52 data points). We validated that the conditional association between cumulative N-deposition and changes in herbivory was statistically non-discernable from zero (Pearson's  $\rho = 0.08$ ; Supplementary Fig. [8](#)), and hence these predictors did not covary in the model. Model syntaxes for the main models can be found on figshare at <https://doi.org/10.6084/m9.figshare.21596844>.

Reporting summary

Further information on research design is available in the [Nature Portfolio Reporting Summary](#) linked to this article.

## Data availability

The data generated in this study have been made available in the Supplementary Information. Source data for figures are provided with this paper. The underlying species composition data were available from forestplot.ugent.be, but restrictions apply to the availability of these data, which were used under license for the current study and so are not publicly available. These data were, however, available from the authors upon request and with the permission of the forestREplot consortium. [Source data](#) are provided with this paper.

## Code availability

The R code for all analyses is available on figshare at <https://doi.org/10.6084/m9.figshare.21596844>.

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## Contributions

J.S. and I.R.S. conceived the study, with input from H.M.P. J.S. performed the analyses. J.S. and I.R.S. made figures. J.S. wrote the manuscript, with significant input from I.R.S., contributions from M.B.-R., N.F., F.S.G., J.L., A.O.-A., K.V., and D.W. and input at an advanced stage from H.M.P., L.B., P.D.F., I.B., J.B., M.C., G.D., T.D., R.H., T.H., B.J., M.K., M.M., F.M., T.N., A.O, K.R., W.S., J.S., A.S.-S., T.S., K.S., B.T., O.V., M.W. The authorship order was determined as follows: (1) core authors, (2) core contributors (alphabetical), and (3) authors contributing community composition data to an advanced version of the manuscript (alphabetical).

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## Ethics declarations

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The authors declare no competing interests.

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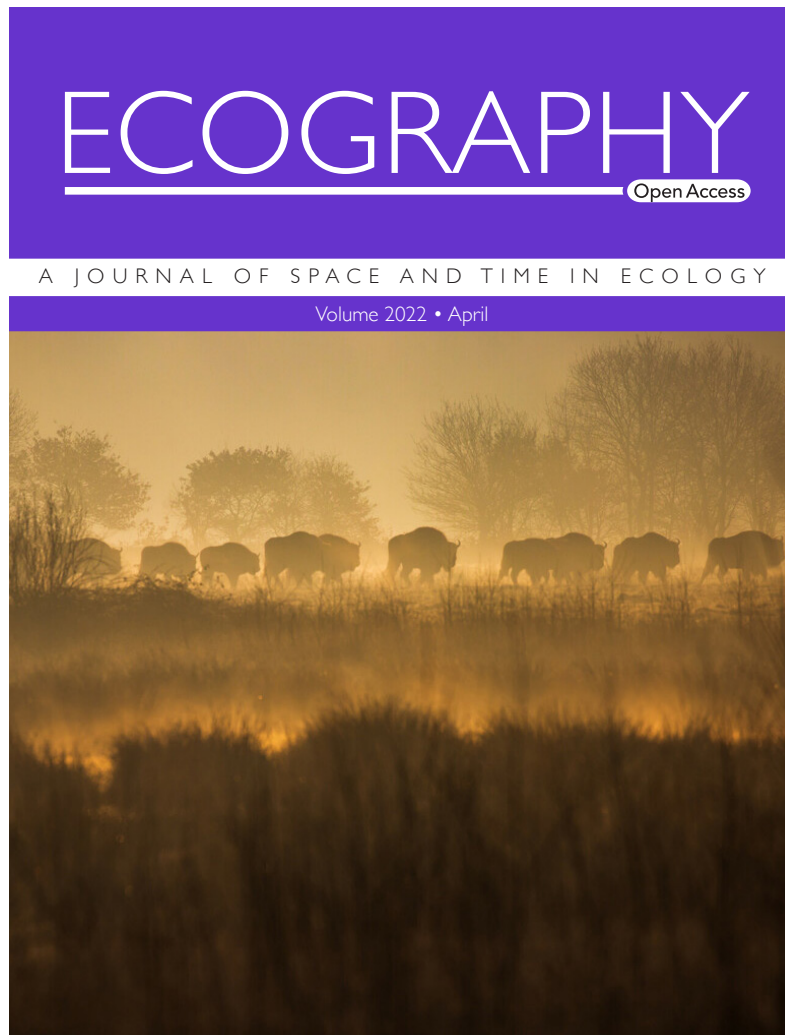
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## Chapter 3

# Expert-based assessment of rewilding indicates progress at site-level, yet challenges for upscaling



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## Abstract

Rewilding is gaining importance across Europe, as agricultural abandonment trajectories provide opportunities for large-scale ecosystem restoration. However, its effective implementation is hitherto limited, in part due to a lack of monitoring of rewilding interventions and their interactions. Here, we provide a first assessment of rewilding progress across seven European sites. Using an iterative and participatory Delphi technique to standardize and analyze expert-based knowledge of these sites, we 1) map rewilding interventions onto the three central components of the rewilding framework (i.e. stochastic disturbances, trophic complexity and dispersal), 2) assess rewilding progress by quantifying 19 indicators spanning human forcing and ecological integrity and 3) compile key success and threat factors for rewilding progress. We find that the most common interventions were keystone species reintroductions, whereas the least common targeted stochastic disturbances. We find that rewilding scores have improved in five sites, but declined in two, partly due to competing socio-economic trends. Major threats for rewilding progress are related to land-use intensification policies and persecution of keystone species. Major determinants of rewilding success are its societal appeal and socio-economic benefits to local people. We provide an assessment of rewilding that is crucial in improving its restoration outcomes and informed implementation at scale across Europe in this decade of ecosystem restoration.

## Introduction

The large-scale restoration of functioning ecosystems is essential in halting two of the most pressing issues of this century; species extinctions and climate change (IPBES [2019](#), IPCC [2019](#)). Rewilding has emerged as an important tool to restore natural, dynamic processes in a self-sustaining way across large areas of degraded or abandoned land, as well as promoting the comeback of threatened keystone species (Svenning et al. [2016](#), Fernández [2017](#), Perino et al. [2019](#)). Widespread land abandonment and recoveries in populations of many megafauna species across Europe are leading to passive rewilding, as well as increasing the potential for active rewilding (Navarro and Pereira [2015](#), Linnell et al. [2020](#)). Consequently, the concept of rewilding is gaining interest among conservation practitioners and the public as a tool to restore nature at scale (Jepson [2019](#)). However, both the application and upscaling of rewilding beyond pilot sites remains limited, in part, due to a lack of monitoring, with the long-term



consequences of rewilding interactions still poorly understood (Torres et al. [2018](#)).

To date, our understanding of rewilding progress has often been limited to studying non-intentional rewilding events, or the consequences of one dimension of rewilding in isolation, e.g. the impact of one species reintroduction (Bakker and Svenning [2018](#)). Furthermore, there is little understanding of what interventions are being used by rewilding practitioners and how these impact the ecological integrity of a site. With limited empirical evidence underlying the conceptual framework of rewilding, there is, in turn, limited capacity either to persuade policy-makers and funders to support the implementation of rewilding at scale or to inform more targeted interventions in the future (Pettorelli et al. [2018](#)). Therefore, there remains the urgent need to support comprehensive assessments of rewilding sites over time and to understand how interventions have translated into ecological and socio-economic changes.

A key challenge of quantifying rewilding progress lies in the ability to capture its multiple dimensions, spanning socio-economic and ecological responses. In response to data paucity, expert elicitation is an increasingly common tool to assess dynamic and complex systems (Martin et al. [2012](#)). Environmental and conservation organizations often use expert-based assessments to make informed and quick decisions for policy-relevant questions, such as for the red-listing of ecosystems or evaluating the effectiveness of conservation interventions (IUCN [2015](#), Bolam et al. [2020](#)). However, just as with empirical data, expert assessments must be scrutinized to minimize biases. Substantial effort has been placed on developing techniques to deal with these issues (Kynn et al. [2008](#)).

One increasingly popular method for minimizing biases and standardizing expert assessments is the Delphi technique. This is an iterative, participatory method used for collecting and formalizing expert-based knowledge (Hemming et al. [2018](#)). The technique provides the possibility for reconsideration of initial responses in the light of the comments of others in the panel (Sutherland et al. [2011](#)), and has been shown to generate more accurate and transparent assessments in conservation ecology (Burgman et al. [2011](#)). It fills in data gaps through the lived experience of the participants (O'Neill et al. [2008](#), Ochoa-Gaona et al. [2010](#)) and aims to integrate different disciplines and/or geographic locations (Bolam et al. [2020](#)). This is particularly relevant in assessments where the outcome is dependent on different perspectives and expertise of respondents. Applying the Delphi

technique can thus provide an inclusive expert judgment of complex and participatory restoration interventions.

Here, we apply the Delphi technique to a multidimensional monitoring framework to a) improve a reproducible process for cost-effective periodic assessment of rewilding and b) produce the first comprehensive assessment of rewilding progress across seven sites in Europe. More specifically, we assess whether the Delphi technique can help generate standardized, calibrated applications of the monitoring framework across sites. We identify what interventions are being applied to rewilding sites and at what scale. Further, we measure the progress made across sites and identify the challenges for upscaling rewilding in these sites. Finally, we assess the major factors benefitting or threatening rewilding progress as identified by rewilding practitioners. The process and assessment presented here are a critical step towards understanding and predicting the factors that are important for rewilding success and scaling up its implementation in this decade of ecosystem restoration.

## Methods

### Quantifying rewilding progress

We quantified rewilding progress in seven sites across Europe: Central Apennines, Greater Côa Valley, Oder Delta, southern Carpathians, Rhodope Mountains and Danube Delta (Fig. 3, Table 1). These sites form part of a coordinated rewilding network (<<https://rewildingeurope.com/>>) which aim to trial the implementation of rewilding on pilot sites. The sites were established in areas of ongoing land abandonment and span different ecological and geographical regions across Europe. We quantified changes over time across the three central components of rewilding identified in a recently proposed rewilding framework: stochastic disturbance, trophic complexity and dispersal (Perino et al. 2019). These components aim to encompass key ecological processes that are essential for self-organizing and complex systems. In order to do so, we expanded these three components into a total of 19 indicators that quantify the amount of human forcing and the state of ecological integrity over time (Torres et al. 2018). These indicators were specifically designed to be scale-independent and to account for a wide range of ecological and societal contexts, as well as active and passive rewilding processes. For each of the indicators, the baseline (i.e. starting year of intervention, Table 1) and the current (November 2020) state of the site were assessed by the local experts. We calculated the rewilding score as the geometric mean across the 19 indicator scores in accordance with Torres et

al. (2018). Score changes over time were calculated as the relative percentage difference between baseline and current scores.

Site (yr)	Size (km <sup>2</sup> )	Interventions			
		Connectivity and Trophic complexity composition	Trophic complexity	Stochastic disturbances	Socio-economic
Central Apennines (2012)	75.5	- Wildlife corridors created between protected areas- Infrastructure permeability measures (e.g. wildlife passages)- Removal of linear infrastructure	- Reintroduction of herbivore and threatened species	NA	- Outreach and education- Human-wildlife coexistence measures (e.g. compensation programs)- Ecotourism established
Greater C�a Valley (2012)	44.7	- Wildlife corridors created- Native seed planting	- Herbivore reintroductions (semi-wild horses, wild cattle, roe deer)- No-take hunting zones created- Vulture feeding stations established	- Removal of sheep grazing- Grazing for fire regime regulation	- Ecotourism established
Danube Delta (2011)	63.9	- Dam removals- Restoration of water channels- Lateral river connectivity improved- Protected area establishment- Halt of invasive species stocking in water bodies	- Reintroduction of herbivore and threatened species (water buffalo, semi-wild horses, red and fallow deer, eagle owl, steppe marmot, kulan)- Supplementary feeding of recently reintroduced, threatened populations	- Rewetting and flooding of lakes and polders	- Ecotourism established
Velebit Mountains (2012)	95.5	- Water body restoration	- No-take hunting zones established- Reintroduction of herbivore species (semi-wild horses, wild cattle, red deer)	NA	- Stakeholder engagement- Ecotourism established
Oder Delta (2014)	78.3	- Lateral river connectivity improved- Halt of invasive species stocking in water bodies	- No-take fishing zones established- Spawning sites restored	- Rewetting of polder and grassland areas- Ecological alluvial forest management introduced	- Land purchases- Ecotourism established

Site (yr)	Size (km <sup>2</sup> )	Interventions			
		Connectivity and composition	Trophic complexity	Stochastic disturbances	Socio-economic
Rhodope Mountains (2011)	13.5	NA	- Herbivore species reintroductions (red and fallow deer, bison, semi-wild horses)	NA	- Ecotourism established
Southern Carpathians (2012)	13.8	- Hunting pressures reduced	- Herbivore species reintroductions (bison)	NA	- Ecotourism established- Education and outreach- Wildlife-human coexistence measures

**Table 1. Inventory of the main rewilding interventions applied per site, characterized by the three ecological rewilding components and socio-economic measures.**

### Applying the Delphi technique

We ran a six-step Delphi expert elicitation technique following the IDEA protocol (Investigate, Discuss, Estimate, Aggregate; Hemming et al. [2018](#)) as outlined by Mukherjee et al. ([2015](#)) for ecological and biological conservation (Fig. [1](#)). We applied this process to account for subjective and biased reporting on the indicator scores, as well as a lack of original consensus over the indicators' meaning and the data that should be used for scoring. As part of the process, we also compiled an inventory of the main rewilding interventions categorized by the three central components of the rewilding framework, and one additional socio-economic dimension to incorporate measures that were societally, and not ecologically, focused. Within the process, we further elicited a list of key success and threat factors as identified by the practitioners for their sites.



**Figure 1. Steps taken for the iterative monitoring process.** Graphic representation of the steps taken for applying the Delphi technique to score rewilding progress across sites at different scales and across varying landscapes.

We adapted the original indicators into an accessible questionnaire for a non-scientific audience (Supporting information). Then, we selected and invited experts for each site to participate (n = 18). These included local practitioners, technicians, scientists and regional managers who work with and understand the sites. This approach ensures a wide range of perspectives and can improve on information biases (Hemming et al. [2018](#)). The process for choosing the participants was purposive, with experts selected conditional on whether they fit into at least one of the following criteria:

1. local practitioners/experts who have a long-term overview of the site and are able to provide detailed information about how the site has changed over time ( $\geq$  one per site) and/or,
2. regional managers who have worked across several sites and are able to provide comparative information to 'control' for scoring the

indicators and complement the local practitioners' knowledge of their site and/or,

3. technicians and GIS experts who work across all or at least one site and who helped collect and analyze the data used to score the indicators wherever available and/or,
4. scientists who are considered experts in rewilding and are familiar with the monitoring methodology (published at least one peer-reviewed paper on the topic).

We had at least one participant from each criterion that was an expert for one or multiple sites to ensure that the range of different perspectives was kept constant across the sites.

We started by providing individual clarification sessions informing on the objective of this analysis. Participants were then asked to complete the questionnaire individually per team and were given time to collect relevant data. We analyzed responses and compiled them into a report, which was used in the next scoring iteration. For each indicator, we prepared results with the summary of scores across sites at baseline, and score changes over time (Supporting information). This stage was essential for participants to be able to evaluate the results in comparison to other sites, as well as be able to explain and reconsider their assessment in the next iteration. Subsequently, we conducted a workshop with all participants together. Per indicator, two sites were chosen randomly to report the methodology for scoring and the context of their site for that score. We then specifically asked:

1. Given the scorings and explanations provided for other sites, did you score similarly or differently?
2. Did you apply the indicator in the same way as the other sites, and if not, why not?

This stimulated discussion on the context of the sites, their reasons for scoring, as well as the indicators themselves. The discussions elicited a consensus agreement on the interpretation of the indicator and what should be taken into account for scoring. Each participant was then given time to evaluate, and if necessary, rescore their sites in light of the group responses.

## Results

### Rewilding interventions

The active rewilding interventions that most often occurred across the sites in various landscapes were predominately focused on species reintroductions or population reinforcements. These measures focused on keystone and large herbivore species and in some cases, threatened, culturally important species. Cattle and horses are fenced, except in Danube Delta, and all other species are free roaming. In three areas, no-take zones were established to increase the viability of hunted and reintroduced species. Additionally, work was conducted across five sites to improve the connectivity of sites and establish wildlife corridors, either by removing infrastructure such as dams and fences, or through land purchases and protected area designations. However, the major ecological components of rewilding (i.e. connectivity and composition, trophic complexity, stochastic disturbances) were dissimilarly addressed across sites, with only three sites including interventions for all components and only three sites addressing the restoration of stochastic disturbances (Table 1). In addition to the ecological components outlined by the original framework, socio-economic measures were also widespread across all the sites aiming at improving human-wildlife coexistence and introducing alternative nature-based economic opportunities. The most common intervention was the establishment of ecotourism through wildlife safaris, bird watching hides and guided tours. Another important socio-economic intervention was human-wildlife coexistence measures, e.g. through compensation programs for wildlife damage.

### Changes in rewilding score

We recorded increases in rewilding score over time in five of the seven sites, whilst two sites reported decreases (Fig. 2). The five sites with overall increases in rewilding scores reported decreases in human forcing, and four of the sites reported increases in ecological integrity (Supporting information for all indicator scores per site). The biggest improvement over time was reported in the Central Apennines, with a relative increase of 47.1% from 2012 to 2020, and improvements in 14 of the 19 indicators. Rhodope Mountains reported the largest decrease in rewilding score over time, with a change of -13% from 2011 to 2020. Both, the Rhodope Mountains and Velebit Mountains decrease are attributable to an increase in the amount of human forcing on the site over time (43.4% and 9.8% respectively), despite a minor improvement in ecological integrity for the Rhodope Mountains (1.1%). The increases in human forcing were attributable to a) population reinforcements and artificial feeding of wildlife, either due to hunting or

temporary rewilding interventions and b) increases in land-use intensity such as agricultural expansion.

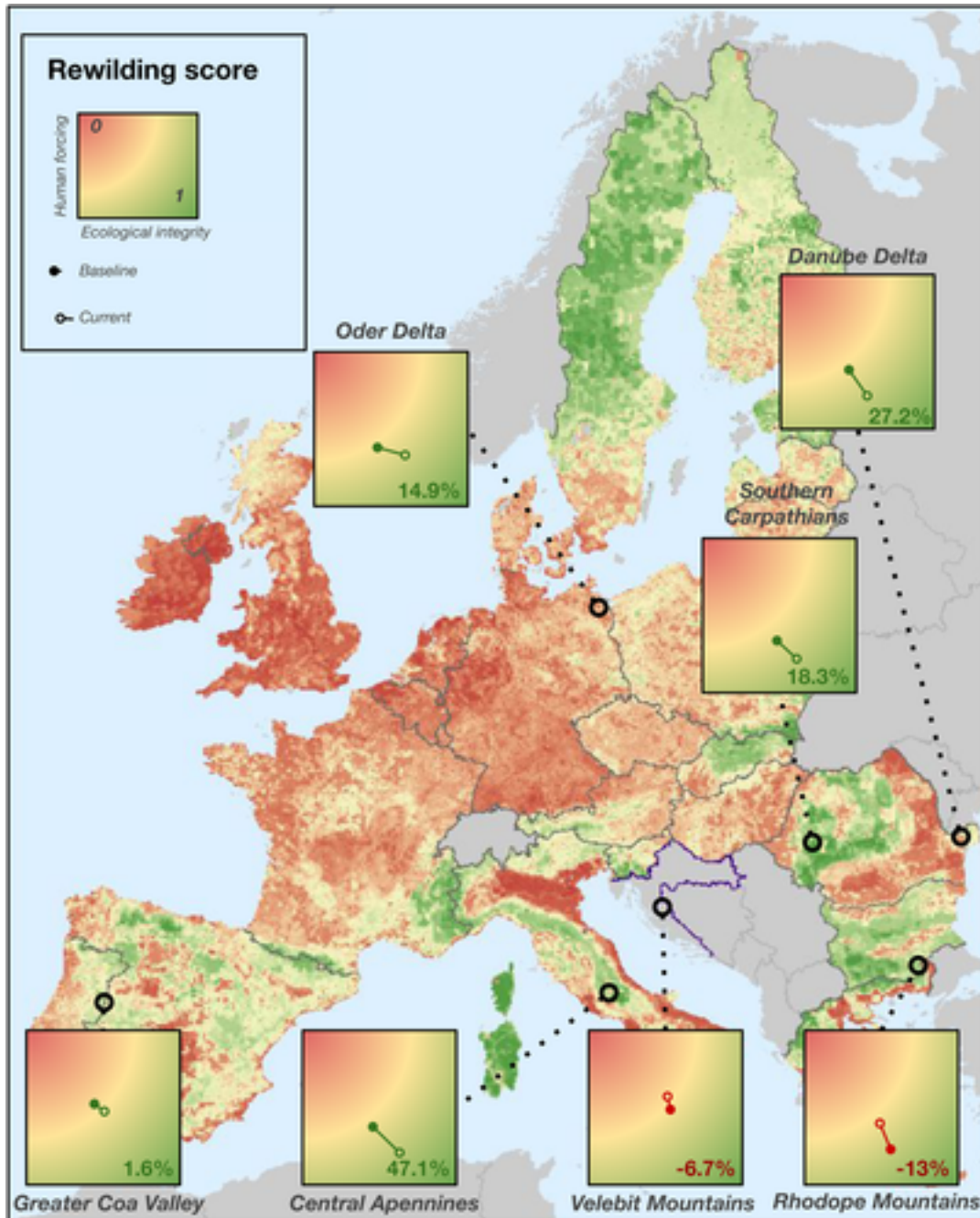


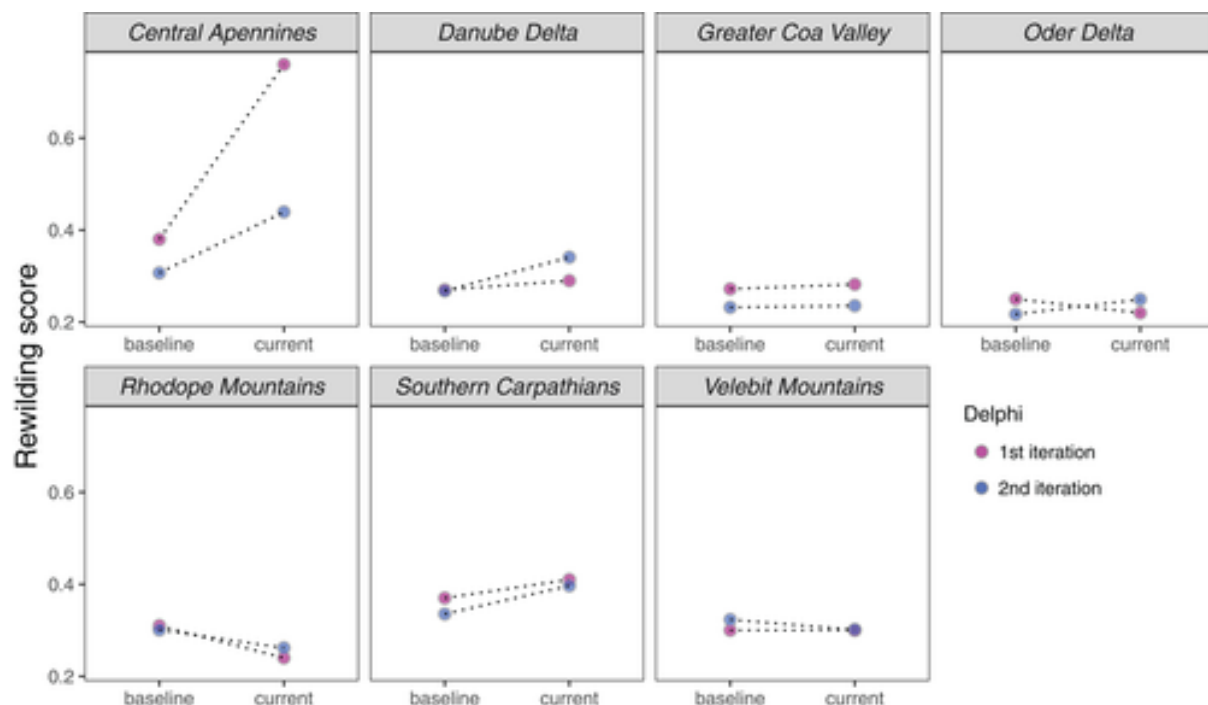
Figure 2. Map of the seven study sites across Europe and their corresponding changes in rewilding score over time. The underlying base map represents the ecological integrity measured at the European scale for the year 2012 (the average baseline year for the sites), and assessed using the same underlying rewilding framework from Torres et al. (2018) (base map credit: Fernández et al. 2020). The study sites are measured using the rewilding score which integrates ecological integrity (x-axis) and human forcing (y-axis), whereas the base map comprises just ecological integrity.



For each site, the baseline rewilding score is depicted by the filled circle and the current rewilding score is depicted by the empty circle.

### *Effects of the Delphi technique*

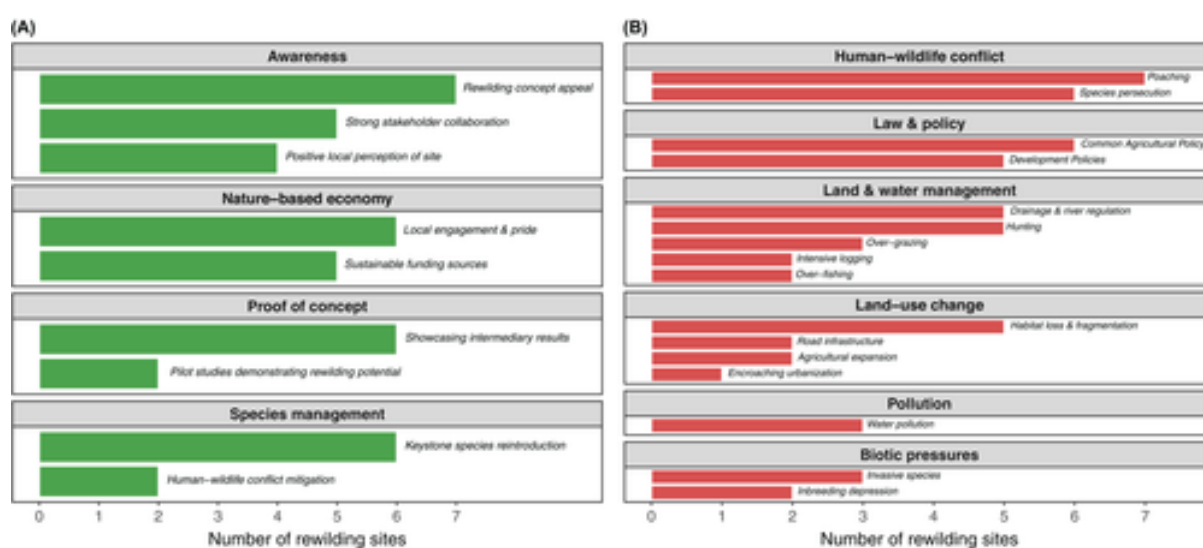
The Delphi technique allowed participants to reevaluate their scores in light of standardized information and consensus understanding of the indicators (Fig. 3, Supporting information for all indicator changes per site). Absolute changes in rewilding score as a result of the Delphi exercise ranged from 2.1 to 56.8% across sites. Furthermore, the results became more similar as a result of the process with reduced extreme values. The range of % change across sites decreased from  $-22.6$  to  $100\%$  (SD = 40.3) pre-Delphi to  $-13.0$  to  $43.2\%$  (SD = 19.7) post-Delphi. Overall, four sites reported increased scores and three sites reported decreased scores after the Delphi process. The main drivers of score change were misunderstandings about the meaning of each indicator, what data should be used to evaluate the indicators and what components should be taken into consideration for scoring, e.g. illegal activity for management indicators. Furthermore, a revised set of indicator descriptions and reference scores was then produced from the consensus agreement about what should be measured (see the Supporting information for the updated list).



**Figure 3. The change in rewilding score over time as a result of the Delphi exercise per study site.** The first iteration scores were those conducted per team and the second iteration scores were those elicited collaboratively from the workshop with all experts across sites together.

## Rewilding progress and threat factors

The most important progress factors were predominately focused around the appeal of rewilding as a concept and effective communication about the sites' results (Fig. 4a). Socio-economic factors were also commonly highlighted, such as bringing economic opportunities to the area and having good working relationships with stakeholders. Alongside the socio-economic factors, effective species management was also considered to play an important role in driving rewilding progress. The threat factor which affected all sites was poaching. These were attributed by the experts to lead to declines in species' populations that cannot be officially monitored or regulated. Additionally, policies, specifically subsidies from the Common Agricultural Policy were also considered a major threat to many sites due to economic incentives for increasing intensive land use through agricultural expansion. Other important factors which were perceived as threatening rewilding progress were land/water use change and management factors which referred to actions that could increase the amount of human forcing on the site.



**Figure 4. The (A) progress and (B) threat factors considered most important for the study sites by the practitioners.** The length of each bar indicates the number of sites that each factor applies to. The factors were identified by the experts themselves during the workshop without previous input or classification.

## Discussion

In the UN decade of restoration, it is increasingly vital that we understand how restoration has progressed, in order to use resources more effectively

and scale up efforts accordingly. In spite of substantial efforts to improve monitoring, there remains a paucity of long-term, comprehensive assessments in restoration and in particular, rewilding sites (Wortley et al. [2013](#), Rubenstein and Rubenstein [2016](#)). Using a participatory, iterative technique for eliciting expert-based knowledge, we calibrated and standardized 19 indicators in order to undertake the first comprehensive assessment of rewilding progress across seven sites in Europe. By quantifying changes in human forcing and ecological integrity, we found that sites are improving in several ecological parameters, with five of the seven sites seeing overall progress along the rewilding scale. However, several indicators consistently failed to change or indicated degradation. Score changes were both the result of directed rewilding interventions and broader, socio-economic trends or competing land uses. Overall, our results suggest that whilst there have been improvements across several dimensions of rewilding, current efforts cannot always revert broader land use and policy pressures.

We employed the Delphi technique in order to improve on the main challenges that we identified in the first scoring iteration, such as differences in understanding and quantifying the indicators among experts. Through consensus decision, we co-produced revised indicator definitions that more fully captured which components should be measured and how these indicators can be quantified (Supporting information). Furthermore, we came to a consensus as to how the reference scoring for each indicator should be standardized, and what state or process constitutes a low, mid or high score. This was important in order to calibrate measurements across sites and spatiotemporal scales, which has often been a limitation of expert-based monitoring schemes (Kapos et al. [2008](#), Eycott et al. [2011](#)). The technique also allowed participants to discuss and formalize what data should be used to score the indicators and what components should be taken into consideration for scoring, as well as clarify misunderstandings about the meaning of each indicator. This led to considerable score changes for some of the sites, most noticeably, Central Apennines and Oder Delta. Through fostering these group discussions and an improved understanding of the indicators, scores changed considerably across indicators and became more similar to each other across sites (Fig. [3](#), Supporting information).

Whilst the consensus indicator list is a further step towards facilitating and standardizing monitoring of rewilding progress across sites in Europe, there remain several challenges that should be addressed through future research. The process of scoring indicators currently remains limited in terms of

attribution of rewilding interventions, with the scoring reflecting both directed and non-targeted actions in the landscape, potentially confounding the analysis. Future assessments may consider the potential for quasi-experimental methods such as synthetic controls for comparison studies to improve on this issue (Baylis et al. [2016](#)). Furthermore, there is the need to combine expert judgement with analytical, data-driven approaches in order to empirically assess changes and determine whether the iterative scoring process brings the expert-based assessments closer to 'accurate' measurements. Where the monitoring of large-scale projects using ground-based measurements remains unfeasible due to resource restrictions, complementary data-driven approaches could harness remote sensing techniques and other cost-effective, repeatable methods for capturing the multi-dimensional components of landscape change (Andersen et al. [2017](#), Pettorelli et al. [2018](#)).

The results of the iterative monitoring process revealed that while some indicators improved across sites, others remained consistently unchanged or deteriorated. Consistent improvements in trophic complexity across sites likely resulted from actions such as implementing no-take zones, mitigating human-wildlife conflicts and reintroducing or reinforcing keystone species populations, as well as European-wide natural recoveries in species populations (Navarro and Pereira [2015](#)). In contrast, indicators related to stochastic disturbance regimes or land-use intensity consistently remained unchanged. This may be, in part, due to spatiotemporal constraints. Given that we report on intermediary progress (< 10 years), this time span may not have been long enough to capture shifts in natural disturbance regimes. Additionally, the spatial scale of the rewilding interventions is still limited and often restricted to small pilot sites, whilst broad-scale interventions are often required before regime shifts can be detected. For example, in the Greater Côa Valley, herbivore grazing was introduced to an area of ~ 9 km<sup>2</sup> within the site to regulate fire, however patterns of pyric herbivory establish at larger scales in a mosaic landscape (Falk et al. [2007](#), Fuhlendorf et al. [2009](#)). Among other factors, the sites are mostly operating outside of protected areas and within a diverse land ownership matrix where there are often competing desires for land use that may undermine the ability for rewilding action to be implemented at scale.

Our findings further suggest that rewilding progress is often limited by regulations and policies that dictate land management and enable competing land uses (Fig. [4](#)). For instance, regional regulations to support hunting practices, such as supplementary feeding and carrion removal can

undermine scavenger ecology (Cortes-Avizanda et al. [2016](#), Kuijper et al. [2016](#)), and regulations to reduce fire risk, such as deadwood removal, has been linked to reduced saproxylic biodiversity in forests (Seibold et al. [2015](#)). More broadly, key funding mechanisms within the EU, such as agricultural subsidies under the Common Agricultural Policy are also either preventing increases in the rewilding score or actively reversing progress. Although rewilding operates predominately in areas of land abandonment, land trajectories are not static and can revert to agriculture given appropriate incentives (Munroe et al. 2021). For example, in the Rhopode Mountains, the trajectory towards land abandonment that began in the 1990s has recently been reversing back towards agricultural intensification and encroachment as a result of Common Agricultural Policy subsidies (Dobrev et al. [2014](#)), with negative implications for rewilding progress in this area. In order to counterbalance this threat, rural policies may need to be better targeted to allow people to make better use of the socio-economic benefits that rewilding can provide.

Overall, our results highlight that the long-term ability for rewilding to progress and scale-up is often subject to external pressures dictated outside the sites themselves. Many important, desired changes rely on legal or policy mechanisms which can only be affected through policy change at the national and EU scale. Therefore, whilst rewilding measures are beginning to make positive changes at local scales, future intervention efforts should be better complemented by policy and advocacy if rewilding is to become scalable across entire landscapes. Moreover, this highlights the need for better land use planning at the national level to determine where there is potential for rewilding, in order for subsidies and conservation efforts to be more effective long term. The public enthusiasm that has been instrumental for rewilding success (Genes et al. [2019](#), Jepson [2019](#); Fig. [4](#)) thus far may be harnessed and channeled towards achieving these goals, allowing rewilding to scale up in this decade of ecosystem restoration.

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Data are available from the Dryad Digital Repository: <<http://dx.doi.org/10.5061/dryad.s7h44j174>> (Segar et al. 2021).

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## Chapter 4

### Urban conservation gardening in the decade of restoration



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## Abstract

Global commitments and policy interventions for conservation have failed to halt widespread declines in plant biodiversity, highlighting an urgent need to engage novel approaches and actors. Here we propose that urban conservation gardening, namely the cultivation of declining native plant species in public and private green spaces, can be one such approach. We identify policy and complementary social mechanisms to promote conservation gardening and reform the existing horticultural market into an innovative nature-protection instrument. Conservation gardening can be an economically viable and participatory measure that complements traditional approaches to plant conservation.

## Main

Declines in native floral richness can lead to cascading effects across trophic levels and impair the functioning of key ecosystem services upon which humanity relies<sup>1</sup>. Despite species conservation being high on the political agenda, with national and global targets to halt biodiversity loss, species populations have continued to decline<sup>2</sup>. Similarly, the key global commitment to halt biodiversity loss by the end of this decade, the Post-2020 Global Biodiversity Framework, is anticipated to miss its species conservation target, in part because the current draft fails to explicitly state that population declines of native species must be halted<sup>3</sup>. To maintain unique ecosystem functions and services and global biodiversity, it is critical that nations find and implement measures to conserve their declining native species.

Conservation measures of threatened plant species have a strong focus on preserving habitat in protected areas<sup>4</sup><sup>5</sup>. While these efforts are integral to successful species conservation, they also face several long-term challenges. Maintaining adequate conservation conditions is resource intensive, with an estimated financial cost of meeting global conservation goals of US\$76.1 billion annually<sup>6</sup>, requiring sustained policy support. Conservation often relies heavily on non-market, poorly scalable funding mechanisms, leaving it under-funded or forced to meet an overwhelming number of diverse socio-economic objectives<sup>5</sup>. Consequently, conservation often competes with other political targets, potentially compelling landowners who are currently implementing conservation measures to opt for more economically attractive land uses. A stark example of this is biodiversity funding competing with subsidies such as the Common Agriculture Policy,

representing 7.5% and 36% of the total European Union (EU) budget, respectively<sup>7</sup>. The cumulative pressures on traditional conservation approaches are exemplified in the continued declines of species, despite high-level efforts to increase the size and spread of protected areas<sup>5</sup>.

Continued species declines, even in protected areas, highlight the need for reconciliation ecology. This means redesigning anthropogenic areas such as cities, suburbs, towns and villages (hereafter referred to as urban areas<sup>8</sup>) to be compatible for a broad array of species<sup>9</sup>. Urban ecosystems represent a rapidly increasing land surface area (projected to be 1.9 million km<sup>2</sup> by 2030 and 3.6 million km<sup>2</sup> by 2050<sup>8</sup>), where conservation can and should be implemented<sup>8,10</sup>. Urban ecosystems can have higher biodiversity than surrounding natural areas<sup>11</sup>. Although often dominated by human-tolerant, widespread species, urban areas also have the potential to harbour many threatened species<sup>12,13</sup>. Furthermore, conserving and restoring biodiversity in urban area can provide multiple co-benefits, such as unique socio-cultural services and health benefits to a substantial proportion of people<sup>14,15</sup>. Today, 55% of people live in urban areas, a value projected to rise to 92% by 2100<sup>16</sup>. This means that urban areas are and will be where most people experience nature regularly, making them key places to expand people's understanding of biodiversity, foster nature stewardship and strengthen societal commitment to biodiversity conservation<sup>13,17</sup>. Novel mechanisms that encourage and integrate the conservation of biodiversity and promote nature stewardship in an increasingly urban world are urgently needed.

We propose that the widespread implementation of conservation gardening in both private and public urban green spaces can act as a form of community-based conservation for the protection of native species. While the idea of native plant gardening is not novel (otherwise known as, for example, wildlife-friendly, native/indigenous, wildscape and pollinator-friendly plant gardening<sup>18,19,20,21,22</sup>), the potential for urban green spaces to contribute actively to the conservation of declining and threatened native species is rarely reported in the scientific literature. Demonstrated justifications for native plant gardening include enhancing biodiversity, particularly insect and bird conservation, and associated social, cultural and psychological benefits<sup>14,21,23</sup>. We argue that native plant species can and should be protected in their own right through conservation gardening and that this may advance the science and practice of sustainable landscaping in multiple useful ways. Here we use Germany as a case study to illustrate this potential, where comprehensive long-term biodiversity data are available,

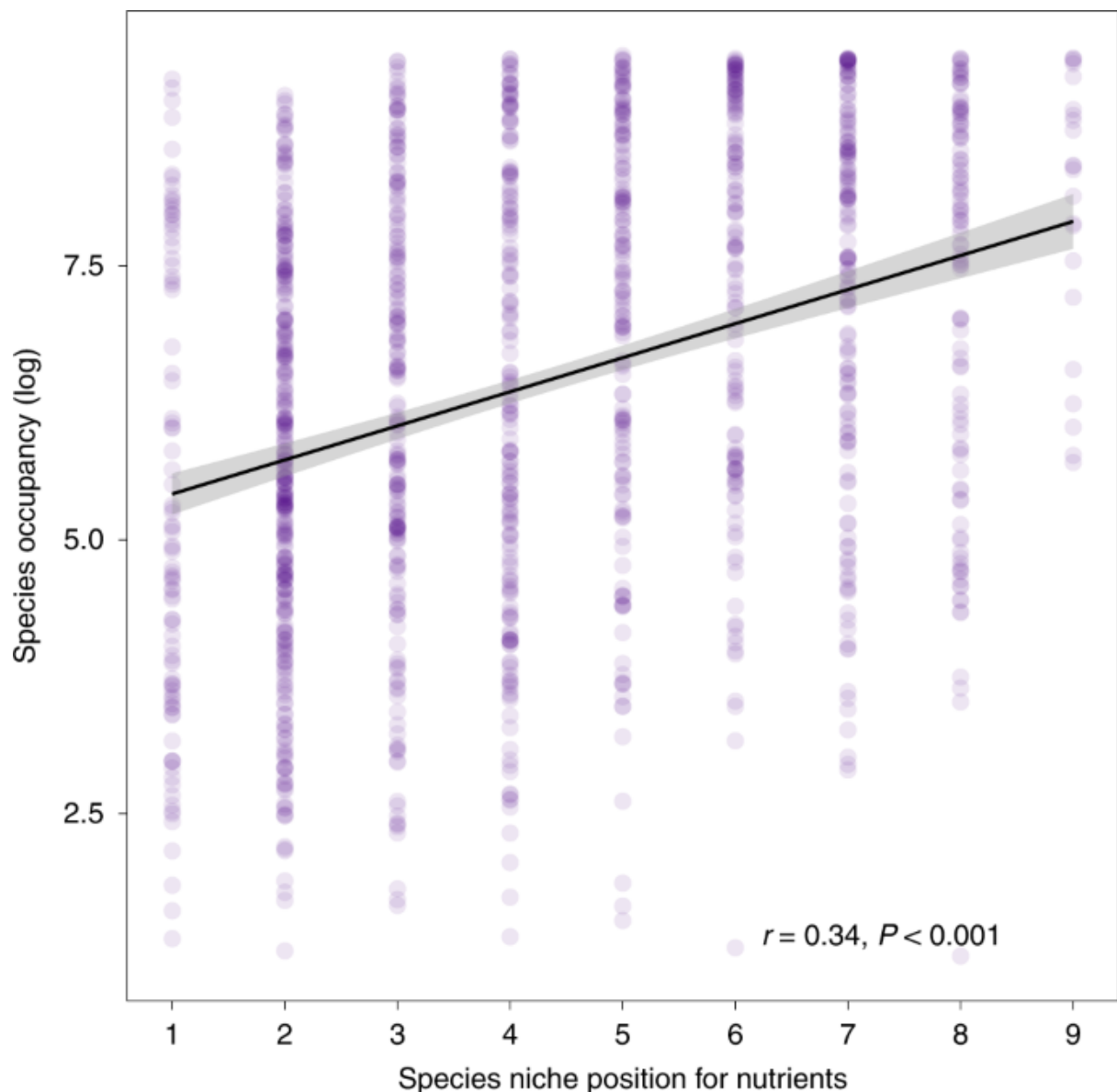
the political system is becoming more attuned to biodiversity concerns and the socio-economic dimensions are largely exemplary for higher-income countries<sup>24,25</sup>. We (1) provide ecological arguments for conservation gardening, (2) suggest economic and policy mechanisms for mainstreaming this approach via the horticultural market, (3) present a tiered system to select appropriate candidate species for planting and (4) propose community-led, participatory approaches to broadly implement conservation gardening. In addition to this initial Eurocentric focus, we suggest our proposals hold insights that can be useful in any region and include examples from outside Europe.

## Ecological arguments

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### Drivers of plant species declines and gains

Globally, two out of five plant species are estimated to be at risk of extinction<sup>26</sup>. This negative trend is also reflected in the German Red List, whereby 27.5% of vascular plant species are currently classified as threatened<sup>27</sup>. Moreover, it has recently been estimated that 70% of plant species are in decline across Germany, and species richness at the landscape scale has decreased by an average of 1.9% per decade over the past 60 years<sup>25</sup>. Drivers of species decline can be grouped by (1) abiotic pressures caused by more intensive land use, atmospheric nitrogen deposition and climate change, and (2) biotic pressures from the arrival of novel competitors, including invasive species<sup>2,27</sup>. In contrast, species associated with nutrient-rich, often anthropogenic habitats are increasing their populations across a wide range of habitats<sup>28,29</sup>. With the advent of the Green Revolution, anthropogenic habitats were made increasingly productive<sup>30</sup>. These conditions have probably benefited nutrient-demanding species, creating (1) a greater availability of suitable habitat and (2) pathways for their dispersal, allowing them to colonize new sites as indicated by the increase of nutrient-demanding species in semi-natural habitats<sup>29</sup>. The success of nutrient-demanding species may be partially reflected in their relatively larger area of occupancy, a pattern that we also found across Germany (Fig. 1). Conservation efforts therefore need to address biotic and abiotic drivers of species decline while harnessing mechanisms of species increases.



**Fig. 1. A species' niche position for nutrients is positively associated with its occupancy across Germany.** Positive association between a species' grid-cell ( $5 \times 5$  km) frequency during the years 1960–1987 (data taken from ref. [25](#)) and Ellenberg indicator values for nutrients (data taken from [sci.muni.cz/botany/juice/ELLENB.TXT](http://sci.muni.cz/botany/juice/ELLENB.TXT)). From ref. [25](#), 1,249 species also had  $N$  values. Larger  $N$  values indicate that a species is associated with more nutrient-rich habitats. The black line and grey ribbon indicate the fitted mean regression line and the  $\pm 95\%$  confidence interval, respectively. Points are coloured semi-transparently, darker shades represent overlaps and higher point density. [Source data](#)

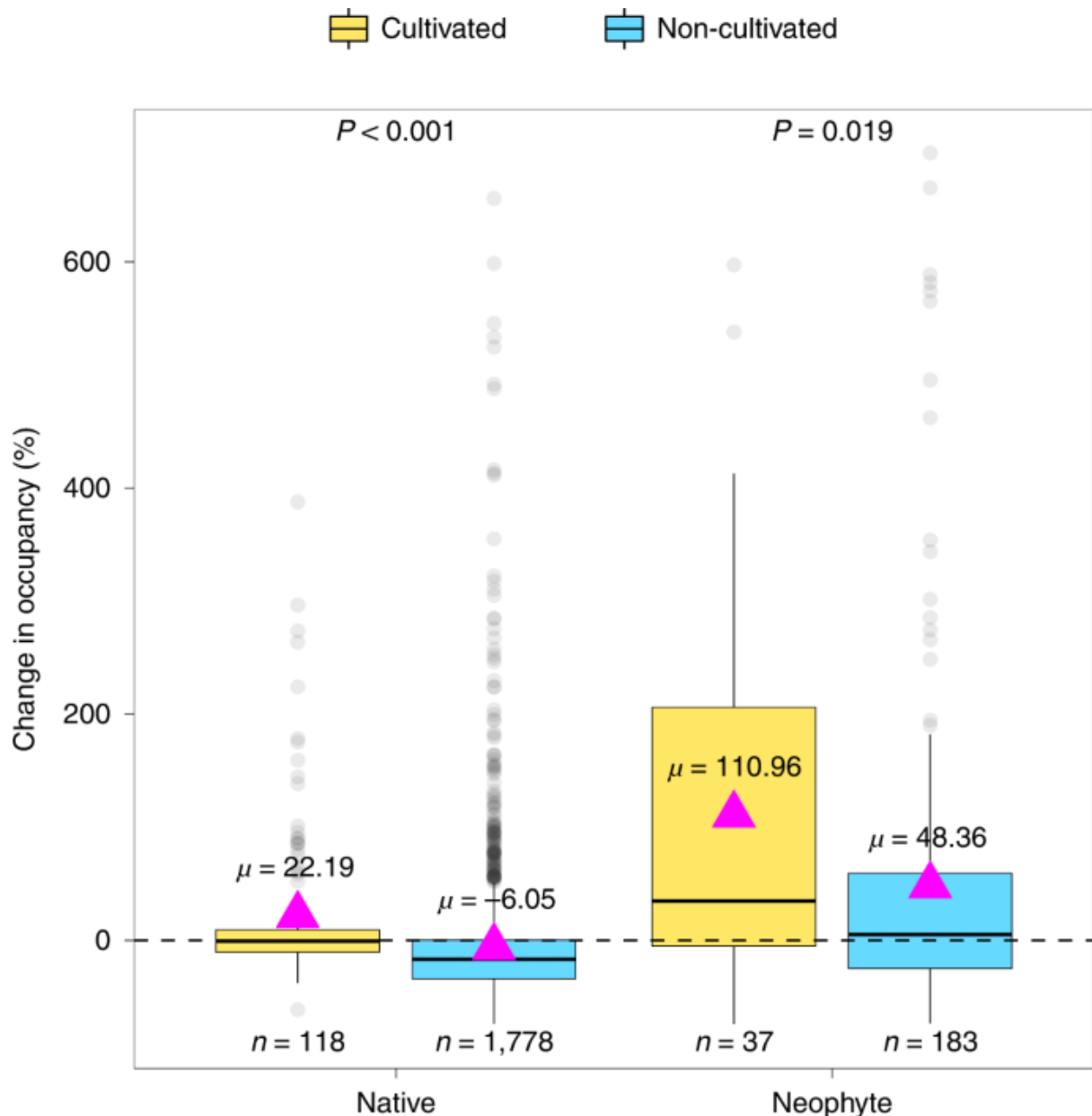
### Reversing population trends

Conservation gardening in urban green spaces may address the two main drivers of plant species decline. First, when building green infrastructure,

humans can, in many cases, actively create adequate abiotic conditions that correspond to the habitat of threatened species (for example, nutrient-poor soils, low soil pH, sandy soils)[31](#). Many threatened plant species have high light demands and occur on nutrient-poor soils[32](#). Certain soil characteristics could be created by incorporating soil amendments, removing topsoil, and selecting specific soil substrates, with novel approaches such as constructed technosols having a high potential to provide multiple soil functions[33](#). High light demands of threatened species could be met in open parks or on roof spaces, for example, with 80 million m<sup>2</sup> of rooftop area having been built in 2019 in Germany alone[34](#). Second, humans can support slower-growing, declining native species by creating competition-free spaces through the regulation of biotic pressure (for example, removing faster-growing, competitive plants), where in urban green spaces, management effort per unit area can be particularly high. Thus, intentional gardening of declining native plant species may address both abiotic and biotic drivers of species decline.

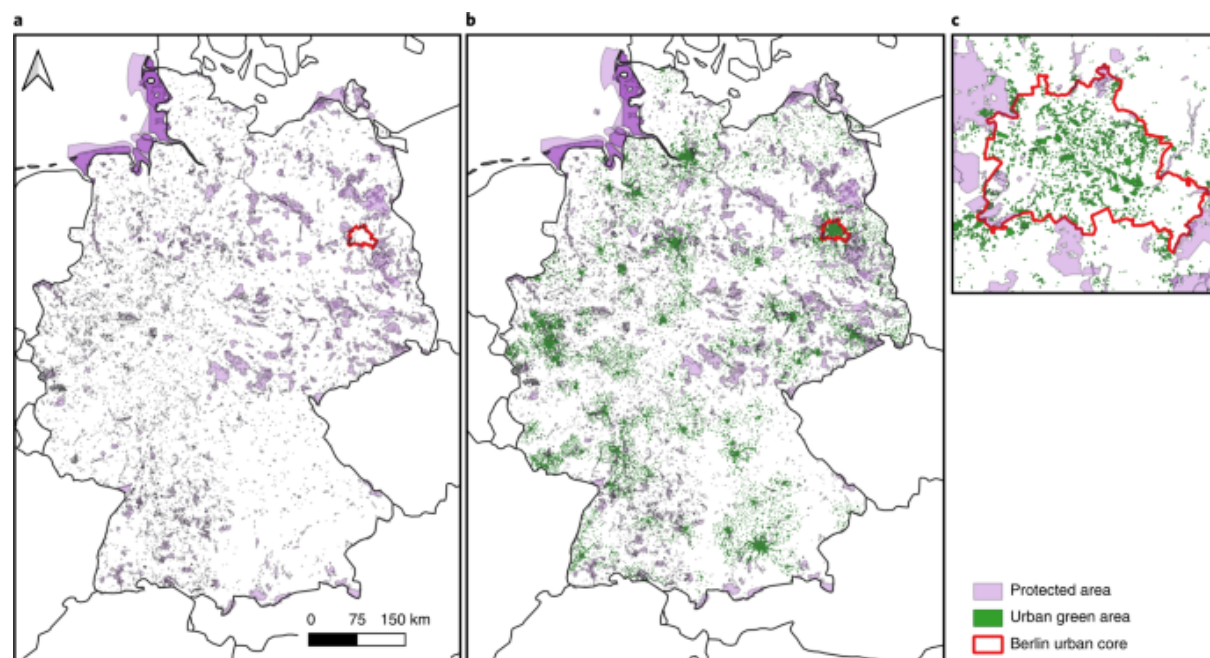
Horticulture is well documented for its key role in the population trend of plant species. Historically, horticulture has had a problematic association with the spread of exotic, weedy and invasive species worldwide[35](#). However, horticulture may similarly be leveraged to facilitate the spread of species with conservation value. For instance, the garden ornamental plant *Muscari botryoides*, classified as 'Vulnerable' on the German Red List, has increased its population by 65% in recent decades[25](#). Accordingly, we find that the cultivation of native plant species is positively associated with their occupancy change over time (Fig. [2](#)). The effect of cultivation could be overestimated, as cultivation is likely to be biased towards species that spread more easily. However, even for neophytes (species introduced after 1492) that show a strong overall positive population trend in Germany, cultivation still proves beneficial (Fig. [2](#)). Adding declining native species to urban environments via conservation gardening may therefore promote secondary dispersal[28](#)[36](#). This could increase the chance of vulnerable species to find additional suitable wild habitat, where a larger area of occupancy may be associated with higher phenotypic plasticity and thus greater resilience to continued global environmental change[37](#).





**Fig. 2. Cultivation has a positive impact on the occupancy trend of both native plants and neophytes.** Boxplot for the percentage change in occupancy across Germany of cultivated (yellow) and non-cultivated (blue) plants for native plants and neophytes (species introduced to Germany after 1492). Changes in occupancy over the past six decades are taken from ref. [25](#); plants with extreme trends according to ref. [25](#) are removed from this analysis. Supplementary Table [1](#) includes a list of plants that are commonly cultivated in Germany and used for this analysis. Displayed is the sample size ( $n$ ), the estimated mean ( $\mu$ , purple triangles) and the  $P$  value of a Mann–Whitney  $U$  test. The box bounds the interquartile range (IQR) divided by the median and whiskers extend up to a maximum of  $1.5 \times$  IQR beyond the box. [Source data](#)

As such, conservation gardening could create considerable additional area for conservation measures alongside protected areas (Fig. 3a,b; ref. 38) and act to complement ex situ conservation areas, such as botanical gardens, which often fall short in providing sufficient space for—and hence have low intra-genetic diversity of—threatened species<sup>39,40</sup>. In Germany, public green spaces amount to 65,000 ha across the country’s 50 major cities<sup>41</sup>. Although some of this area will be unavailable for conservation use due to competing societal needs, this estimate does not account for the other urban areas within these cities potentially available for conservation gardening (for example, allotments, private gardens, balconies, roofs and pavements) and green spaces in smaller cities, suburban and more rural settings, for which there are currently few data available. As a result, this is therefore probably a conservative estimate of the potential space available. For instance, the area of allotment gardens in Germany alone is an additional 44,000 ha (ref. 42). Importantly, urban green spaces also have high spatial complementarity and can be well connected to current protected areas (Fig. 3c); this can minimize isolation and increase primary and anthropogenic dispersal from urban areas to protected habitats<sup>38,43</sup>. Conservation gardening can therefore not only create additional land for conservation but also be an approach to expand habitat networks.



**Fig. 3. Urban green spaces can increase and better connect the area for conservation activities.** a–c, A map of Germany displaying the spatial extent and distribution of protected areas only (available from [protectedplanet.net](https://protectedplanet.net); a), protected and urban green spaces for the largest 96 cities in Germany (available from Urban Atlas

2012, [land.copernicus.eu/local/urban-atlas](http://land.copernicus.eu/local/urban-atlas); **b**) and the urban core of Berlin (**c**), the most populous city in Germany, depicting both the spatial complementarity of the two networks and their connectedness. Note that while urban green spaces may not be classified as protected here, they can be weakly protected, for example, under Berlin's Green Spaces Law, and thus have comparable status to Landscape Protection Areas.

Urban green spaces are increasingly recognized as important pieces of the conservation puzzle<sup>12:13:44</sup> that can support viable populations of threatened native species<sup>13:40:44</sup>. Of all threatened plant taxa assessed by the International Union for Conservation of Nature (IUCN), 17.4% were already found to occur in domestic garden collections<sup>40</sup>, probably a conservative estimate of those actually present, as floristic inventory data of domestic gardens are far from complete, especially in biodiverse, lower-income countries<sup>40:45</sup>. Importantly, occurrences of declining native flora are not restricted to natural vegetation remnants or gardens but are found across diverse, heavily modified land-use types including roadsides, railways, golf courses and cemeteries<sup>13:38:44</sup>. Due to the documented potential for native species in urban areas, several initiatives have sprung up to implement their planting in anthropogenic ecosystems, despite this being rarely reported in the scientific literature<sup>40</sup>. In New Zealand, city councils promote threatened native plants in various urban environments<sup>46</sup>. On oceanic islands, where many native species are threatened, they are often used for landscaping as a mechanism for conservation<sup>47</sup>, and in China, a case study suggests that cultivation of threatened plants in urban green spaces contributes towards their conservation<sup>48</sup>. These findings and initiatives highlight that while the protection of natural habitats for many species remains essential, conservation gardening, implemented in anthropogenic ecosystems, could complement the protection of declining native plant species.

## **Economic arguments**

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### Market potential

The global horticulture market is currently estimated to be valued at US\$109 billion and is projected to reach US\$127 billion by 2024<sup>49</sup>. The German garden market is also a substantial source of economic revenue. Consumer spending on flowers and ornamental plants was €8.7 billion in 2018 alone (per capita spending ~€105), with Germans continuing to spend money on gardening in economic downturns<sup>50</sup>. In Germany, 12% of the active population (5 million people) own a small garden<sup>42</sup>, reflecting a high

consumer potential for conservation gardening. In parallel, strategies to improve the quality and availability of urban green spaces are also gaining momentum. For example, the EU Green City Accord mobilizes European cities to safeguard biodiversity, with several EU funding programmes and financial instruments available to support such measures (for example, European Agricultural Fund for Rural Development, LIFE and URBACT). Germany alone had €790 million available in 2017 to fund sustainable urban infrastructure (for example, federal spending programmes such as ‘Zukunft Stadtgrün’, ‘Soziale Stadt’ and ‘Stadtumbau’). This funding landscape clearly provides a facilitating context for participatory conservation endeavours. With the proliferation of societal awareness and political will to tackle the biodiversity crisis, the green economy and the demand to actively participate in species conservation are both growing rapidly<sup>51</sup>. We therefore expect that garden businesses focusing on declining natives can be profitable in the future by tapping into green consumer spending.

### An incomplete market

The formation of an ecologically meaningful market for conservation gardening is currently limited, however, by various factors, despite there being several declining natives already available for purchase online. We estimate through a random sample of 100 threatened species from the German Red List (~10%) that 35% of the species are readily available from various online retailers (Supplementary Table 2 provides search criteria). For example, *Iberis amara* is classified as extinct in Germany<sup>27</sup> but can be ordered for €3 per 100 seeds (Fig. 4 includes more examples). However, the majority of declining plant species are unavailable for purchase, and there is no comprehensive and accessible database for customers to find plant material that is available. This limited supply is probably due to the historical focus of the horticultural industry on ‘winning’ cultivars that are aesthetic and easy to establish and maintain with little concern for the origin or provenance of species<sup>52</sup>. This also means that there are generally (and not only in Germany) a lack of standards and quality certification for plants and seeds for use in conservation gardening<sup>53</sup>. Currently, it is not clear to consumers whether what they are buying is risk free and conservation oriented. One such risk is that seeds may come from spatially distant populations or they may be cultivars and selectively bred, potentially leading to reduced genetic diversity and outbreeding depression if they mix with wild populations<sup>54</sup>. Policy therefore needs to boost the supply of native plant material, while ensuring quality certification.



**Fig. 4. Many threatened native plant species are already available for purchase online.** Examples of declining native plant species in Germany that can be bought from online retailers (Supplementary Table 2). Potential uses in urban settings (as specified by retailers) range from private balconies (for example, *Muscari botryoides*), green roofs (for example, *Juniperus sabina*), ponds (for example, *Nymphoides peltata*) and parks (for example, *Sorbus domestica*). German Red List criteria 0–3 were translated to IUCN Red List categories EX–VU, where EX is Extinct, EW is Extinct in the Wild, CR is Critically Endangered, EN is Endangered and VU is Vulnerable. Photographs © Michael Hassler ([www.worldplants.de](http://www.worldplants.de)).

## Policy mechanisms

### Cross-sectoral integration

Integrating the emerging native seed sector into the mainstream horticulture market could greatly catalyse the multiplication of certified plant material for conservation gardening<sup>52:55</sup>. The native seed industry is projected to have substantial economic growth as ecological restoration activities and funding mechanisms gain momentum in the post-2020 policy environment<sup>56</sup> and could thus be a major source of native plant material for commercial enterprises. Moreover, the native seed sector already often has science-based standards for the production of native plant material<sup>52:55</sup>. These could therefore be adopted by the mainstream horticultural industry, using policies such as the ‘International Standards for Native Seeds’ to develop directives to ensure quality certification<sup>55</sup> with the potential to involve third party, publicly funded adjudicators to verify standards. To incentivize that certified producers are contracted by garden centres, financial support (for example, a lower value-added tax rate on native seeds) and national policy initiatives (for example, a requirement that city gardening projects use a certain percentage of native seeds) could be created.

We further expect an increase in interest from the horticultural industry and government support for this cross-sector integration, as in many countries, species decline is accompanied by a growing awareness among owners of private gardens and the authorities responsible for the maintenance of public green spaces<sup>51</sup>. Structural support of the native seed sector will therefore allow native seeds to become more readily available for the horticulture market to meet increasing demand.

Currently, the native seed sector still faces several challenges, such as poorly scalable seed production techniques and lack of integration of applied knowledge. One of the biggest bottlenecks is that the industry often relies on wild stands for seed supply<sup>53</sup>. Funding needs to target initiatives that boost and stabilize the production capacity of native seeds, for example, through the creation of seed production areas and native seed farms. Rural regions in particular could share in these economic opportunities; in Europe, such funding provisions may come from the Common Agricultural Policy to support this<sup>7</sup>. In addition, Indigenous land, people and knowledge could be part of this native seed-farming enterprise, especially in lower-income countries, where initiatives such as the Tree Conservation Fund ([treeconservationfund.org/](http://treeconservationfund.org/)) may help unlock private capital to support local communities for the production of native plant material. Moreover, botanical gardens could play a key role in giving access to the best science and practical advice and suitable native plant material for conservation gardening in commercial settings<sup>57</sup>. The world's botanical gardens grow at least one-third of all known plant species<sup>58</sup>, can cultivate many threatened plants (even in mega-diverse countries such as China<sup>39</sup>) and comprise a community of >60,000 experts who can offer advice for plant collection, germination and propagation techniques<sup>57</sup>. A prominent example of such a cross-sectoral collaboration between botanical gardens and the native seed sector to boost seed supplies is Greening Australia<sup>39</sup>. Funding for the native seed and botanical garden communities (for example, through tax credits, grants, donations, fees for service) alongside better coordination of these sectors will be key to the uptake of garden-led plant conservation<sup>57</sup>.

### Conservation gardening label

In conjunction with cross-sectoral integration and certification, we posit that labelling schemes are needed to enable a shift of the demand curve towards 'conservation gardening' species. Appropriate and informative labelling on the trend and overall status of declining native species are typically lacking, hindering consumer choice between these and conventional species.

Increasing awareness of biodiversity loss is frequently reported in surveys<sup>51</sup> and could therefore turn into a preference for buying conservation gardening-labelled species, potentially marketed at a premium. A conservation gardening label could therefore have the triple benefit of generating a price premium while ensuring quality certification and creating awareness of native plant diversity loss. Such a label could distinguish ‘conservation gardening’ species, guarantee that seeds are not taken from natural ecosystems at an unsustainable rate, and ensure that seeds have regional provenance or at least originate from spatially proximate populations<sup>59</sup>. A label should also include the following information: (1) the geographic area in which the plant is native, (2) whether the plant species is declining and/or listed as threatened on the national Red List and why, (3) the services it provides (for example, pollinator friendly, medicinal, ornamental) and (4) the habitats where the plant species occurs naturally. Finally, a conservation gardening label could advertise the investment of a percentage of profits into active conservation and restoration projects of habitats from which these species originate, thereby helping to redirect private consumer spending towards biodiversity conservation measures.

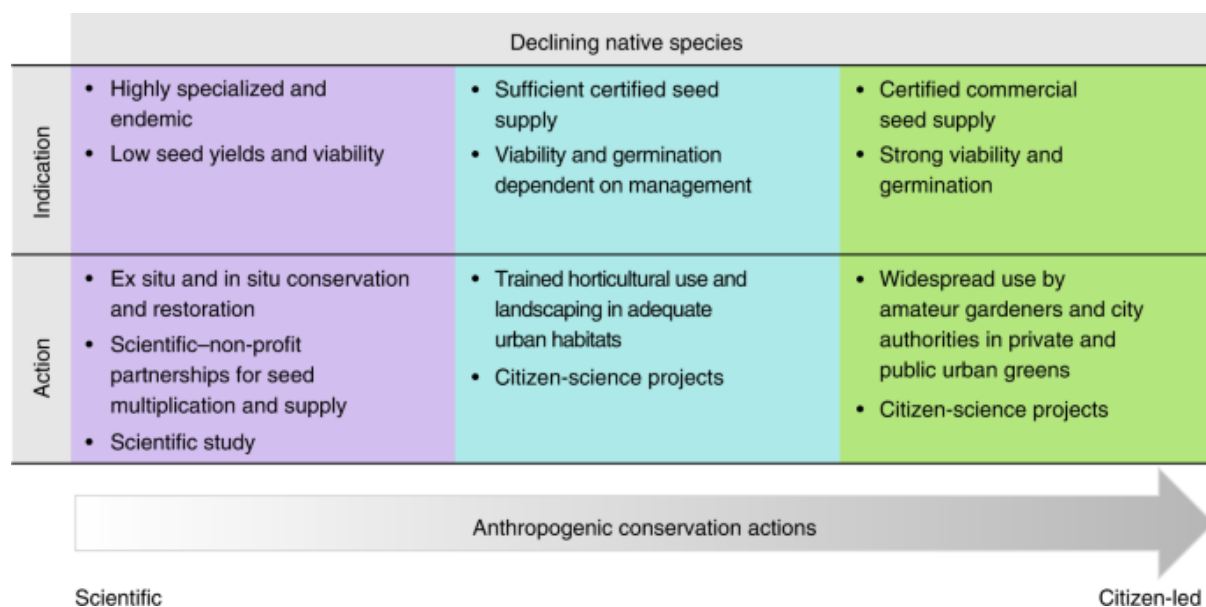
### **Candidate species**

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Conservation gardening targets the use of declining native species. For this, two fundamental concepts must be considered: the spatial scale of (1) species nativeness and (2) decline. Native status defined by political boundaries can be problematic in large countries where a species native to one state may be ecologically harmful in another (for example, *Sollya heterophylla* in Australia<sup>60</sup>). Considering nativeness at the scale of botanical countries<sup>61</sup> may help address this issue, with comprehensive data available at that scale (for example, Plants of the World Online, [powo.science.kew.org](http://powo.science.kew.org)). Yet, the concept of nativeness should also go beyond geographic origin, focusing on environmental outcomes such as potential for invasiveness<sup>62</sup>. Such assessments could in turn be guided by global databases on invasiveness (for example, GloNAF, [glonaf.org](http://glonaf.org)). Finally, species population trends depend on spatial scale. Where fine-grained monitoring data are available, species declines may be considered at local scales, especially for emblematic species that are important for culture and heritage<sup>63,64</sup>. In the absence of fine-grained long-term monitoring data, regional and national Red Lists provide a basis for defining decline, where databases such as ThreatSearch ([tools.bgci.org/threat\\_search.php](http://tools.bgci.org/threat_search.php)) readily provide such information. The recent availability of these comprehensive

global databases makes the definitions of nativeness and decline operational across applied contexts.

Accounting for these considerations, we propose a tiered approach to integrating appropriate declining natives with anthropogenic activities (Fig. 5). We also outline those species that will probably not be suitable. Declining species, which are specialized to habitats that do not occur in urban settings, are difficult to propagate or require specific and complex ecological mechanisms to survive (for example, specialized pollinators, fire and so on), need ongoing habitat-preservation efforts and professional ex situ conservation<sup>65</sup>. Similarly, declining endemics may have small populations or seed yields that are too low and variable for public use<sup>66</sup> or do not propagate with seeds and can so far only be reproduced effectively in vitro<sup>67</sup>. Many declining plants are, however, not endemic, having parts of their range in adjacent regions or countries where they are not listed as threatened<sup>68</sup>, potentially providing sustained plant material sources. In many cases, ‘near-local’ provenances provide similarly for biodiversity as local populations<sup>18</sup>. Similarly, local provenance defined at larger spatial scales may justify the use of populations that occur in neighbouring areas with warmer or drier climates to prepare for species migrations with climate change<sup>69</sup>. Flexibility in the definition of the exact provenance must, however, go in tandem with ensuring that threatened species will not further be depressed by processes such as crossing and reduced genetic diversity<sup>18,54</sup>.



**Fig. 5. A tiered approach for selecting appropriate declining native species.**



We provide a tiered approach for determining which declining native species are appropriate to use in anthropogenic conservation and restoration activities. Boosting declining native species through conservation actions can gradually move from more scientific (purple) efforts to more citizen-led (green) ones. We highlight here both the indications for choosing which species should belong to each category (top), as well as the respective appropriate conservation actions for each category (bottom).

Appropriate species for conservation gardening are those where a sufficient seed supply can be established (Fig. 5, middle and right). Species where germination and viability are strongly dependent on habitat management could be directed for use by trained gardeners and landscapers in appropriate urban habitats and be a basis for citizen-science projects. Species with a strong viability could be mainstreamed for use in private and public green spaces. Overall, conservation gardening can be considered as a socio-ecological restoration action at the anthropogenic end of the ‘restoration continuum’, providing an opportunity for urban and regional administrations—and the public—to become involved in participatory restoration and conservation activities<sup>70</sup>. Fostering integration of specialist plant knowledge on the amenability of species for urban gardening programmes, academic research on species provenance zones (for example, refs. <sup>56</sup><sup>70</sup><sup>71</sup>) and existing guidelines from the native seed industry<sup>55</sup> will be integral to putting this tiered approach into practice.

### **Promoting social uptake**

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For conservation gardening to become scalable, initiatives must be accepted and adopted at the individual-community level. Although surveys often report an increasing awareness of biodiversity loss (for example, ref. <sup>51</sup>) and signal a willingness for purchasing species for conservation gardening, a considerable barrier to widespread citizen participation is a continuing preference for tidy gardens. Additionally, many of the declining native plants may not have comparable aesthetic appeal to common garden ornamental plants. Social norms (for example, a duty to maintain neighbourhood standards<sup>72</sup>) and human perception of nature therefore have a strong influence on behaviours associated with maintaining urban green spaces. While research has shown that ecological aspects of conservation gardening can strongly align with cultural conceptions of aesthetic beauty, the aforementioned barriers often prevent transitions to a more conservation-minded ethos<sup>73</sup>.

Studies have shown that promoting connections to place and nature and disseminating practical information is key to overcoming these barriers<sup>19:63:64:73</sup>. Improving people's understanding of the importance of native biodiversity in their garden has been demonstrated to lead to a positive shift in people's attitudes, values and behaviours with regards to wildlife-friendly gardening<sup>74</sup>. Practical advice on which plants to remove and sow was found to be one of the most effective ways of encouraging previously non-engaged actors to participate in biodiversity-friendly gardening<sup>75</sup>. Encouraging influential actors such as government agencies and municipalities to disseminate this practical guidance can target a critical mass of residents<sup>76</sup>. The act of participating in conservation gardening, especially in a community setting, has further been shown to enhance people's commitment to nature stewardship, increase community linkages and create strong attachments to their sense of place and identity<sup>15:63:64</sup>. Therefore, there must be emphasis placed on bolstering information campaigns and nature connections to direct individual preferences and neighbourhood perceptions towards conservation gardening<sup>75</sup>.

Specific mechanisms to enable this uptake should harness the use of social diffusion and neighbour mimicry<sup>77</sup>. Tested strategies include: (1) community outreach programmes that engage local residents (for example, using a block leader approach) and place emphasis on 'learning by doing'<sup>64:75:78</sup>; (2) social organizations (for example, homeowner and neighbourhood associations) that influence and allow the coordination of biodiversity-friendly management across gardens and provide ongoing advice and materials<sup>79</sup>; (3) collaborative networks (for example, UrBioNet, [sites.rutgers.edu/urbionet/](https://sites.rutgers.edu/urbionet/), and URBIO, [urbionetwork.com](http://urbionetwork.com)) that engage diverse stakeholders in urban biodiversity management, design and planning and engage local residents to partake in scientific research regarding the ecological role of declining native plant species (for example, habitats for insects); (4) urban biodiversity stewardship networks that foster partnerships between local government and community member actors across both private and public land and place particular emphasis on nature and species of 'place'<sup>63:76</sup>; (5) citizen-science initiatives that further increase participant knowledge and skills, enhance conservation actions and inform future research priorities on the topic<sup>78</sup>; and (6) environmental community awards for conservation gardens (for examples, see review by ref. <sup>72</sup>) that encourage competition among neighbours and justify the perception of an unkempt garden<sup>80</sup>. Finally, botanical gardens can again play a key role here by advocating for and supporting these initiatives. Given the 500 million

(predominantly urban) visitors to botanical gardens each year<sup>58</sup>, they can provide a platform both for educational purposes, for example, courses for training ([ncbg.unc.edu/learn/adult-programs/conservation-gardening/](https://ncbg.unc.edu/learn/adult-programs/conservation-gardening/)) and for contributing towards providing suitable plant material<sup>81</sup>. Through the promotion and support of community actions, powerful social mechanisms can be harnessed to implement and mainstream conservation gardening.

### **The time for conservation gardening**

Species extinction rates are currently 10 to 100 times higher than background rates<sup>2</sup>. In response to these threats, the United Nations General Assembly declared 2021–2030 the UN Decade on Ecosystem Restoration to safeguard species and their habitats. Here we propose an opportunity for ecosystem restoration at the anthropogenic end of the ‘restoration continuum’ in the form of conservation gardening, whereby large-scale planting of declining native species in human-managed urban areas could not only result in additional land used for conservation but also help declining species find suitable wild habitat faster than they can naturally. Implementing conservation gardening at scale does not require wholesale changes to the existing architecture for conservation and can be cost-effective and self-sustainable while allowing for a more proactive, citizen-led approach to conservation. Furthermore, this effort could provide a platform to educate the public about the threats declining species face and thus promote awareness of the biodiversity crisis while providing positive, actionable steps to remedy it. By introducing such measures, conservation can become a tangible and integrated practice of urban living. We argue that integrating the native seed sector within the larger horticultural market, adding conservation gardening labels, and community dissemination of practical support will be key to scaling up and mainstreaming conservation gardening. While we recognize that this cannot be a panacea for native species conservation and that specific measures will always need to be adjusted for context, there is potential for conservation gardening to be implemented broadly and become ever more important in an increasingly urbanized world. Scaling up and mainstreaming conservation gardening can increase demographic rates of declining species, facilitate dispersal, promote human stewardship of nature, raise awareness of mostly unknown but disappearing species, be economically viable and sustainable, and potentially be used to co-fund other conservation initiatives.

## Data availability

Data used for Figs. 1 and 2 are taken from ref. 25 and [sci.muni.cz/botany/juice/ELLENB.TXT](https://sci.muni.cz/botany/juice/ELLENB.TXT). Source data are provided with this paper.

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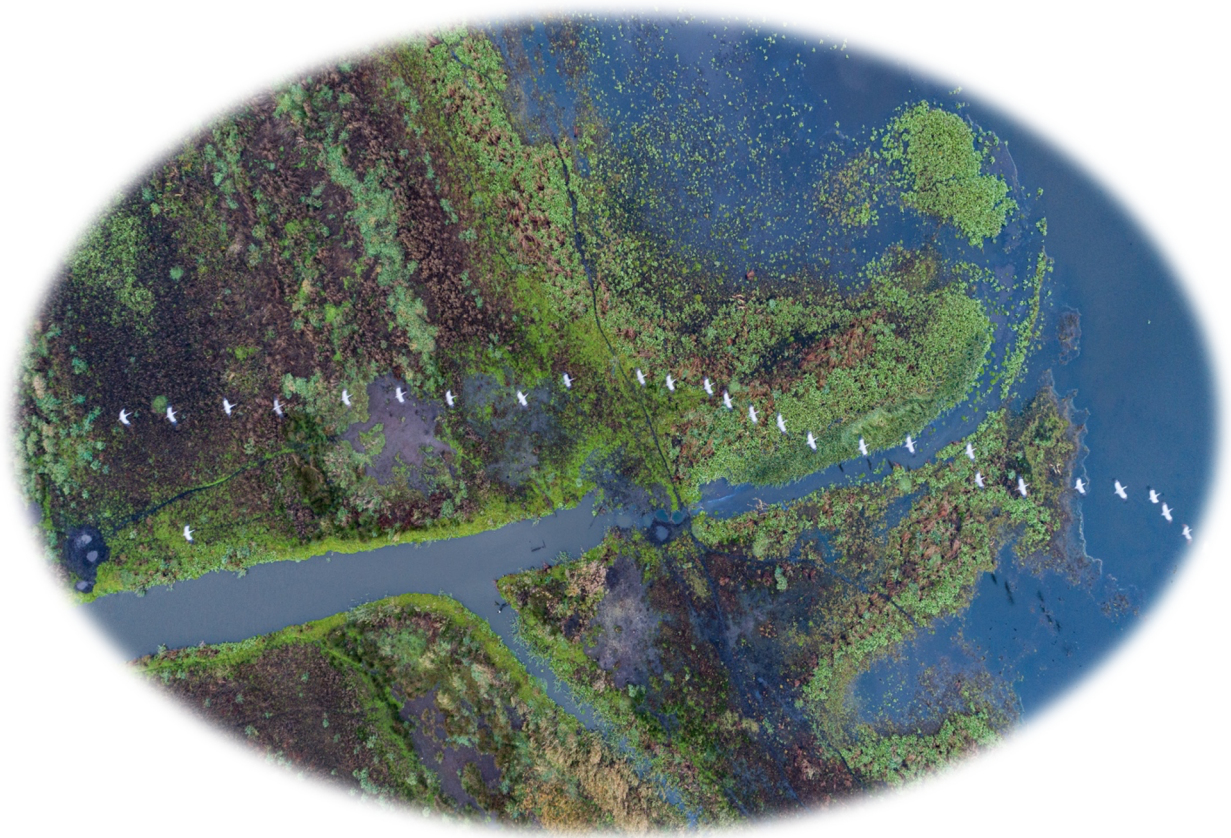
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### **Contributions**

J.S. and I.R.S. devised the project and the main conceptual ideas with contributions from C.T.C., E.L., A.P., H.M.P. and J.N.M. J.S. and I.R.S. performed the analytical calculations. J.S., I.R.S. and E.L. produced figures. J.S. and I.R.S. wrote the manuscript with contributions from E.L., C.T.C., J.N.M., A.P. and H.M.P. I.R.S. supervised the project.

## Chapter 5

## Synthesis



*Photo credit: Florian Möllers / Rewilding Europe*

In this thesis, I used a variety of different methodologies to investigate approaches to promote biodiversity in changing landscapes. I explored how and where rewilding and urban conservation gardening can be implemented to tackle socio-economic shifts in land use across Europe. I found that rewilding sites are making some progress at the site-scale, however, socio-political pressures currently prevent them from scaling up to the landscape scale. I additionally found that rewilding approaches, such as bolstering herbivore populations, interact with other human pressures in novel landscapes, and that these must be accounted for when planning rewilding actions. Finally, I explored complementary, participatory approaches to restoration actions in urban areas where rewilding or reserves may not be appropriate. I found that horticultural practices are partially responsible for the expansion of species' occurrence and can play a key role in species conservation. Subsequently, I postulate that implementing this approach would not require wholesale changes to current conservation and horticultural practices, but rather political and behavioural nudges. Here, I will further investigate the scientific and societal implications of the work, as well as provide ideas for future research directions.

The third chapter built on theoretical work from Perino et al. (2019) and Torres et al. (2018), who proposed rewilding frameworks from which meaningful monitoring could occur. My third chapter was, in part, also testing some of the more theoretical assumptions and predictions of these two papers. The societal boundaries and ecological challenges to rewilding identified by Perino et al. (2019) aligned with the hinderances we found in our interview process with rewilding practitioners and experts. The Common Agricultural Policy subsidises intensive and extensive agriculture in low-production and other areas prone to abandonment (Pe'er et al. 2014). Whilst there are certainly some benefits in doing so, it can greatly undermine the rewilding work that has been conducted in these areas and prevent upscaling. Local policies can similarly work in opposition to rewilding initiatives, such as requiring carrion and deadwood removal or expanding infrastructural development. Therefore, policy changes are required before rewilding can hope to become a mainstream and integrated restoration activity. Furthermore, we found that public support, both at the general and local level is essential for ensuring the continuation of rewilding work at any scale. Entire rewilding projects have been decommissioned or abandoned due to lacking public support and it can severely undermine established projects' abilities to do meaningful work (Rewilding Britain, 2019). This should be an equally important task alongside policy change when

developing rewilding projects and plans. Lastly, the context within which rewilding programs are established matters. We further illustrate this in chapter 2 when we examined the long-term consequences of ungulate herbivore population increases on forest vegetation. Rewilding and the specific rewilding measures that come with it, must make both ecological and social sense for the context they are in otherwise they can lead to detrimental and unintended consequences (Nogués-Bravo et al. 2016). This is not to say that rewilding cannot have meaningful and welcome effects, but they should be carefully considered and, most importantly, effectively monitored in the long-term.

The reality of many rewilding (and restoration) sites is that there are often a paucity of long-term data collection and monitoring (Brooks et al. 2006). Resource limitations can mean that monitoring is not prioritized or even implemented, and time-limited funding sources may not accommodate for monitoring (Clark et al. 2019; Cooke et al. 2019). First and foremost, it prevents a deeper understanding of ecological processes that occur following rewilding actions, and secondly, it hinders meaningful management actions (Nicol et al. 2015). Furthermore, it also undermines the credibility of rewilding projects, not only for scientists, but also the public and policy makers (Pettorelli et al. 2018). Again, we find, for example, in chapter 2 that herbivore reintroductions interact in unexpected ways with modern human pressures, and that rewilding actions in novel landscapes may lead to unintended consequences. Monitoring is, therefore, essential for understanding and responding to these events, but has not been a priority for most projects. A major impediment is often funding. In most cases, there is either no additional funding for monitoring or specific monitoring requirements are attached to precarious, short-term funding cycles that prevent meaningful, long-term data collection and analysis (Cooke et al. 2019). It may also be that monitoring requirements are unsuitable for practitioners, either due to their complexity, technical or resource requirements (Margoluis et al. 2009; Stem et al. 2005; Torres et al. 2018) This lack of consistent monitoring was initially a major barrier to effectively evaluating rewilding in chapter 3. Whilst we were able to make effective use of expert opinion and interviews alongside a Delphi Process, our understanding would greatly benefit from complementary empirical evidence, including on the ground ecological monitoring and remote sensing data that does current not exist or remains hidden in local institutions (Pereira et al., 2013).

Furthermore, rewilding forms part of a larger restoration community (Svenning et al. 2016). Restoration efforts can be vital to save both species and ecosystems, but when conducted poorly or with only specific goals in mind, it can also be extremely damaging, perhaps more so than if we did nothing (Overbeck et al. 2015). For example, tree planting efforts can be appropriate under certain conditions, in areas that have lost tree cover historically and when a diversity of tree species are used to ensure a functioning ecosystem (Pereira et al. 2020). However, the prevailing focus on afforestation has also led to many destructive restoration efforts (Hoekstra et al. 2005). Ecosystems such as grasslands, peatlands and tundra that would not normally support trees are often considered reasonable habitats to plant trees, outcompeting the native species in the long run. This may be in part due to the long-standing perception that forest is considered the natural baseline habitat for many places (Pausas and Bond 2019; Vera 2000). In part this is also due to the prevailing attention that carbon mitigation gets in environmental policy (di Sacco et al. 2021). Often the desire is to offset carbon with tree planting considered the best way to do so (decadeonrestoration.org). This oversimplistic focus obscures other endangered ecosystems, such as grasslands. For example, the IUCN and World Resources Institute misidentified 9 million km<sup>2</sup> of grassy systems as potential areas for forest restoration (Veldman et al. 2015). To this end, perhaps passive restoration, or rewilding, is a preferable option in some cases where the restoration goals and pathways remain unclear. Particularly as it is unclear when and whether active restoration efforts result in faster or more complete recovery sites than passive efforts (Crouzeilles et al. 2017; Strassburg et al. 2019). These questions have enormous implications for the type of restoration that should be done, and for how limited restoration resources are used in the future. To this end, I worked on a project to highlight grassland restoration efforts (Staudé et al. 2023)\* and have previously called for better informed restoration efforts (Pereira et al. 2020)\*.

As with rewilding, urban conservation gardening remains conceptionally in its infancy and there are several important gaps in our knowledge. It is unclear whether it is, in fact, essential for gardeners to use native plant species to promote trophic complexity in urban spaces (Matteson and Langellotto 2011). Some experiments and observational studies suggest that native species are essential for promoting insect diversity, whereas other studies suggest that non-native and even invasive species can fulfil the same functional role (Liebhold et al. 2018; Mata et al. 2021). This begs the question whether it is necessary to focus on native species themselves or whether our

gardening focus should instead be on improving floral diversity, composition and other important metrics (Schaffers et al. 2008). Fundamental basic relationships between specialized insects and plant species remain poorly understood and synthesis work is required to better understand host switching and novel species associations (Braga and Janz 2021; Tallamy et al. 2021). Secondly, it is unclear exactly which native species are appropriate for use in conservation gardening. It is uncertain which seeds can be commercially harvested for manufacture and distribution and therefore which species can be gardened by non-experts (Ladouceur et al. 2018). It is also unclear which species can be grown together and in which urban environments, e.g., balconies, green roofs, gardens, parks, roadside strips etc. In order to address this, we have produced a shiny app that provides easily accessible information for gardeners to find appropriate declining, native species online and understand their care requirements (Marius et al., *in review*)\*. Many more experimental studies are required, however, to determine appropriate species lists for different areas and needs.

One fundamental concern that arose from the urban conservation gardening chapter was that of provenance. This has significant practical repercussions for which species can be planted and where, but also which evolutionary process is more important for conservation, genetic diversity for resilience to future change or genetic distinction to prevent hybridization and species loss (Wilkinson 2001)? Zooming out, this also has important implications for rewilding and restoration more broadly. Should we introduce species populations into other areas to bolster population sizes of endangered species? Should we proactively introduce species to countries where we believe habitat will become available due to climate change in the future (Thomas 2011)? On the one hand, local provenance is essential for conserving locally adapted genes. There are concerns that hybrids from two provenances may have lower long-term fitness due to the loss of local adaptations or epistasis (Broadhurst et al. 2008). On the other hand, low population genetic diversity may also lower a species' fitness through genetic bottlenecks (Bischoff 2010; Wilkinson 2001). Our ability to use seeds or populations from different provenances has major implications for seed and population availability, particularly for endangered species, and therefore, which species are available for conservation gardening, as well as other restoration efforts. In chapter 4, we advocate for some flexibility in the definition of provenance, particularly when accounting for future climate

change, however, more research is certainly required to understand the limitations thereof.

My thesis sparked many additional questions and scientific directions for future research, yet it also touched upon philosophical considerations that are important for the ongoing work in this field. There are several semantic challenges that arise within the field of ecology, with implications for the scientific work itself. Most notable, “rewilding” as a term is fraught with controversy, both politically and scientifically (Gammon 2018; Hayward et al. 2019). Questions such as “what does wild mean”, “when constitutes the right kind of wilderness in history” and “should humans form part of wilderness” have plagued rewilding throughout its 20-year history (Lorimer 2015; Lorimer et al. 2015). Whilst some of these issues were addressed by the establishment of a rewilding framework (Perino et al., 2019), some of these concerns remain. The questions and feelings that a term evokes in people are important, as they can play a significant role in the outcome of projects themselves. Rewilding Britain had to renounce a rewilding project in Wales before it even began due to enormous public outcry and concern over what “rewilding” would mean (Rewilding Britain 2019). On the other hand, the term itself has garnered considerable positive attention from other segments of society, with conservation and restoration projects using the label to attract both funding and for galvanizing support (Jepson 2019). What a term includes and excludes also plays a large role in how initiatives and science are conducted. Within my work, I use another term “stochastic disturbances” to refer to random environmental events that cause large change in the biophysical surroundings, e.g., fire events. The use of the term disturbance implies something negative, undesired or unnatural, “a state in which normal functioning is disrupted” (Fraterrigo 2020). In actuality, these events are recalibration mechanisms, upon which species functioning *relies* (Brose and Hillebrand 2016). Many plant species require pyric events for regeneration (Fuhlendorf et al. 2016). Again, this may have implications for how we understand and even monitor such events, as well as how public respond to them emotionally.

Another intriguing aspect of this work was determining species responses to different land use drivers. Although it is well established that there will inevitably be both winner and loser species for any form of ecological and land change (or lack thereof), the extent and type of species composition change is of particular relevance and importance (Newbold et al., 2018). Also important are the value judgements that are assigned to the drivers that



promote either “good” or “bad” species. In restoration and conservation work, we add value to particular sets of species that we wish to bolster, typically declining, culturally-important, iconic and native species, whereas we devalue others, typically non-native, competitive species (Pereira et al., 2012; Heink et al. 2018; Hobbs 2016; Verbrugge 2016). These assumptions are prevalent throughout the literature, as well as this thesis. In chapter 2, I consider the increase of threatened and small-ranged species as “good” and the increase of nitrophilous and non-natives as “bad”. In chapter 3, the rewilding experts focus on the reintroduction or bolstering of specific species, e.g., bison, whilst the rewilding framework also rewards sites that don’t have invasive, “harmful” species. In chapter 4, I advocate for the mainstreaming of specifically native, declining species’ planting. In all cases, these are expert judgements informed by values that assume a hierarchy of species (Pereira et al., (2012) and the approach that scientists and conservationists take are often driven by the underlying conservation focus (Queiroz et al., 2014). Non-native species, for example, may provide important functional substitutes and can be more resilient to future ecological changes (Schlaepfer et al. 2011; Thomas and Palmer 2015). They can also lead to hybridization and therefore rapid speciation in the Anthropocene, potentially offsetting other species losses (Thomas 2013).

However, there are a couple of logical reasons why certain species may have more *conservation* value than others. Firstly, certain species may be at particular risk of anthropogenic pressures and therefore require more anthropogenic attention in turn (Chichorro et al. 2019). Secondly, there are many more native species than non-native species in Europe (Keller et al. 2011). Therefore, when we are actively promoting these species, we are able to encompass many more species as a result. Finally, rewilding pays particular attention to keystone species which create habitat for many other species in turn (Jordan 2009). It makes logical sense to focus on these species if the aim of biodiversity restoration is indeed to conserve as many species as possible. Regardless, it is important that our implicit judgements should be acknowledged and taken into consideration when assessing the findings in these papers. There are many biases amongst scientists against non-natives, with value-laden language used to describe and discuss them (Sagoff 2005), which influences our decision-making. To this end, I supervised a master’s student to investigate the impact of non-native and invasive species on vegetation diversity in local plots at a global scale to understand their potential impact. We found that both overall and native diversity increased in plots with both non-native and invasive species

present, potentially affecting our conception of non-native species and their impacts (Lefebvre et al. *in prep*)\*.

The aim of my thesis was to investigate mechanisms by which biodiversity can be better supported within a rapidly changing landscape. I found that the efficacy potential for these mechanisms remain highly context-dependent, both on societal, as well as ecological, factors. Rewilding projects are able to make some progress, yet are often hindered from becoming scalable by competing land use pressures. Ungulate herbivory can play divergent roles within the same habitat depending on ambient environmental conditions. Urban conservation gardening may work for certain amenable species under certain socio-political conditions in urban areas. However, it is a combination of all these different approaches, under regulated and understood conditions, that will allow us to make tangible changes for the world that we and other species live in. Considering the complexity of the world we are operating in; it will take a diversity of approaches to support a diversity of species to continue to thrive within it.

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# Appendices



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## Supplementary Information: Chapter 2

# Supplementary Information for Divergent roles of herbivory in eutrophying forests

### Supplementary Figures

**Supplementary Figure 1:** *Vegetation cover changes under different forest management types.*

**Supplementary Figure 2.** *Association between shrub cover and nitrophilous, non-native spp.*

**Supplementary Figure 3.** *N-deposition effects on community composition.*

**Supplementary Figure 4.** *Species richness change and exchange ratio versus herbivory change in relation to Ndeposition.*

**Supplementary Figure 5.** *Threatened and native spp. have lower N-numbers on average.*

**Supplementary Figure 6.** *Correlation between herbivory weighted with and without body mass.*

**Supplementary Figure 7.** *Histograms of herbivore pressure and N-deposition across sites.*

**Supplementary Figure 8.** *Conditional association between N-deposition and herbivore pressure.*

### Supplementary Tables

**Supplementary Table 1.** *Study site info.*

**Supplementary Table 2.** *Dataset.*

**Supplementary Table 3 - 11.** *Model summaries for Figure 2: Herbivory and shrub, herb and tree layer cover changes.*

**Supplementary Table 12 - 15.** *Model summaries for Figure 3: Herbivory, species richness and temporal turnover.*

**Supplementary Table 16 - 23.** *Model summaries for Figure 4: Herbivory and community composition.*

**Supplementary Table 24 - 25.** *Model summaries for Supplementary Figure 2: Shrub cover versus non-native, nitrophilous spp.*

**Supplementary Table 26 - 29.** *Model summaries for Supplementary Figure 3: N-deposition and community composition.*

**Supplementary Table 30 - 37.** *Model summaries for Figure 4: Interaction between herbivory and N-deposition.*

**Supplementary Table 38 - 39.** *Model summaries for Supplementary Figure 4: Differences in N-numbers.*

**Supplementary Table 40 - 43.** *Model summaries for changes in herbivory versus community composition, accounting for productivity.*

**Supplementary Table 44 - 47.** *Model summaries for changes in herbivory versus community composition, accounting for tree cover*

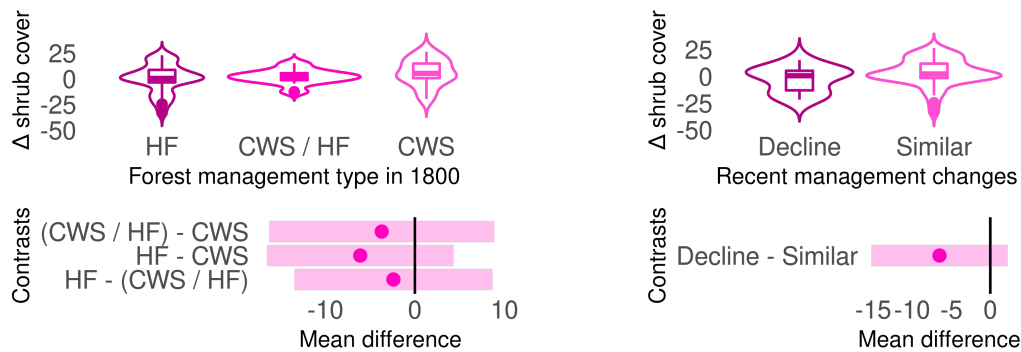
**Supplementary Table 48 - 51.** *Model summaries for changes in herbivory versus community composition, excluding baseline herbivory.*

## Supplementary Note

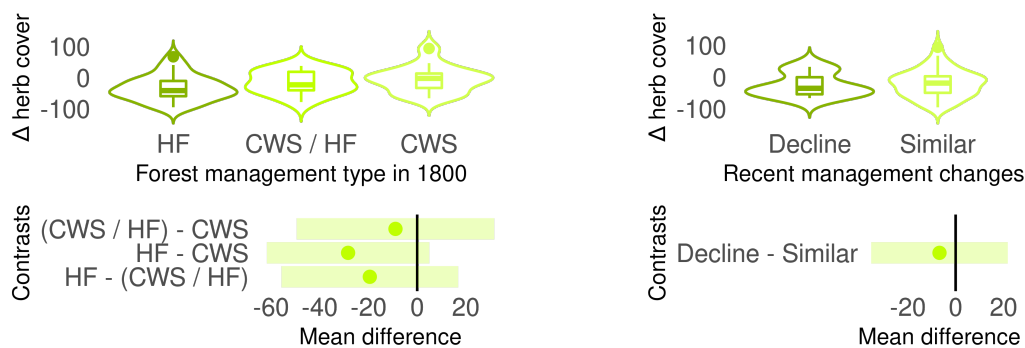
**R code** for all main analyses are available on figshare at: <https://doi.org/10.6084/m9.figshare.21596844>

## Supplementary Figures

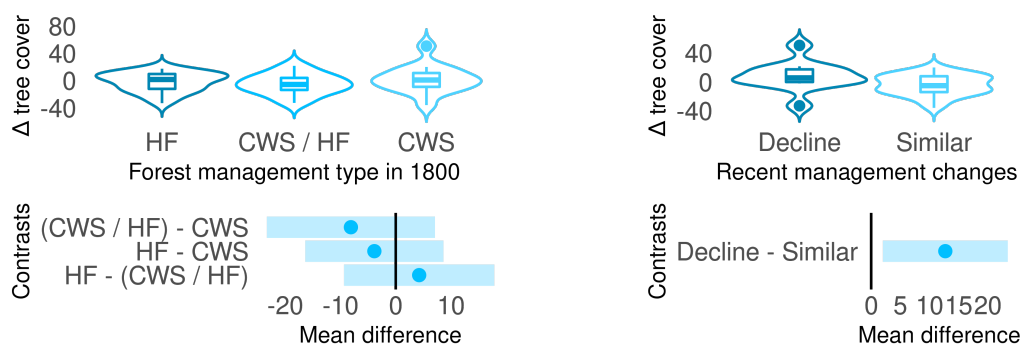
**a**



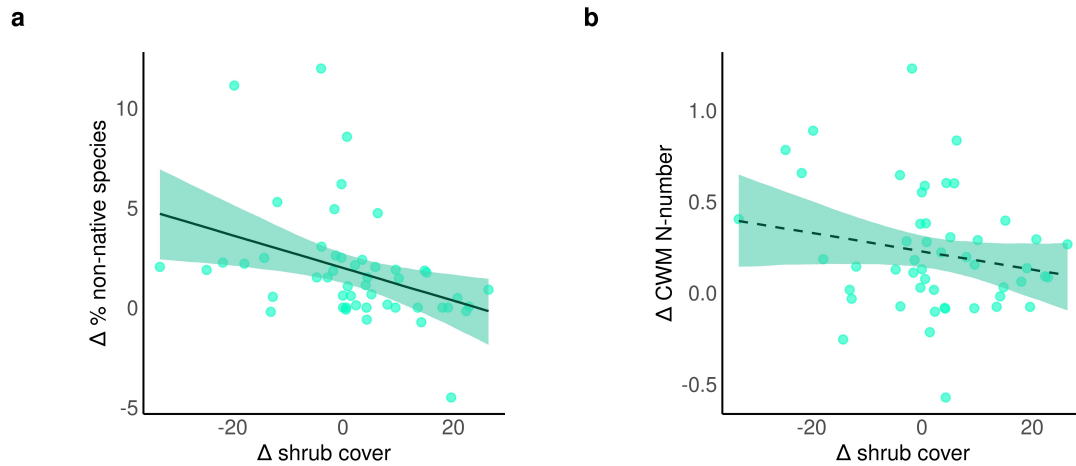
**b**



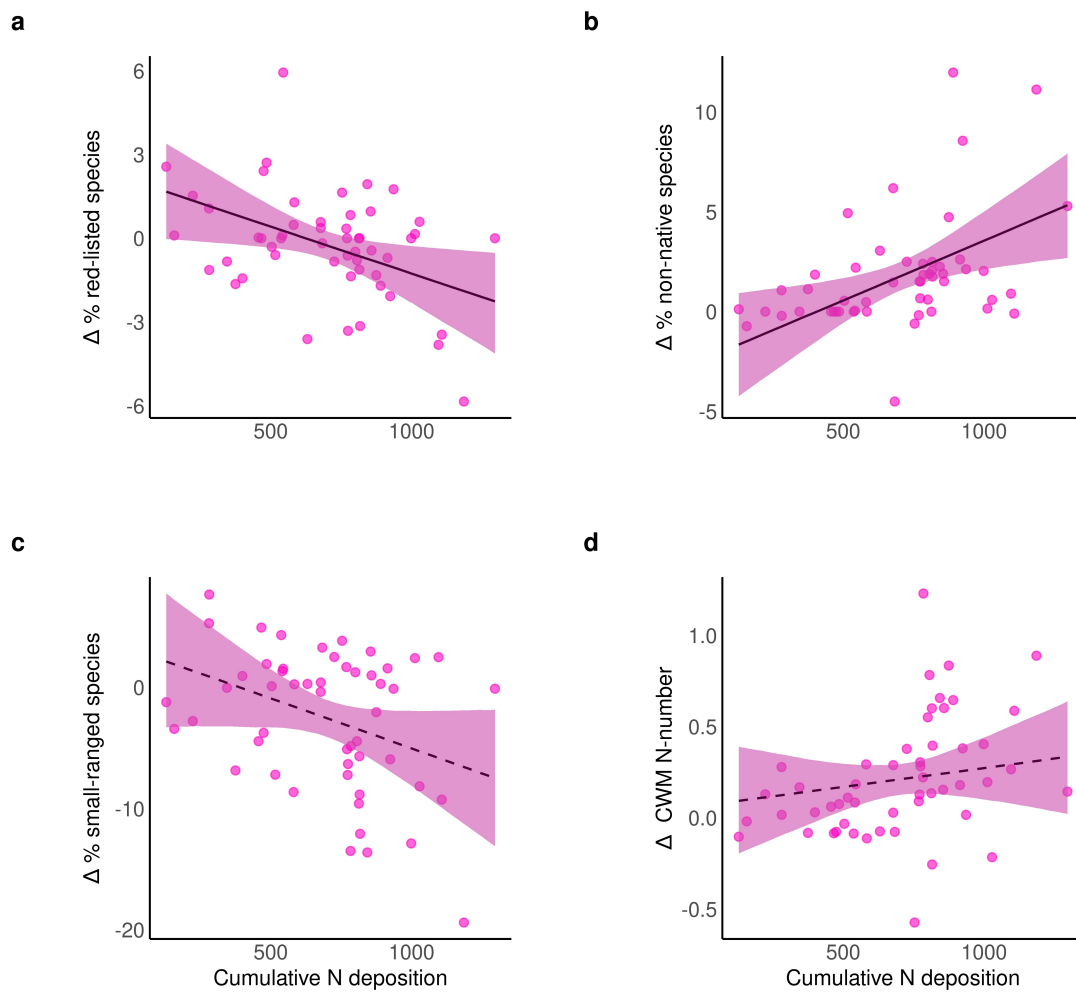
**c**



Supplementary Figure 1: **Relationship of (left) historical management practices and (right) recent management changes between changes in a, shrub cover; b, herb cover and c, tree cover.** The box and violin plots show that there is no association between forest management and changes in **a**, shrub cover or **b**, herb cover, either in the year 1800 (left) or due to recent management changes (resurvey - baseline). There is no association between historical forest management and **c**, changes in tree cover, however, there is an increase in tree cover in sites that experienced declines in management intensity between baseline and resurvey. Boxplots bound the interquartile range (IQR) divided by the median and whiskers extend up to a maximum of 1.5 x IQR beyond the box. Note that two sites lacked shrub and tree cover and one site also lacked herb cover data so that there were n=50 and n=51 independent resurvey sites for **a**, **c** and **b** respectively.



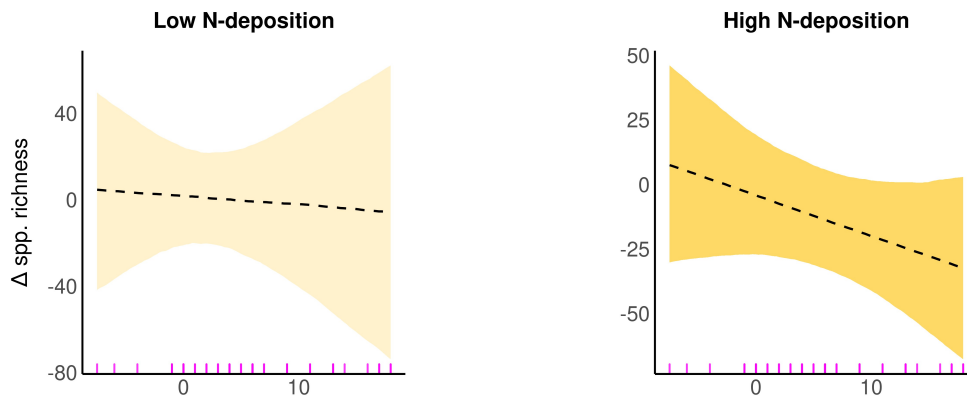
Supplementary Figure 2: **Relationship between changes in shrub layer cover and a, % non-native species and b, the CWM N-number.** Lines and transparent ribbons represent the posterior mean line and the 95% credible interval. The dotted line represents marginal non-significance here. Note that two sites lacked shrub cover data so that there were n=50 independent resurvey sites for this analysis (Supplementary Table 24 and 25).



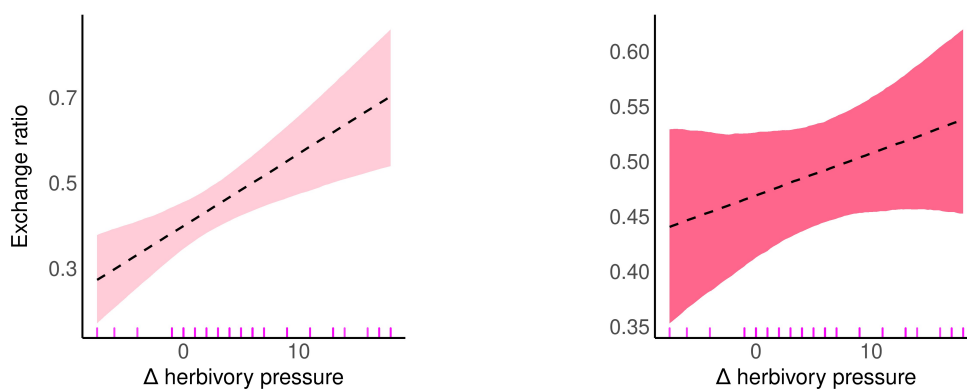
Supplementary Figure 3: **Relationship between cumulative N-deposition and changes in a, % red-listed species, b, % non-native species, c, % small-ranged species and d, CWM N-number.** Lines and

transparent ribbons represent the posterior mean line and the 95% credible interval. Dotted lines represent marginal nonsignificance here. Models included inter-census time span, and site area as covariates, with n=52 independent resurvey sites (Supplementary Table 26 and 30).

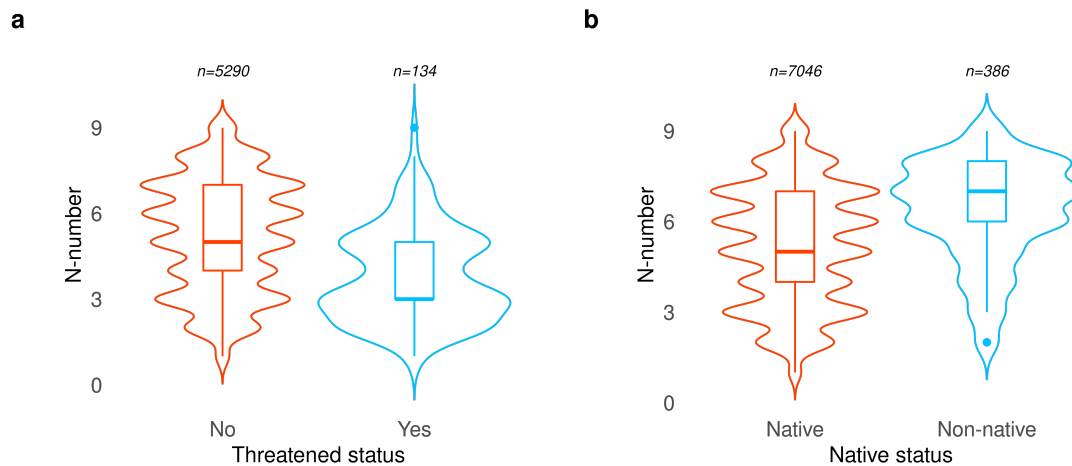
**a**



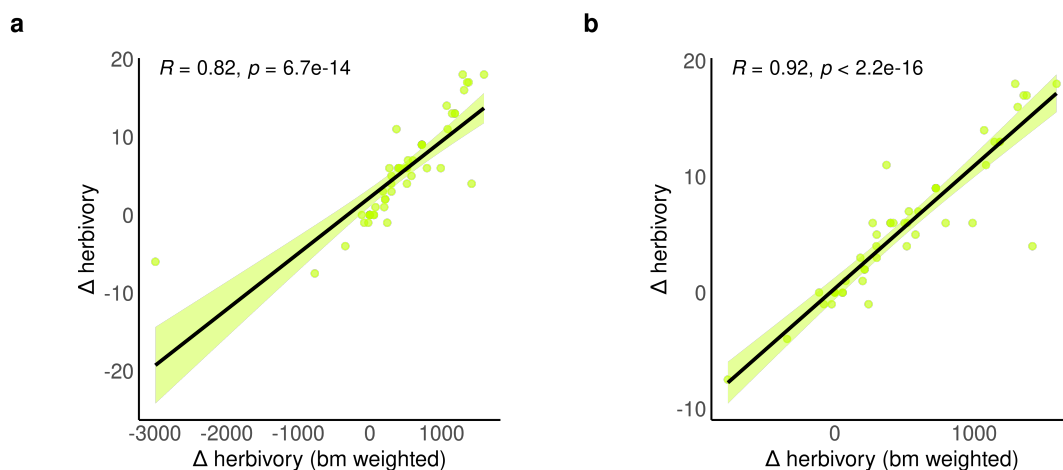
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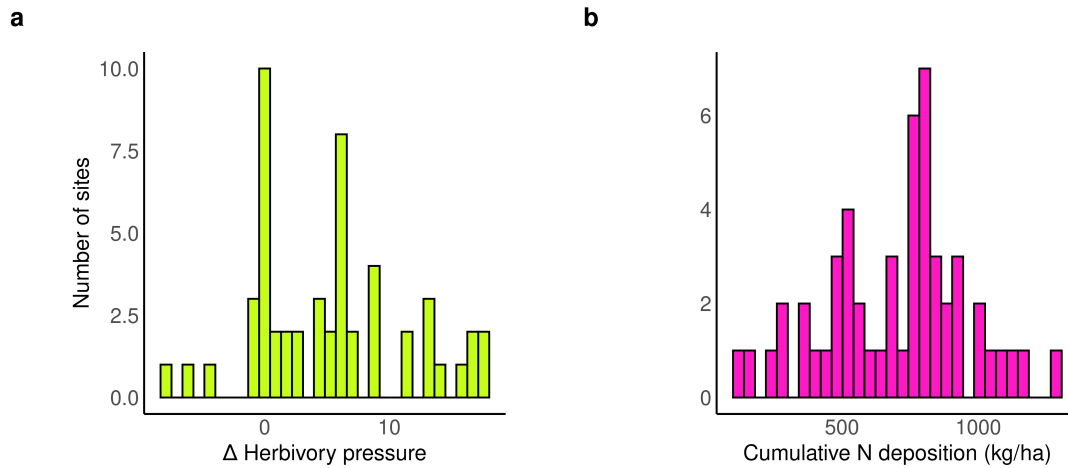
Supplementary Figure 4: **Counterfactual plots of the association between changes in herbivore pressure and species richness change/exchange ratio under low and high N-deposition.** Counterfactuals are depicted at the 10th (348 kg/ha; left) and 90th (1010 kg/ha; right) percentile of cumulative N-deposition in the data. The negative slope for the association with species richness became more pronounced under higher N-deposition, yet the interaction effect was statistically uncertain (beta = -2.83, se = 6.66, 95% CI [-15.97, 9.80]). Species exchange ratio was higher under high N-deposition and low herbivory than under low N-deposition and low herbivory. The association between herbivory and species exchange ratio weakened under high N-deposition, but the interactive effect was statistically uncertain (beta = -0.03, se = 0.02, 95% CI[-0.06, -0.002]). The results reveal that especially under low N deposition herbivore pressure is associated with high number of both species losses and gains (no net change in richness, but up to 70% of species changed), while at high N deposition herbivore pressure is associated with more species lost than gained (richness tends to decrease by up to 25 species, max 55% of species changed), yet these results remain statistically unclear. All models with n=52 independent resurvey sites. Lines and ribbons represent the posterior mean line and the 95% credible interval. Dashed lines represent statistically unclear relationships. Rugs at figure bottom in **a** and **b** depict the marginal distribution of the predictor. Cumulative N-deposition is calculated between the baseline and resurvey year per site.



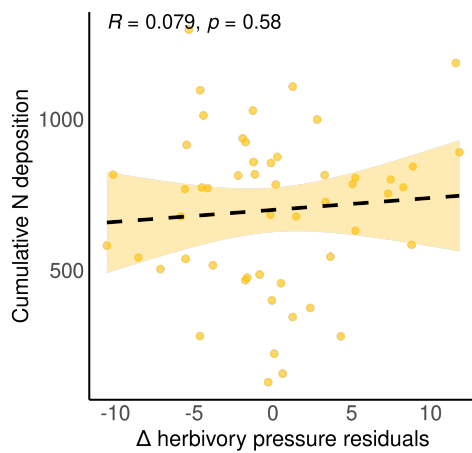
Supplementary Figure 5: **Differences in N-number depending on a, threatened and b, native status.** The box and violin plots show that **a**, species threatened on a national Red List and **b**, native species have lower Ellenberg N-values than non-threatened and non-native species across sites, respectively. Boxplots bound the interquartile range (IQR) divided by the median and whiskers extend up to a maximum of 1.5 x IQR beyond the box. Note threatened and native classifications depend on the respective country, hence one species may be native / threatened in a given country but not in another. Sample size (n) is indicated across sites; n can be higher than the total number of species in our data set as classifications count cumulatively across sites. Our statistical model evaluates differences in N-number at the site level by including a random intercept for study site (Supplementary Table 38 and 39).



Supplementary Figure 6: **Relationship between changes in herbivory pressure and body-mass weighted herbivory pressure with a, the full range of values and b, an outlier value removed.** The lines and ribbons represent the posterior mean line and the 95% credible interval. n=52 independent resurvey sites. R is Pearson's rho correlation coefficient.



Supplementary Figure 7: **Histogram of herbivore pressure and N-deposition across forest sites.**



Supplementary Figure 8: **Conditional association between cumulative N-deposition and changes in herbivore pressure.** The line and ribbon represent the posterior mean line and the 95% credible interval for the conditional association between N-deposition and herbivory change in the interaction models. On the x-axis are the partial residuals of herbivore pressure change, namely the variation left unexplained by the other variables in the model (inter-census time span and site area).  $R$  is Pearson's rho correlation coefficient,  $p$  is the p-value.

## Supplementary Tables

### Supplementary Table 1. Study site info.

Supplementary Table 1: **Dataset ID, country, site name, year of the baseline survey and resurvey** [when one survey (baseline or resurvey) was carried out over several years, the list shows the earliest baseline survey and the latest resurvey in which all vegetation layers were sampled] **and coordinates**.

Dataset		Site name	Baseline	Resurvey	Lat	Long
ID	Country		yr	yr		
1	Belgium	Meerdaalwoud	1954	2000	50.799	4.708
2	Sweden	Dalby	1935	1976	55.692	13.330
3	Sweden	Dalby	1976	2002	55.692	13.330
4	Germany	Elbe-Weser	1986	2008	53.552	8.984
5	Czech Republic	Děvín Wood	1953	2002	48.867	16.630
6	Czech Republic	Milovice Wood	1953	2006	48.838	16.690
7	Czech Republic	Rychlebské hory Mts.	1942	1998	50.267	17.083
8	United Kingdom	Wytham Woods	1974	1999	51.773	-1.334
9	Germany	Göttingen, SFB	1980	2001	51.530	10.048
10	Germany	Göttingen, Carici-Fagetum	1960	2011	51.333	9.820
11	Germany	Göttingen, Hordelymo-Fagetum	1960	2009	51.556	10.019
12	Austria	Zöbelboden	1993	2005	46.840	14.440
13	Hungary	Heves	1989	2008	47.988	20.501
14	Germany	Brandenburg	1962	2012	52.059	13.857
15	Slovakia	Slovakia, South-West	1966	2007	48.398	17.341
16	Slovakia	Slovakia, Central	1964	2005	48.258	19.378
17	Slovakia	Slovakia, North-East	1965	2006	49.215	21.850
18	Czech Republic	České Středohoří	1965	2012	50.586	14.116
19	Czech Republic	Krumlov Wood	1964	2012	49.053	16.384
20	Czech Republic	Hodonínská Důbrava	1965	2012	48.882	17.104
21	Czech Republic	Ždánice Wood	1959	2012	49.099	17.030



22	Poland	Białowieża	1966	2012	52.700	23.870
23	Sweden	Skåne	1983	2014	55.881	13.719
24	Hungary	Zselic	1958	2018	46.295	17.861
25	Germany	Göttingen, Hünstollen	1992	2002	51.578	10.047
26	Poland	Bazaltowa Mt	1992	2010	51.008	16.132
27	Poland	Buki Sudeckie beech forest	1990	2014	50.943	16.028
28	Poland	Trzebnickie Hills	1962	2011	51.262	16.816
29	Germany	Prignitz	1954	2014	53.080	12.280
30	Germany	Brandenburg Nord	1963	2014	53.064	13.471
31	Germany	Brandenburg Süd	1960	2014	51.792	13.801
32	Germany	Unteres Spreewald-Randgebiet	1965	2010	52.088	13.934
33	Slovenia	Strmec	1983	2015	45.622	14.819
34	Slovenia	Rajhenavski Rog	1983	2015	45.663	15.012
35	Slovenia	Pecka	1983	2015	45.755	14.999
36	France	Compiègne forest	1970	2015	49.364	2.887
37	Hungary	Bakony és Gerecse	1955	2015	47.202	18.075
38	Hungary	Bükkalja és Dél-Cserehát	1953	2014	47.909	20.399
39	Hungary	Gödöllői-dombság	1950	2014	47.589	19.396
40	Hungary	Mátra-Bükk-Zemplén	1958	2015	48.194	20.903
41	Hungary	Őrség	1954	2014	46.916	16.567
42	Hungary	Visegrádi-hegység	1953	2015	47.730	18.963
43	Germany	Großer Staufenberg	1988	1998	51.625	10.636
44	Germany	Riedried	1986	2018	49.033	8.230
45	Czech Republic	Śnieżnik Massif	1955	2013	50.231	16.917
46	Germany	Göttinger Wald (Fliehburgen)	1955	2015	51.576	10.008
47	Poland	N-E Puszcza Niepołomska	1966	2019	50.093	20.373
48	Ukraine	Zakarpatska oblast	1935	1997	48.400	23.100
49	Ukraine	Zakarpatska oblast	1935	1997	48.400	23.100
50	Ukraine	Zakarpatska oblast	1935	1997	48.400	23.100
51	Poland	Riparian forests of the Oder Valley (near Wrocław)	1959	2019	50.930	17.350
52	Poland	Dolina Wapienicy (Wapienica Valley)		1991	2020	49.757

**Supplementary Table 2. Dataset.**

Supplementary Table 2: **Data table with key variables.** Shown here is the dataset ID; HP = change in herbivore pressure; Cum N-dep = cumulative N-deposition; RL% = % change in red list species/; Non-native % = % change in Non-native species; SR = change in species richness; herb cover; shrub cover; CWM-N = change in community weighted mean N value; Man 1800 = management in year 1800 (CWS = coppicing with standards; HF = high forest), Mgmt change = management change between baseline and resurvey.

Dataset ID	Δ HP	Cum Ndep	Δ RL %	Δ Nonnative %	Δ SR	Δ Herb cover	Δ Shrub cover	CWM-N	Man 1800	Mgmt change
1	0.0	1295.51	0.00	5.29	-4	-66.67	-11.90	0.14	CWS	Decline
2	6.0	544.46	5.94	2.20	-21	-14.14	-17.88	0.18	HF	Similar
3	6.0	630.31	-3.61	3.06	5	-46.96	-3.90	-0.07	HF	Similar
4	0.0	503.80	-0.31	0.54	26	-78.76	-12.73	-0.03	CWS / HF	Similar
5	6.0	1107.00	-3.45	-0.10	-93	-56.30	0.52	0.59	CWS	Decline
6	18.0	1185.39	-5.85	11.13	-32	-36.41	-19.72	0.89	CWS	Decline
7	6.0	1028.09	0.59	0.59	-33	-94.05	1.44	-0.22	HF	Similar
8	11.0	583.97	1.29	0.00	-18	24.87	NA	-0.11	CWS	Similar
9	0.0	456.89	0.03	0.00	-2	93.60	18.02	0.06	CWS	Similar
10	2.0	1095.38	-3.82	0.90	-15	46.47	26.39	0.27	CWS	Similar
11	2.0	1011.71	0.15	0.15	-13	10.86	8.07	0.20	CWS	Similar
12	0.0	223.66	1.53	0.00	4	-46.84	0.01	0.13	HF	Similar
13	0.0	344.98	-0.83	0.00	-34	NA	NA	0.17	HF	Similar
14	9.0	935.83	1.76	2.13	21	37.56	2.19	0.02	CWS / HF	Similar
15	7.0	783.12	0.83	2.40	-9	-3.06	3.50	0.22	CWS / HF	Similar
16	3.0	773.06	-0.62	0.67	-4	-3.90	5.17	0.30	CWS	Similar
17	3.0	770.90	0.00	1.52	-2	-24.73	-4.75	0.13	CWS / HF	Similar
18	7.0	874.61	-1.32	4.74	-10	-34.42	6.31	0.83	CWS / HF	Decline
19	18.0	890.17	-1.70	11.99	90	-24.56	-3.97	0.65	CWS	Similar
20	6.0	854.62	0.96	1.90	25	14.36	9.57	0.15	CWS / HF	Similar
21	6.0	923.88	-2.07	8.57	4	-51.24	0.73	0.38	CWS / HF	Similar

22	4.0	812.93	0.00	0.00	-7	-3.89	19.05	0.14	HF	Similar
23	4.0	516.31	-0.60	4.94	-9	-23.27	-1.55	0.11	CWS / HF	Similar
24	11.0	998.39	0.00	2.04	-33	-95.54	-33.20	0.40	HF	Similar
25	0.0	157.96	0.10	-0.73	-13	-15.31	14.21	-0.02	CWS	Similar
26	5.0	281.30	1.07	1.07	43	13.88	0.87	0.28	CWS	Similar
27	4.0	375.06	-1.64	1.12	35	31.91	4.12	-0.08	HF	Decline
28	-7.5	815.47	0.00	2.49	4	-52.73	-14.28	-0.26	HF	Decline
29	5.0	914.52	-0.70	2.61	11	-47.45	-1.32	0.18	CWS / HF	Similar
30	9.0	817.16	-3.14	1.76	4	22.67	15.14	0.40	CWS / HF	Decline
31	9.0	857.72	-0.44	1.52	44	26.20	4.45	0.60	CWS / HF	Decline
32	9.0	725.61	-0.83	2.50	37	-10.14	-0.28	0.38	HF	Similar
33	0.0	485.57	2.71	0.00	-35	-37.86	0.59	0.08	HF	Similar
34	0.0	474.97	2.41	0.00	-16	-46.00	13.56	-0.08	HF	Similar
35	0.0	467.00	0.00	0.00	-21	-75.62	9.51	-0.08	HF	Similar
36	1.0	677.73	0.37	1.46	39	66.96	10.13	0.29	HF	Similar
37	17.0	842.89	1.94	2.26	-51	-60.98	-21.79	0.66	HF	Decline
38	14.0	805.98	-0.79	1.89	-98	-93.10	-24.73	0.78	HF	Similar
39	13.0	814.59	-1.12	2.04	-21	-24.21	5.87	0.60	HF	Decline
40	17.0	774.21	-3.32	1.52	-71	-49.48	-2.77	0.28	HF	Similar
41	13.0	784.58	-1.36	1.84	-77	-56.74	-1.79	1.23	HF	Similar
42	16.0	800.16	-0.48	0.60	-35	-35.65	0.00	0.55	HF	Decline
43	-1.0	129.69	2.56	0.12	-4	-1.41	2.37	-0.10	CWS	Similar
44	1.0	399.87	-1.43	1.85	18	-60.40	14.81	0.03	CWS	Similar
45	13.0	753.30	1.64	-0.60	-36	-2.41	4.32	-0.57	HF	Similar
46	0.0	768.20	0.34	-0.18	-42	-0.73	22.34	0.09	CWS	Similar
47	6.0	683.00	-0.18	-4.51	16	40.37	19.62	-0.08	HF	Similar
48	-6.0	581.37	0.48	0.48	-19	-63.55	20.75	0.29	HF	Similar
49	-4.0	541.78	0.10	0.05	-8	-74.17	22.85	0.08	HF	Similar
50	-1.0	537.33	0.00	0.00	18	-28.19	4.26	-0.09	HF	Similar

51	6.0	677.41	0.58	6.19	9	11.22	-0.27	0.03	HF	Similar
52 Similar	-1.0	282.02	-1.14		-0.21	12	-13.08		-13.09	0.02 HF

**Supplementary Table 3 - 11.** Model summaries for Figure 2: Herbivory and shrub, herb and tree layer cover changes.

Supplementary Table 3: Summary of the model testing the association between changes in herbivory and shrub cover (Figure 2a). Parameter estimates, their standard error (SE) and 95% credible interval (CI). Both the response and predictor variables were scaled.

Predictor	Slope estimate	SE	lower 95% CI	upper 95% CI
Intercept	-0.01	0.14	-0.28	0.25
Herbivore pressure	-0.42	0.17	-0.76	-0.10
Baseline herbivory	0.14	0.15	-0.17	0.42
Time span	0.14	0.16	-0.17	0.45
Site area (log)	0.00	0.16	-0.31	0.33

Supplementary Table 4: Summary of the model testing the association between changes in herbivory and herb cover (Figure 2b). Parameter estimates, their standard error (SE) and 95% credible interval (CI). Both the response and predictor variables were scaled.

Predictor	Slope estimate	SE	lower 95% CI	upper 95% CI
Intercept	0.01	0.14	-0.27	0.28
Herbivore pressure	-0.02	0.17	-0.37	0.32
Baseline herbivory	-0.09	0.16	-0.41	0.22
Time span	-0.27	0.17	-0.59	0.06
Site area (log)	0.12	0.17	-0.23	0.46

Supplementary Table 5: Summary of the model testing the association between changes in herbivory and tree cover (Figure 2c). Parameter estimates, their standard error (SE) and 95% credible interval (CI). Both the response and predictor variables were scaled.

Predictor	Slope estimate	SE	lower 95% CI	upper 95% CI
Intercept	-0.01	0.14	-0.30	0.28
Herbivore pressure	0.13	0.18	-0.22	0.47
Baseline herbivory	0.12	0.17	-0.20	0.44
Time span	0.09	0.16	-0.24	0.41
Site area (log)	0.05	0.17	-0.29	0.38

Supplementary Table 6: Summary of model testing the association between changes in herbivory and shrub layer cover, after accounting for forest management change. Parameter estimates, their standard error (SE) and 95% credible interval (CI). Both the response and predictor variables were scaled.

Predictor	Slope estimate	SE	lower 95% CI	upper 95% CI
Intercept	0.061	0.154	-0.243	0.368
Herbivore pressure	-0.379	0.176	-0.725	-0.029
Baseline herbivory	0.168	0.153	-0.136	0.469
Time span	0.160	0.161	-0.148	0.481
Site area (log)	0.003	0.157	-0.306	0.306
Mgmt change:decline (delta)		-0.364	0.348	-1.037 0.318

Supplementary Table 7: Summary of model testing the association between changes in herbivory and shrub layer cover, after accounting for historical forest management. Parameter estimates, their standard error (SE) and 95% credible interval (CI). Both the response and predictor variables were scaled.

Predictor	Slope estimate	SE	lower 95% CI	upper 95% CI
Intercept	-0.254	0.218	-0.684	0.179
Herbivore pressure	-0.385	0.177	-0.738	-0.034
Baseline herbivory	0.143	0.155	-0.156	0.450
Time span	0.223	0.169	-0.107	0.555
Site area (log)	-0.121	0.235	-0.595	0.335
Mgmt: CWS/HF	0.472	0.508	-0.538	1.467
Mgmt: CWS	0.500	0.347	-0.168	1.169

Supplementary Table 8: Summary of model testing the association between changes in herbivory and herb layer cover, after accounting for forest management change. Parameter estimates, their standard error (SE) and 95% credible interval (CI). Both the response and predictor variables were scaled.

Predictor	Slope estimate	SE	lower 95% CI	upper 95% CI
Intercept	0.006	0.171	-0.330	0.341
Herbivore pressure	-0.017	0.181	-0.384	0.329
Baseline herbivory	-0.092	0.167	-0.428	0.239
Time span	-0.265	0.169	-0.603	0.064
Site area (log)	0.115	0.178	-0.227	0.461
Mgmt change:decline (delta)		0.000	0.370	-0.709 0.711

Supplementary Table 9: Summary of model testing the association between changes in herbivory and herb layer cover, after accounting for historical forest management. Parameter estimates, their standard error (SE) and 95% credible interval (CI). Both the response and predictor variables were scaled.

Predictor	Slope estimate	SE	lower 95% CI	upper 95% CI
Intercept	-0.196	0.224	-0.627	0.245

Herbivore pressure	-0.023	0.190	-0.407	0.346
Baseline herbivory	-0.088	0.161	-0.398	0.239
Time span	-0.177	0.180	-0.532	0.164
Site area (log)	0.085	0.251	-0.418	0.565
Mgmt: CWS/HF	0.246	0.552	-0.821	1.360
Mgmt: CWS	0.545	0.373	-0.210	1.293

Supplementary Table 10: Summary of model testing the association between changes in herbivory and tree layer cover, after accounting for forest management change. Parameter estimates, their standard error (SE) and 95% credible interval (CI). Both the response and predictor variables were scaled.

Predictor	Slope estimate	SE	lower 95% CI	upper 95% CI
Intercept	-0.152	0.168	-0.485	0.177
Herbivore pressure	0.059	0.178	-0.291	0.408
Baseline herbivory	0.055	0.166	-0.269	0.383
Time span	0.044	0.163	-0.278	0.354
Site area (log)	0.033	0.172	-0.316	0.369
Mgmt change:decline (delta)		0.678	0.373	-0.033 1.410

Supplementary Table 11: Summary of model testing the association between changes in herbivory and tree layer cover, after accounting for historical forest management. Parameter estimates, their standard error (SE) and 95% credible interval (CI). Both the response and predictor variables were scaled.

Predictor	Slope estimate	SE	lower 95% CI	upper 95% CI
Intercept	0.011	0.230	-0.443	0.459
Herbivore pressure	0.025	0.194	-0.338	0.418
Baseline herbivory	0.076	0.173	-0.253	0.411
Time span	0.105	0.180	-0.252	0.456
Site area (log)	0.282	0.254	-0.226	0.788
Mgmt: CWS/HF	-0.572	0.566	-1.683	0.534
Mgmt: CWS	0.354	0.366	-0.379	1.087

Supplementary Table 12 - 15. Model summaries for Figure 3: Herbivory, species richness and temporal turnover.

Supplementary Table 12: Summary of the model testing the association between changes in herbivory and spp. richness (Figure 3a). Parameter estimates, their standard error (SE) and 95% credible interval (CI). Both the response and predictor variables were scaled.

Predictor	Slope estimate	SE	lower 95% CI	upper 95% CI
Intercept	0.00	0.14	-0.27	0.27

Herbivore pressure	-0.23	0.17	-0.56	0.10
Baseline herbivory	0.02	0.14	-0.27	0.31
Time span	-0.28	0.16	-0.59	0.04
Site area (log)	0.28	0.16	-0.04	0.60

Supplementary Table 13: Summary of the model testing the association between herbivory change and spp. exchange ratio (Figure 3b). Parameter estimates, their standard error (SE) and 95% credible interval (CI). Both the response and predictor variables were scaled.

Predictor	Slope estimate	SE	lower 95% CI	upper 95% CI
Intercept	0.001	0.117	-0.228	0.232
Herbivore pressure	0.518	0.141	0.240	0.790
Baseline herbivory	0.036	0.122	-0.207	0.279
Time span	0.321	0.133	0.057	0.587
Site area (log)	-0.248	0.137	-0.510	0.023

Supplementary Table 14: Summary of model testing the association between changes in herbivory and species richness, after accounting for forest management change. Parameter estimates, their standard error (SE) and 95% credible interval (CI). Both the response and predictor variables were scaled.

Predictor	Slope estimate	SE	lower 95% CI	upper 95% CI
Intercept	0.011	0.163	-0.315	0.327
Herbivore pressure	-0.223	0.173	-0.555	0.114
Baseline herbivory	0.022	0.148	-0.260	0.310
Time span	-0.270	0.162	-0.591	0.048
Site area (log)	0.275	0.167	-0.057	0.606
Mgmt change:decline (delta)		0.065	0.373	-0.662 0.810

Supplementary Table 15: Summary of model testing the association between changes in herbivory and species exchange ratio, after accounting for forest management change. Parameter estimates, their standard error (SE) and 95% credible interval (CI). Both the response and predictor variables were scaled.

Predictor	Slope estimate	SE	lower 95% CI	upper 95% CI
Intercept	-0.048	0.133	-0.317	0.210
Herbivore pressure	0.495	0.146	0.207	0.783
Baseline herbivory	0.018	0.127	-0.234	0.268
Time span	0.308	0.136	0.045	0.578
Site area (log)	-0.251	0.141	-0.529	0.022
Mgmt change:decline (delta)		0.242	0.311	-0.373 0.855

**Supplementary Table 16 - 23. Model summaries for Figure 4: Herbivory and community composition.**

Supplementary Table 16: Summary of the model testing the association between changes in herbivory and CWM N number (Figure 4a). Parameter estimates, their standard error (SE) and 95% credible interval (CI). Both the response and predictor variables were scaled.

Predictor	Slope estimate	SE	lower 95% CI	upper 95% CI
Intercept	-0.001	0.117	-0.226	0.229
Herbivore pressure	0.432	0.149	0.138	0.725
Baseline herbivory	0.011	0.127	-0.228	0.264
Time span	0.162	0.137	-0.107	0.431
Site area (log)	0.116	0.144	-0.169	0.401

Supplementary Table 17: Summary of the model testing the association between changes in herbivory and % non-native spp. (Figure 4c). Parameter estimates, their standard error (SE) and 95% credible interval (CI). Both the response and predictor variables were scaled.

Predictor	Slope estimate	SE	lower 95% CI	upper 95% CI
Intercept	0.0025	0.1331	-0.2593	0.2614
Herbivore pressure	0.3665	0.1651	0.0452	0.6916
Baseline herbivory	-0.0868	0.1370	-0.3554	0.1816
Time span	0.0463	0.1523	-0.2549	0.3460
Site area (log)	0.0122	0.1591	-0.3047	0.3110

Supplementary Table 18: Summary of the model testing the association between changes in herbivory and % red-listed spp. (Figure 4e). Parameter estimates, their standard error (SE) and 95% credible interval (CI). Both the response and predictor variables were scaled.

Predictor	Slope estimate	SE	lower 95% CI	upper 95% CI
Intercept	0.0028	0.1408	-0.2854	0.2848
Herbivore pressure	-0.1929	0.1690	-0.5250	0.1367
Baseline herbivory	-0.0667	0.1458	-0.3545	0.2200
Time span	-0.0690	0.1534	-0.3742	0.2347
Site area (log)	-0.1379	0.1652	-0.4625	0.1941

Supplementary Table 19: Summary of the model testing the association between changes in herbivory and % small-ranged spp. (Figure 4g). Parameter estimates, their standard error (SE) and 95% credible interval (CI).

Both the response and predictor variables were scaled.

Predictor	Slope estimate	SE	lower 95% CI	upper 95% CI
Intercept	0.0047	0.1356	-0.2564	0.2710



Herbivore pressure	-0.2463	0.1684	-0.5731	0.0860
Baseline herbivory	-0.1852	0.1471	-0.4743	0.1032
Time span	-0.0521	0.1606	-0.3592	0.2671
Site area (log)	-0.1261	0.1607	-0.4433	0.1923

Supplementary Table 20: Summary of model testing the association between changes in herbivory and CWM-N, after accounting for forest management change. Parameter estimates, their standard error (SE) and 95% credible interval (CI). Both the response and predictor variables were scaled.

Predictor	Slope estimate	SE	lower 95% CI	upper 95% CI
Intercept	-0.123	0.134	-0.385	0.142
Herbivore pressure	0.376	0.142	0.102	0.660
Baseline herbivory	-0.035	0.124	-0.277	0.216
Time span	0.129	0.132	-0.130	0.389
Site area (log)	0.108	0.138	-0.168	0.379
Mgmt change:decline (delta)		0.578	0.315	-0.054 1.199

Supplementary Table 21: Summary of model testing the association between changes in herbivory and % non-native spp., after accounting for forest management change. Parameter estimates, their standard error (SE) and 95% credible interval (CI). Both the response and predictor variables were scaled.

Predictor	Slope estimate	SE	lower 95% CI	upper 95% CI
Intercept	-0.077	0.155	-0.385	0.227
Herbivore pressure	0.331	0.170	-0.004	0.669
Baseline herbivory	-0.115	0.143	-0.386	0.174
Time span	0.022	0.153	-0.275	0.326
Site area (log)	0.004	0.163	-0.311	0.334
Mgmt change:decline (delta)		0.367	0.361	-0.341 1.079

Supplementary Table 22: Summary of model testing the association between changes in herbivory and % red-listed spp., after accounting for forest management change. Parameter estimates, their standard error (SE) and 95% credible interval (CI). Both the response and predictor variables were scaled.

Predictor	Slope estimate	SE	lower 95% CI	upper 95% CI
Intercept	0.130	0.159	-0.177	0.432
Herbivore pressure	-0.134	0.174	-0.474	0.216

Baseline herbivory	-0.018	0.147	-0.308	0.274
Time span	-0.029	0.159	-0.338	0.288
Site area (log)	-0.130	0.162	-0.444	0.190
Mgmt change:decline (delta)		-0.614	0.367	-1.350 0.103

Supplementary Table 23: Summary of model testing the association between changes in herbivory and % small-ranged spp., after accounting for forest management change. Parameter estimates, their standard error (SE) and 95% credible interval (CI). Both the response and predictor variables were scaled.

Predictor	Slope estimate	SE	lower 95% CI	upper 95% CI
Intercept	0.156	0.154	-0.143	0.457
Herbivore pressure	-0.174	0.166	-0.506	0.146
Baseline herbivory	-0.127	0.139	-0.400	0.142
Time span	-0.012	0.153	-0.312	0.286
Site area (log)	-0.112	0.158	-0.422	0.193
Mgmt change:decline (delta)		-0.736	0.356	-1.446 -0.030

Supplementary Table 24 - 25. Model summaries for Supplementary Figure 2: Shrub cover versus non-native, nitrophilous spp.

Supplementary Table 24: Summary of the model testing the association between changes in shrub cover and % non-native spp. Parameter estimates, their standard error (SE) and 95% credible interval (CI). Both the response and predictor variables were scaled.

Predictor	Slope estimate	SE	lower 95% CI	upper 95% CI
Intercept	-0.0106	0.1369	-0.2834	0.2594
Shrub cover	-0.3696	0.1383	-0.6367	-0.0913
Time span	0.1261	0.1482	-0.1595	0.4160
Site area (log)		0.0850	0.1533	-0.2121 0.3874

Supplementary Table 25: Summary of the model testing the association between changes in shrub cover and CWM N number. Parameter estimates, their standard error (SE) and 95% credible interval (CI). Both the response and predictor variables were scaled.

Predictor	Slope estimate	SE	lower 95% CI	upper 95% CI
Intercept	-0.0263	0.1256	-0.2715	0.2205
Shrub cover	-0.1939	0.1314	-0.4557	0.0590

	Time span	0.2763	0.1409	-0.0126	0.5518
Site area (log)	0.2557		0.1423	-0.0147	0.5450

**Supplementary Table 26 - 29.** Model summaries for Supplementary Figure 3: N-deposition and community composition.

Supplementary Table 26: Summary of the model testing the association between cumulative N-deposition and the %-change in red-listed spp. (Supplementary Figure 3a). Parameter estimates, their standard error (SE) and 95% credible interval (CI). Both the response and predictor variables were scaled.

Predictor	Slope estimate	SE	lower 95% CI	upper 95% CI	
Intercept	0.00097	0.13410	-0.25931	0.26405	
N-dep	-0.45777	0.21303	-0.88617	-0.05272	
Time span	0.16616	0.19624	-0.21195	0.55649	
Site area (log)		-0.07654	0.15470	-0.38173	0.22986

Supplementary Table 27: Summary of the model testing the association between cumulative N-deposition and the %-change in non-native spp. (Supplementary Figure 3c). Parameter estimates, their standard error (SE) and 95% credible interval (CI). Both the response and predictor variables were scaled.

Predictor	Slope estimate	SE	lower 95% CI	upper 95% CI	
Intercept	-0.0010	0.1307	-0.2593	0.2533	
N-dep	0.5613	0.2041	0.1658	0.9601	
Time span	-0.2072	0.1904	-0.5818	0.1691	
Site area (log)		0.0053	0.1530	-0.2960	0.3019

Supplementary Table 28: Summary of the model testing the association between cumulative N-deposition and the %-change in small-ranged spp. (Supplementary Figure 3b). Parameter estimates, their standard error (SE) and 95% credible interval (CI). Both the response and predictor variables were scaled.

Predictor	Slope estimate	SE	lower 95% CI	upper 95% CI	
Intercept	0.00341	0.13545	-0.26353	0.27257	
N-dep	-0.37813	0.21241	-0.79709	0.04114	
Time span	0.12171	0.20231	-0.28083	0.51614	
Site area (log)		-0.09509	0.15906	-0.41251	0.21813

Supplementary Table 29: Summary of the model testing the association between cumulative N-deposition and the change in CWM N-number. (Supplementary Figure 3d). Parameter estimates, their standard error (SE) and 95% credible interval (CI). Both the response and predictor variables were scaled.

Predictor	Slope estimate	SE	lower 95% CI	upper 95% CI
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Intercept	-0.0017	0.1314	-0.2593	0.2582
N-dep	0.1685	0.2081	-0.2512	0.5776
Time span	0.1702	0.1936	-0.2068	0.5472
		Site area (log)	0.2327	0.1542
			-0.0727	0.5366

**Supplementary Table 30 - 37.** Model summaries for Figure 4: Interaction between herbivory and N-deposition.

Supplementary Table 30: Summary of the model testing the interactive effect between herbivore pressure and N-deposition on CWM N-number. (Figure 4b). Parameter estimates, their standard error (SE) and 95% credible interval (CI). Both the response and predictor variables were scaled.

Predictor	Slope estimate	SE	lower 95% CI	upper 95% CI
Intercept	-0.14346	0.13834	-0.41861	0.12963
Herbivore pressure	0.28525	0.15601	-0.01979	0.59231
N-dep	0.24089	0.19410	-0.14276	0.62363
Time span	0.10411	0.16984	-0.23513	0.44001
Site area (log)	0.12390	0.14429	-0.15784	0.41086
Herbivore:N-dep		0.32971	0.16528	0.00489 0.65462

Supplementary Table 31: Summary of the model testing the interactive effect between herbivore pressure and N-deposition on % non-native spp. (Figure 4d). Parameter estimates, their standard error (SE) and 95% credible interval (CI). Both the response and predictor variables were scaled.

Predictor	Slope estimate	SE	lower 95% CI	upper 95% CI
Intercept	-0.15823	0.14254	-0.43938	0.12451
Herbivore pressure	0.19529	0.16362	-0.12837	0.51561
N-dep	0.66243	0.20276	0.26629	1.06086
Time span	-0.26308	0.17790	-0.61263	0.08861
Site area (log)	-0.07403	0.15048	-0.37599	0.21962
Herbivore:N-dep		0.36221	0.17277	0.02477 0.70093

Supplementary Table 32: Summary of the model testing the interactive effect between herbivore pressure and N-deposition on % red- listed spp. (Figure 4f). Parameter estimates, their standard error (SE) and 95% credible interval (CI). Both the response and predictor variables were scaled.

Predictor	Slope estimate	SE	lower 95% CI	upper 95% CI
Intercept	0.16467	0.15405	-0.14038	0.46590
Herbivore pressure	0.01358	0.17541	-0.32855	0.36299
N-dep	-0.60393	0.21945	-1.03893	-0.17028

Time span	0.19537	0.19105	-0.18431	0.57162
Site area (log)	-0.06133	0.16282	-0.38160	0.26048
Herbivore:N-dep		-0.37769	0.18673	-0.74862 -0.00935

Supplementary Table 33: Summary of the model testing the interactive effect between herbivore pressure and N-deposition on % small-ranged spp. (Figure 4h). Parameter estimates, their standard error (SE) and 95% credible interval (CI). Both the response and predictor variables were scaled.

Predictor	Slope estimate	SE	lower 95% CI	upper 95% CI
Intercept	0.22165	0.15068	-0.07421	0.51683
Herbivore pressure	0.03988	0.17192	-0.29525	0.38004
N-dep	-0.56607	0.21418	-0.98972	-0.14858
Time span	0.14544	0.18769	-0.22306	0.51553
Site area (log)	-0.08430	0.15878	-0.39849	0.22959
Herbivore:N-dep		-0.50683	0.18215	-0.86508 -0.14563

Supplementary Table 34: Summary of model testing the interaction between changes in herbivory and Ndeposition on CWM-N, after accounting for forest management change. Parameter estimates, their standard error (SE) and 95% credible interval (CI). Both the response and predictor variables were scaled.

Predictor	Slope estimate	SE	lower 95% CI	upper 95% CI
Intercept	-0.261	0.151	-0.561	0.046
N-dep	0.113	0.205	-0.284	0.528
Herbivore pressure	0.234	0.163	-0.075	0.561
Baseline herbivory	-0.090	0.131	-0.351	0.168
Time span	0.148	0.174	-0.188	0.490
Site area (log)	0.142	0.144	-0.142	0.421
Mgmt change:decline (delta)	0.558	0.320	-0.084	1.186
Herbivore:N-dep		0.329	0.167	-0.003 0.655

Supplementary Table 35: Summary of model testing the interaction between changes in herbivory and Ndeposition on % non-native spp., after accounting for forest management change. Parameter estimates, their standard error (SE) and 95% credible interval (CI). Both the response and predictor variables were scaled.

Predictor	Slope estimate	SE	lower 95% CI	upper 95% CI
Intercept	-0.185	0.163	-0.511	0.135
N-dep	0.631	0.222	0.192	1.068
Herbivore pressure	0.158	0.176	-0.193	0.502
Baseline herbivory	-0.089	0.141	-0.366	0.190
Time span	-0.237	0.185	-0.601	0.125

Site area (log)	-0.065	0.154	-0.368	0.240
Mgmt change:decline (delta)	0.075	0.347	-0.609	0.756
Herbivore:N-dep		0.386	0.182	0.032 0.748

Supplementary Table 36: Summary of model testing the interaction between changes in herbivory and Ndeposition on % red-listed spp., after accounting for forest management change. Parameter estimates, their standard error (SE) and 95% credible interval (CI). Both the response and predictor variables were scaled.

Predictor	Slope estimate	SE	lower 95% CI	upper 95% CI
Intercept	0.230	0.173	-0.113	0.570
N-dep	-0.537	0.234	-0.997	-0.075
Herbivore pressure	0.019	0.184	-0.348	0.378
Baseline herbivory	-0.034	0.151	-0.326	0.263
Time span	0.186	0.196	-0.200	0.571
Site area (log)	-0.070	0.162	-0.388	0.250
Mgmt change:decline (delta)	0.358	0.362	-0.359	1.071
Herbivore:N-dep		-0.351	0.191	-0.728 0.025

Supplementary Table 37: Summary of model testing the interaction between changes in herbivory and Ndeposition on % small-ranged spp., after accounting for forest management change. Parameter estimates, their standard error (SE) and 95% credible interval (CI). Both the response and predictor variables were scaled.

Predictor	Slope estimate	SE	lower 95% CI	upper 95% CI
Intercept	0.311	0.164	-0.012	0.632
N-dep	-0.484	0.225	-0.930	-0.045
Herbivore pressure	0.023	0.174	-0.316	0.368
Baseline herbivory	-0.111	0.142	-0.388	0.165
Time span	0.154	0.189	-0.215	0.527
Site area (log)	-0.090	0.155	-0.396	0.216
Mgmt change:decline (delta)	-0.544	0.350	-1.232	0.139
Herbivore:N-dep		-0.447	0.181	-0.804 -0.092

Supplementary Table 38 - 39. Model summaries for Supplementary Figure 4: Differences in N-numbers.

Supplementary Table 38: Summary of the model testing for differences in N-number between threatened and non-threatened spp. (Supplementary Figure 4a). Parameter estimates, their standard error (SE) and 95% credible interval (CI). Both the response and predictor variables were scaled.

Predictor	Slope estimate	SE	lower 95% CI	upper 95% CI		
Intercept	5.34	0.09	5.17	5.51		
Threatened - Yes			-1.41	0.17	-1.73	-1.08

Supplementary Table 39: Summary of the model testing for differences in N-number between native and nonnative species. (Supplementary Figure 4b). Parameter estimates, their standard error (SE) and 95% credible interval (CI). Both the response and predictor variables were scaled.

Predictor	Slope estimate	SE	lower 95% CI	upper 95% CI	
Intercept	6.52	0.12	6.29	6.75	
Native - Yes		-1.25	0.10	-1.46	-1.05

Supplementary Table 40 - 43. Model summaries for changes in herbivory versus community composition, accounting for productivity.

Supplementary Table 40: Summary of the model testing the association between changes in herbivore pressure and CWM-N, with productivity measured as AP:PET as a covariate. Parameter estimates, their standard error (SE) and 95% credible interval (CI). Both the response and predictor variables were scaled.

Predictor	Slope estimate	SE	lower 95% CI	upper 95% CI	
Intercept	0.000	0.127	-0.247	0.256	
Herbivore pressure	0.420	0.151	0.117	0.722	
Baseline herbivory	0.016	0.128	-0.235	0.269	
Time span	0.173	0.148	-0.112	0.453	
Site area (log)	0.119	0.146	-0.166	0.406	
Productivity - AP:PET		0.032	0.136	-0.230	0.294

Supplementary Table 41: Summary of the model testing the association between changes in herbivore pressure and % non-native spp., with productivity measured as AP:PET as a covariate. Parameter estimates, their standard error (SE) and 95% credible interval (CI). Both the response and predictor variables were scaled.

Predictor	Slope estimate	SE	lower 95% CI	upper 95% CI	
Intercept	0.001	0.134	-0.266	0.260	
Herbivore pressure	0.348	0.173	0.011	0.688	
Baseline herbivory	-0.078	0.146	-0.379	0.208	
Time span	0.057	0.160	-0.265	0.368	
Site area (log)	-0.001	0.161	-0.319	0.315	
Productivity - AP:PET		0.059	0.150	-0.228	0.354

Supplementary Table 42: Summary of the model testing the association between changes in herbivore pressure and % red-listed spp., with productivity measured as AP:PET as a covariate. Parameter estimates, their standard error (SE) and 95% credible interval (CI). Both the response and predictor variables were scaled.

Predictor	Slope estimate	SE	lower 95% CI	upper 95% CI	
Intercept	0.005	0.146	-0.286	0.287	
Herbivore pressure	-0.187	0.181	-0.547	0.162	
Baseline herbivory	-0.070	0.159	-0.384	0.244	
Time span	-0.072	0.167	-0.396	0.254	
Site area (log)	-0.107	0.167	-0.440	0.215	
Productivity - AP:PET		-0.037	0.157	-0.349	0.263

Supplementary Table 43: Summary of the model testing the association between changes in herbivore pressure and % small-ranged spp., with productivity measured as AP:PET as a covariate. Parameter estimates, their standard error (SE) and 95% credible interval (CI). Both the response and predictor variables were scaled.

Predictor	Slope estimate	SE	lower 95% CI	upper 95% CI	
Intercept	0.005	0.143	-0.275	0.280	
Herbivore pressure	-0.239	0.176	-0.585	0.102	
Baseline herbivory	-0.182	0.149	-0.464	0.108	
Time span	-0.010	0.168	-0.343	0.315	
Site area (log)	-0.127	0.169	-0.469	0.202	
Productivity - AP:PET		0.057	0.160	-0.258	0.376

**Supplementary Table 44 - 47.** Model summaries for changes in herbivory versus community composition, accounting for tree cover

Supplementary Table 44: Summary of the model testing the association between changes in herbivore pressure and CWM-N, with tree cover as a covariate. Parameter estimates, their standard error (SE) and 95% credible interval (CI). Both the response and predictor variables were scaled.

Predictor	Slope estimate	SE	lower 95% CI	upper 95% CI	
Intercept	-0.018	0.121	-0.252	0.218	
Herbivore pressure	0.411	0.143	0.128	0.702	
Baseline herbivory	0.033	0.130	-0.226	0.279	
Time span	0.163	0.138	-0.114	0.428	
Site area (log)	0.135	0.142	-0.148	0.414	
Tree cover		0.172	0.127	-0.084	0.415



Supplementary Table 45: Summary of the model testing the association between changes in herbivore pressure and % non-native spp., with tree cover as a covariate. Parameter estimates, their standard error (SE) and 95% credible interval (CI). Both the response and predictor variables were scaled.

Predictor	Slope estimate	SE	lower 95% CI	upper 95% CI	
Intercept	-0.005	0.140	-0.281	0.270	
Herbivore pressure	0.353	0.168	0.020	0.685	
Baseline herbivory	-0.118	0.153	-0.420	0.180	
Time span	0.030	0.156	-0.281	0.336	
Site area (log)	0.000	0.162	-0.326	0.316	
Tree cover		0.000	0.140	-0.271	0.273

Supplementary Table 46: Summary of the model testing the association between changes in herbivore pressure and % red-listed spp., with tree cover as a covariate. Parameter estimates, their standard error (SE) and 95% credible interval (CI). Both the response and predictor variables were scaled.

Predictor	Slope estimate	SE	lower 95% CI	upper 95% CI	
Intercept	0.018	0.143	-0.260	0.297	
Herbivore pressure	-0.207	0.174	-0.557	0.125	
Baseline herbivory	-0.128	0.166	-0.461	0.201	
Time span	-0.088	0.160	-0.406	0.235	
Site area (log)	-0.176	0.169	-0.508	0.154	
Tree cover		0.023	0.150	-0.282	0.312

Supplementary Table 47: Summary of the model testing the association between changes in herbivore pressure and % non-native spp., with tree cover as a covariate. Parameter estimates, their standard error (SE) and 95% credible interval (CI). Both the response and predictor variables were scaled.

Predictor	Slope estimate	SE	lower 95% CI	upper 95% CI	
Intercept	0.020	0.141	-0.258	0.296	
Herbivore pressure	-0.241	0.173	-0.584	0.090	
Baseline herbivory	-0.205	0.161	-0.533	0.122	
Time span	-0.059	0.159	-0.382	0.254	
Site area (log)	-0.137	0.169	-0.468	0.196	
Tree cover		-0.066	0.146	-0.349	0.216

Supplementary Table 48 - 51. Model summaries for changes in herbivory versus community composition, excluding baseline herbivory.

Supplementary Table 48: Summary of the model testing the association between changes in herbivore pressure and CWM-N, excluding baseline herbivory. Parameter estimates, their standard error (SE) and 95% credible interval (CI). Both the response and predictor variables were scaled.

Predictor	Slope estimate	SE	lower 95% CI	upper 95% CI
Intercept	0.001	0.117	-0.227	0.231
Herbivore pressure	0.430	0.145	0.142	0.715
Time span	0.163	0.134	-0.104	0.433
Site area (log)		0.114	0.139	-0.167 0.392

Supplementary Table 49: Summary of the model testing the association between changes in herbivore pressure and % non-native spp., excluding baseline herbivory. Parameter estimates, their standard error (SE) and 95% credible interval (CI). Both the response and predictor variables were scaled.

Predictor	Slope estimate	SE	lower 95% CI	upper 95% CI
Intercept	-0.001	0.133	-0.258	0.259
Herbivore pressure	0.387	0.162	0.078	0.715
Time span	0.036	0.152	-0.262	0.336
Site area (log)		0.015	0.156	-0.287 0.315

Supplementary Table 50: Summary of the model testing the association between changes in herbivore pressure and % red-listed spp., excluding baseline herbivory. Parameter estimates, their standard error (SE) and 95% credible interval (CI). Both the response and predictor variables were scaled.

Predictor	Slope estimate	SE	lower 95% CI	upper 95% CI
Intercept	-0.003	0.141	-0.279	0.284
Herbivore pressure	-0.177	0.169	-0.508	0.168
Time span	-0.066	0.158	-0.374	0.255
Site area (log)		-0.135	0.167	-0.469 0.184

Supplementary Table 51: Summary of the model testing the association between changes in herbivore pressure and % small-ranged spp., excluding baseline herbivory. Parameter estimates, their standard error (SE) and 95% credible interval (CI). Both the response and predictor variables were scaled.

Predictor	Slope estimate	SE	lower 95% CI	upper 95% CI
Intercept	0.001	0.140	-0.278	0.274
Herbivore pressure	-0.193	0.171	-0.531	0.139
Time span	-0.062	0.160	-0.371	0.259
Site area (log)		-0.122	0.164	-0.448 0.203

## **Supplementary Information: Chapter 3**

### **Supplementary Material 2 Assessing rewilding interventions and progress in Europe**

#### **Authors:**

**Josiane Segar, Henrique Pereira, Raquel Filgeiras, Deli Saavedra,  
Alexandros Karamanlidis, Nestor Fernandez**

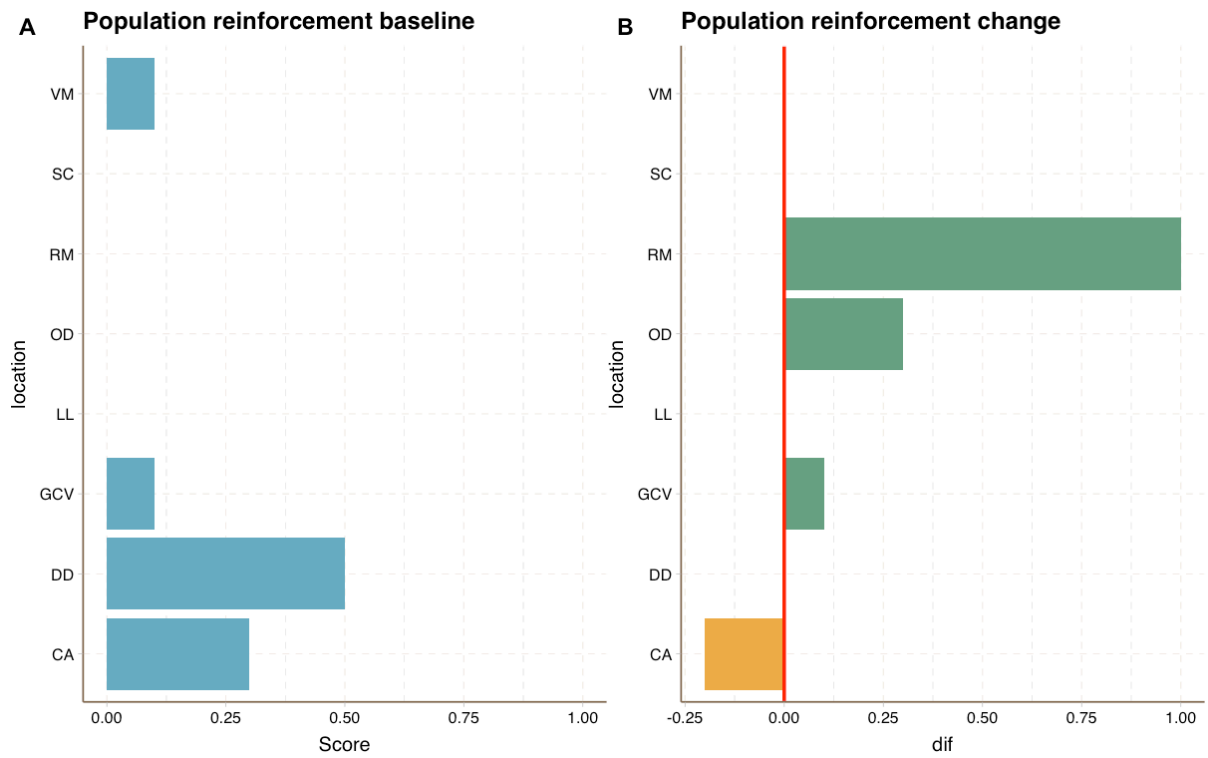
#### **Content:**

**Figure 1: Example summary figure for the workshop**

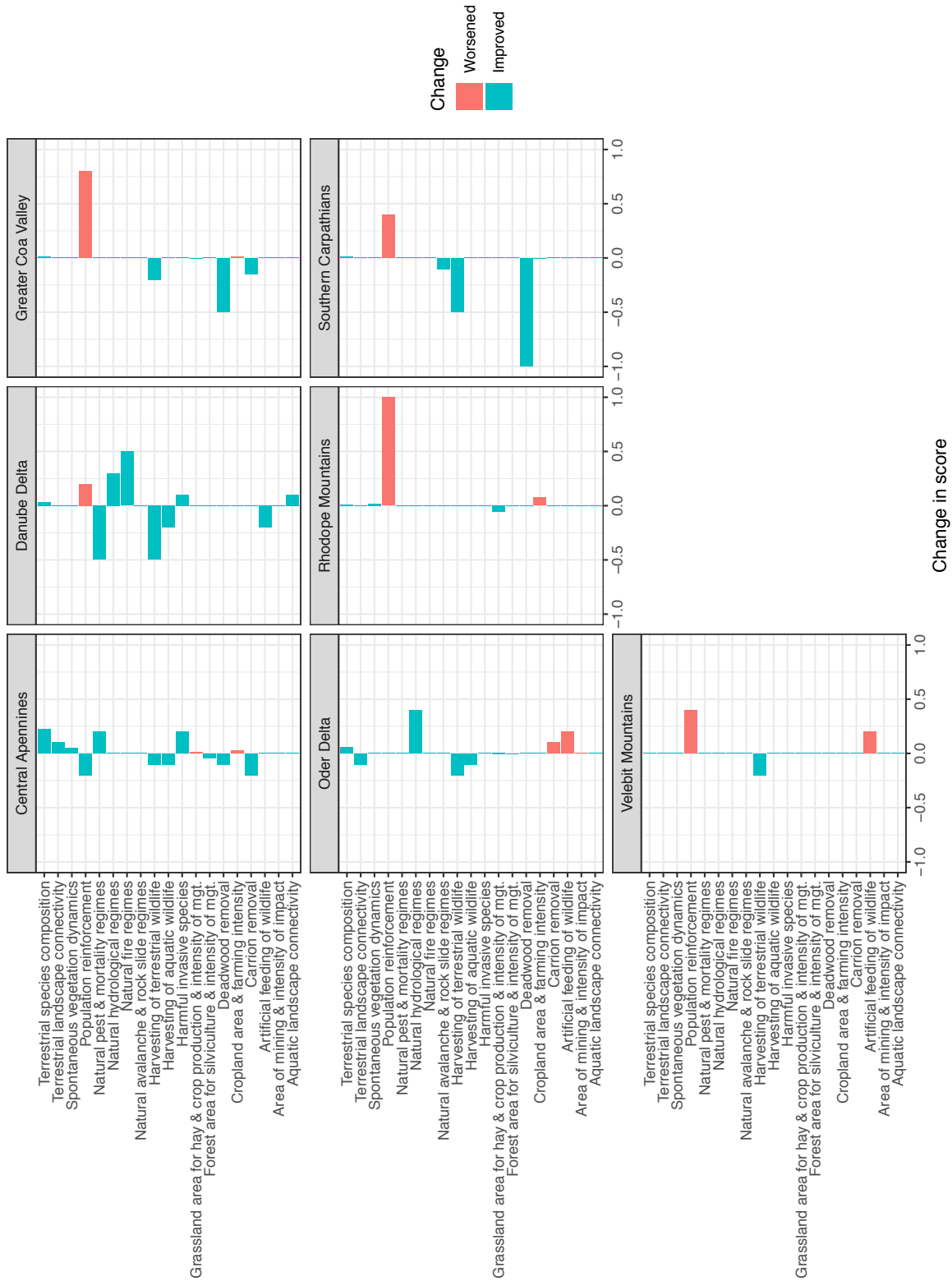
**Figure 2: Changes in indicator scores over time per site**

**Table 1: The full calibrated list of 19 indicators for baseline and current  
for all sites post-Delphi**

**Table 2: The updated indicators and their descriptions elicited from the  
Delphi Technique**



**Figure 1:** An example of the summary figure presented to the practitioners during the second iteration of scoring to stimulate discussion on the indicator and the method of scoring.



**Figure 2:** Indicators of rewilding progress (n = 19) and their change over time across rewilding sites. Human forcing indicators improve if the score decreased over time, whereas ecological integrity indicators improve if the score increased over time.

Indicator	CA_Baseline	CA_Current	GCV_Baseline	GCV_Current	DD_Baseline	DD_Current	RM_Baseline	RM_Current	OD_Baseline	OD_Current	VM_Baseline	VM_Current	SC_Baseline	SC_Current
Artificial feeding of wildlife	0.300	0.300	0.700	0.700	1.000	1.000	0.800	0.800	0.500	0.400	0.600	0.800	1.000	1.000
Population reinforcement	0.300	0.100	0.200	1.000	0.500	0.700	0.000	1.000	1.000	0.000	0.000	0.100	0.500	0.400
Cropland area & farming inter	0.090	0.120	0.028	0.036	0.000	0.000	0.138	0.213	0.109	0.109	0.120	0.120	0.006	0.004
Forest area for silviculture & intensity of mgt.	0.255	0.215	0.000	0.000	0.016	0.016	0.065	0.065	0.157	0.156	0.300	0.300	0.339	0.339
Grassland area for hay & crop production & intensity of	0.080	0.090	0.112	0.110	0.063	0.063	0.072	0.016	0.234	0.225	0.045	0.045	0.100	0.100
Area of mining & intensity of i	0.000	0.000	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.000	0.000	0.000	0.000
Harvesting of terrestrial wildlife	0.500	0.400	1.000	0.800	0.600	0.100	0.700	0.700	0.900	0.700	0.900	0.700	1.000	0.500
Harvesting of aquatic wildlife	0.400	0.300	0.800	0.800	1.000	0.800	0.600	0.600	0.900	0.800	0.500	0.500	0.800	0.800
Carriion removal	0.500	0.300	0.600	0.450	0.500	0.500	0.100	0.100	0.500	0.600	0.600	0.800	0.100	0.100
Deadwood removal	0.600	0.500	1.000	0.500	0.000	0.000	0.500	0.500	0.700	0.700	0.500	0.500	1.000	0.000
Natural avalanche & rock slide regimes	1.000	1.000	NA	NA	0.000	0.000	1.000	1.000	0.000	0.000	1.000	1.000	1.000	0.900
Natural fire regimes	0.000	0.000	0.000	0.000	0.000	0.500	0.000	0.000	0.000	0.000	0.000	0.000	0.500	0.500
Natural hydrological regimes	0.700	0.700	0.500	0.500	0.000	0.300	0.300	0.300	0.400	0.800	0.200	0.200	0.200	0.200
Natural pest & mortality regimes	0.600	0.800	1.000	1.000	1.000	0.500	0.300	0.300	0.500	0.500	0.500	0.500	0.500	0.500
Terrestrial landscape connectivity	0.600	0.700	0.500	0.500	0.500	0.500	0.750	0.750	0.600	0.500	0.900	0.900	1.000	1.000
Aquatic landscape connectivity	0.500	0.500	0.000	0.000	0.800	0.900	0.200	0.200	0.400	0.400	0.200	0.200	0.200	0.200
Harmful invasive species	0.600	0.800	0.500	0.500	0.500	0.600	0.500	0.500	0.600	0.600	0.900	0.900	0.500	0.500
Spontaneous vegetation dyna	0.582	0.628	0.002	0.001	1.060	1.060	0.040	0.061	0.023	0.024	1.075	1.075	0.005	0.005
Terrestrial species composition	0.249	0.475	0.580	0.594	0.427	0.461	0.464	0.473	0.494	0.549	0.494	0.494	0.889	0.903
Human forcing	0.303	0.232	0.444	0.440	0.368	0.298	0.267	0.369	0.390	0.389	0.407	0.447	0.434	0.324
Ecological integrity	0.434	0.580	0.417	0.420	0.424	0.486	0.410	0.415	0.356	0.408	0.544	0.544	0.593	0.587
Rewilding Score	0.303	0.445	0.232	0.236	0.268	0.341	0.301	0.262	0.217	0.249	0.323	0.301	0.335	0.397

**Table 1:** The full calibrated list of 19 indicators for baseline and current for all sites post-Delphi

<b>Human forcing</b>
<b>Artificial feeding of wildlife</b>
To what extent does artificial feeding in the site impact ecological processes, species communities and behaviour? Would these species survive or fundamentally alter their populations if the amount of feeding was changed? If there is legislation regarding feeding, and if so, how well implemented and enforced is it?
0 - no artificial feeding; 0.5 - some artificial feeding that has moderate levels of influence of species communities and population dynamics; 1 - High levels of feeding fundamentally changing ecological processes and species' communities
<b>Population reinforcement</b>
Have animals (scavengers, large herbivores, carnivores and their associated important prey species) been anthropogenically (re-)introduced into the system in the last years? Are managers or hunters regularly (i.e., every year) reinforcing wildlife populations by bringing individuals in from other populations? Consider not only the numbers of animals being introduced, but the effect these numbers are having on ecological communities and the system.
0 - no population reinforcement in the last period of assessment; 0.5 - species sporadically reinforced or reintroduced for conservation purposes; 1 - regular to intensive population reinforcements for the conservation of species that would otherwise decline, or reinforcement of non-declining populations for other purposes such as hunting
<b>Agricultural production</b>
Percentage of the total rewilding area devoted to cropland (data-driven) weighted by a factor of farming intensity (expert-based considering criteria like field size, pesticides, fertilizers, machinery, etc.)
0 - No harvested or fallow for at least 5 years (i.e., land abandonment); 0.5 - Cropped and harvested under traditional, extensive farming practices; 1 - Intensive harvesting, every year
<b>Forestry production</b>
Percentage of the total rewilding area devoted to production forestry (data-driven) weighted by a factor of forest management intensity (expert-based)
0 - No logging (i.e. unmanaged forest) for at least 5 years; 0.5 - Selective logging; 1 - Clear-cut logging (short rotation forestry)
<b>Grassland production</b>
Percentage of the total rewilding area devoted to managed grasslands (data-driven) weighted by a factor of intensity of production (expert-based, e.g., intensity of fertilization, frequency of mowing, intensity of domesticated livestock grazing)
0 - No harvested for at least 5 years (land abandonment); 0.5 - Mowed under traditional, extensive farming practices; 1 - Intensive harvesting or very high livestock stocking densities
<b>Mining</b>
Percentage of the total rewilding area devoted to production forestry (data-driven) weighted by a factor of forest management intensity (expert-based)
0 - No mining for at least 5 years; 0.5 - Mining with non-destructive production practices (e.g., artisanal mining) and strict regulation and mitigation of pollution; 1 - Intensive mining with destructive mining practices and clear evidence of degradation
<b>Harvesting of terrestrial wildlife</b>
To what extent is hunting allowed and practiced on the site? How is this affecting the species and their ecosystem? Consider the area of the site that is covered by hunting practices, the intensity of the hunting relative to the species population size and the ecological effect this is having on community dynamics and ecological processes. Consider poaching and illegal harvesting of wildlife if appropriate.
0 - No hunting or poaching; 0.5 - moderate level of hunting somewhat affecting the growth rates of wildlife populations, animal movements or other affected species in the community; 1 - very high levels of hunting relative to the population size greatly affecting the growth rates, population structure and / or species interactions.
<b>Harvesting of aquatic wildlife</b>
What is the intensity of fishing in the site? Consider the amount of extraction relative to the density of the aquatic species, the size of water bodies affected and the ecological impact this is having on system. Consider also illegal fishing and the effect this has on communities.
0 - No extractive fishing; 0.5 - fishing only in artificial ponds or moderate levels that have small effects on the growth rates of populations, animal movements or other affect species in the community; 1 - very high levels of fishing relative to the population size greatly affecting the growth rates, population structure and / or species interactions.
<b>Carrion removal</b>
Are carcasses left in the field? Consider wild animals dying of natural causes, livestock and hunted animals. If there is a legal obligation to remove these carcasses, is this well enforced or not? If carcasses are removed for feeding stations, this is still considered removal.
0 - carcasses from wild animals, livestock and hunted animals are always left in the field; 0.5 - carcasses of wildlife and hunted animals are left in the field, livestock are removed; 1 - all carcasses are removed from the field.
<b>Deadwood removal</b>
To what extent is deadwood (dead trees and woody debris) removed from the system? What effect is this having on the system, such as the composition and abundance of saproxylic species or on disturbance regimes?
0 - No deadwood removal; 0.5 - moderate levels of removal with some ecological effects on disturbance regimes, animal compositions or movements, or other processes; 1 - very high and systematic removal of deadwood
<b>Ecological integrity</b>

<b>Connectivity &amp; composition</b>
<b>Terrestrial landscape connectivity</b>
To what extent is the landscape fragmented by linear human infrastructure? How permeable is the infrastructure that exists, e.g. wildlife passes, amount of traffic.
0 - Landscape is highly fragmented with high human use (high levels of infrastructure, e.g. roads with heavy traffic); 0.5 - Landscape is crossed by low traffic or semi-permeable infrastructure; 1 - Landscape is completely connected with no linear infrastructure
<b>Aquatic landscape connectivity</b>
To what extent are there migratory paths within the aquatic system and to the sea?
0 - Aquatic systems are heavily fragmented and fish migration is severely limited; 0.5 - Within river migration but migration to sea is limited, dams may be in place but alternative migration routes or fish ladders are provided; 1 - No impediments to fish migration
<b>Spontaneous vegetation dynamics</b>
To what extent are natural and spontaneous vegetation dynamics occurring as a result of land abandonment? [Percentage of total rewilding area abandoned and devoted to open vegetation dynamics (data-driven) weighted by the progress of the vegetation dynamics (expert-based)]
0.1 - Early successional stages (e.g. <50 years); 0.5 - Medium term abandonment (50-200 years); 1 - Long-term abandonment with well-developed successional stages adapted to each ecological region or biome (e.g. > 200 years)
<b>Harmful invasive species</b>
What is the impact of harmful invasive species on the rewilding area? Do they significantly impact natural processes or ecological communities?
0 - Very severe impacts of invasive species on ecological communities in rewilding area; 0.5 - Impacts of invasive species within small, localized communities within rewilding area; 1 - No major invasive species present
<b>Trophic complexity</b>
<b>Terrestrial species composition (&gt;5kg)</b>
Species composition of large-bodied (greater > 5kg) species comprising species viability, occupancy and time present in site where: S is the space occupied by the species in the area, estimated from 0– 1; T is the percentage of the time in a year that species are present in the area they occupy (estimated 0–1, except for migratory species that if present should score 1); V is the viability of the population to which the individuals of the species belong that can be larger than the focal area (estimated 0– 1); curr denotes the values for each species at a given time; and max denotes the maximum possible value for each variable for that species (always equals 1)
<b>Stochastic disturbances</b>
<b>Natural avalanche or rock slide regime</b>
Are there avalanche avoidance measures in place (e.g., artificial slope bombardment, barriers) to reduce the risk of avalanches? Is the avalanche regime regulated?
0 - Regulation of avalanches / rock slides across the whole rewilding area; 0.5 - Regulation of avalanches / rock slides only in certain places; 1 - No regulation of the avalanche / rock slide regime
<b>Natural fire regime</b>
Is the natural fire regime modified by humans and to what extent (this might be in either direction, i.e., fire suppression or prescribed burning)? In the cases where humans do influence fire, do these mimic natural fire patterns? On what land uses do these fires occur and what is the ecological impact of these fires?
0 - Fire regime is heavily modified by human intervention and the fires do not mimic natural patterns causing significant ecological change; 0.5 - Some artificial and localized fire patterns somewhat affecting ecological impacts or human fires largely mimic natural patterns; 1 - No deviations of the natural fire regime with no human influence
<b>Natural hydrological regime</b>
Are there deviations from the natural flooding regimes on the site? Are the hydrological systems a natural shape and have lateral and longitudinal connectivity (connectivity along the river and to the flood beds)? This can be due to actions like dams and deepening and straightening of river beds.
0 - High regulation of hydrological regime; 0.5 - Regulations like dams or channelization with minor impacts on the overall flood regime; 1 - No regulation of the hydrological regime
<b>Natural pest or mortality regimes</b>
To what extent are natural pest and mortality regimes allowed to play a role in the ecosystem or to what extent are they regulated? If there are legislations in place, are they respected or not? Are measurements taken to reduced or remove pests through the use of chemicals? Is deadwood allowed to remain? Have there been any large-scale, disease-related deadwood removals in the last year. Take into account both the state of the system AND the management that is in place.
0 - Management to avoid pests or after mortality events; 0.5 - Low levels of management to avoid pests or after mortality events unlikely to affect disturbance regime, animal movements and other ecological processes significantly; 1 – No management actions implemented to avoid pests (e.g., pesticide use) or after mortality events (e.g., salvage logging, removal of burnt wood)

**Table 2:** The updated indicators and their descriptions elicited from the Delphi Technique



## **Supplementary Information: Chapter 4**

### **Supplementary Information for Urban conservation gardening in the decade of restoration**

#### **This file contains**

Supplementary Table 1. **Commonly cultivated plant species.**

Supplementary Table 2. **Online availability of threatened species from Germany's Red List.**

References

**Supplementary Table 1. Commonly cultivated plants in Germany according to ref.<sup>1</sup>.** This list only includes the species from ref.<sup>1</sup> that matched with species names from the population trend data from ref.<sup>2</sup>.

<i>Abies grandis</i>	<i>Eryngium planum</i>	<i>Papaver somniferum</i>	<i>Viburnum lantana</i>
<i>Acer campestre</i>	<i>Euphorbia lathyris</i>	<i>Phacelia tanacetifolia</i>	<i>Viburnum opulus</i>
<i>Acer platanoides</i>	<i>Fagus sylvatica</i>	<i>Phalaris arundinacea</i>	<i>Vinca minor</i>
<i>Acer pseudoplatanus</i>	<i>Festuca pratensis</i>	<i>Physalis alkekengi</i>	<i>Vitis vinifera</i>
<i>Aesculus hippocastanum</i>	<i>Fraxinus excelsior</i>	<i>Picea abies</i>	<i>Zea mays</i>
<i>Agrostemma githago</i>	<i>Fritillaria meleagris</i>	<i>Pinus cembra</i>	
<i>Agrostis capillaris</i>	<i>Galanthus nivalis</i>	<i>Pinus nigra</i>	
<i>Alchemilla mollis</i>	<i>Galium odoratum</i>	<i>Pinus strobus</i>	
<i>Allium schoenoprasum</i>	<i>Geranium pratense</i>	<i>Pinus sylvestris</i>	
<i>Alnus incana</i>	<i>Geranium sanguineum</i>	<i>Plantago lanceolata</i>	
<i>Amelanchier lamarckii</i>	<i>Hedera helix</i>	<i>Poa compressa</i>	
<i>Anthemis tinctoria</i>	<i>Helianthus annuus</i>	<i>Poa trivialis</i>	
<i>Anthriscus cerefolium</i>	<i>Helianthus tuberosus</i>	<i>Polemonium caeruleum</i>	
<i>Anthyllis vulneraria</i>	<i>Helleborus niger</i>	<i>Populus nigra</i>	
<i>Antirrhinum majus</i>	<i>Hippophae rhamnoides</i>	<i>Populus tremula</i>	
<i>Apium graveolens</i>	<i>Hippuris vulgaris</i>	<i>Primula vulgaris</i>	
<i>Armeria maritima</i>	<i>Hordeum vulgare</i>	<i>Prunella vulgaris</i>	
<i>Arrhenatherum elatius</i>	<i>Iberis amara</i>	<i>Prunus avium</i>	
<i>Aruncus dioicus</i>	<i>Ilex aquifolium</i>	<i>Prunus domestica</i>	
<i>Avena sativa</i>	<i>Iris sibirica</i>	<i>Prunus mahaleb</i>	
<i>Bellis perennis</i>	<i>Juglans regia</i>	<i>Prunus serotina</i>	
<i>Beta vulgaris</i>	<i>Juniperus communis</i>	<i>Pseudotsuga menziesii</i>	
<i>Brassica napus</i>	<i>Laburnum anagyroides</i>	<i>Pulsatilla vulgaris</i>	
<i>Brassica oleracea</i>	<i>Lamium maculatum</i>	<i>Quercus robur</i>	
<i>Buddleja davidii</i>	<i>Larix decidua</i>	<i>Quercus rubra</i>	

<i>Buxus sempervirens</i>	<i>Larix kaempferi</i>	<i>Rhamnus cathartica</i>
<i>Calendula officinalis</i>	<i>Lathyrus latifolius</i>	<i>Ribes alpinum</i>
<i>Calluna vulgaris</i>	<i>Leontodon autumnalis</i>	<i>Ribes nigrum</i>
<i>Caltha palustris</i>	<i>Leucojum vernum</i>	<i>Ribes uva-crispa</i>
<i>Campanula glomerata</i>	<i>Ligustrum vulgare</i>	<i>Robinia pseudoacacia</i>
<i>Campanula persicifolia</i>	<i>Lilium martagon</i>	<i>Rosa rugosa</i>
<i>Carpinus betulus</i>	<i>Lolium multiflorum</i>	<i>Rudbeckia hirta</i>
<i>Centaurea cyanus</i>	<i>Lolium perenne</i>	<i>Rudbeckia laciniata</i>
<i>Centaurea montana</i>	<i>Lonicera caprifolium</i>	<i>Salvia nemorosa</i>
<i>Chrysanthemum segetum</i>	<i>Lonicera tatarica</i>	<i>Sanguisorba minor</i>
<i>Cichorium intybus</i>	<i>Lonicera xylosteum</i>	<i>Scilla siberica</i>
<i>Consolida ajacis</i>	<i>Lycium barbarum</i>	<i>Scorzonera hispanica</i>
<i>Convallaria majalis</i>	<i>Lycopersicon esculentum</i>	<i>Secale cereale</i>
<i>Cornus mas</i>	<i>Lysimachia nummularia</i>	<i>Sedum spurium</i>
<i>Cornus sanguinea</i>	<i>Lysimachia punctata</i>	<i>Silene armeria</i>
<i>Corylus avellana</i>	<i>Mahonia aquifolium</i>	<i>Sinapis alba</i>
<i>Crepis biennis</i>	<i>Malva alcea</i>	<i>Sorbus aucuparia</i>
<i>Crocus vernus</i>	<i>Matteuccia struthiopteris</i>	<i>Symphoricarpos albus</i>
<i>Cynosurus cristatus</i>	<i>Medicago lupulina</i>	<i>Taxus baccata</i>
<i>Cytisus scoparius</i>	<i>Muscari botryoides</i>	<i>Tilia cordata</i>
<i>Daucus carota</i>	<i>Muscari neglectum</i>	<i>Trifolium hybridum</i>
<i>Dianthus deltoides</i>	<i>Narcissus poeticus</i>	<i>Trifolium pratense</i>
<i>Digitalis purpurea</i>	<i>Narcissus pseudonarcissus</i>	<i>Trifolium repens</i>
<i>Eranthis hyemalis</i>	<i>Onopordum acanthium</i>	<i>Triticum aestivum</i>
<i>Erica carnea</i>	<i>Papaver rhoeas</i>	<i>Valerianella locusta</i>

**Supplementary Table 2. Online availability of 100 randomly sampled threatened species from Germany's Red List of Vascular Plants.** Red list category 0, 1, 2, 3 correspond to IUCN category EX, CR, EN, VU,

respectively. To determine online availability, we used Google search and entered the Latin and English name of a species with "buy online" or "nursery" and reviewed the first three Google pages, assuming that this reflected a reasonable effort by an average customer. As of May 2021, 35 species of plants were available online. Given that our search was biased toward mainstream garden centres, we suggest the majority of these species are amenable to gardening. URLs are hyperlinked to save space.

Species	Author	Red List Availability	Available online
<i>Trinia glauca</i>	(L.) Dumort.	2	
<i>Elatine triandra</i>	Schkuhr	3	
<i>Diphasiastrum zeilleri</i>	(Rouy) Holub	2	
<i>Rubus stormanicus</i>	H.E. Weber	2	
<i>Taraxacum platyglossum</i>	Raunk.	3	
<i>Muscari botryoides</i>	(L.) Mill.	3	<a href="#">link</a>
<i>Carlina biebersteinii</i>	Hornem.	3	
<i>Populus nigra</i>	L.	3	<a href="#">link</a>
<i>Sedum dasyphyllum</i>	L.	3	<a href="#">link</a>
<i>Deschampsia wibeliana</i>	(Sond.) Parl.	3	
<i>Hieracium sommerfeltii</i>	Lindeb.	1	
<i>Thesium alpinum</i>	L.	3	
<i>Knautia kitaibelii</i>	(Schult.) Borb'as	0	
<i>Hieracium subramosum</i>	Lonnr."	2	
<i>Verbascum phoeniceum</i>	L.	2	<a href="#">link</a>
<i>Taraxacum heleocharis</i>	Kirschner & Step' anek	2	
<i>Trifolium ochroleucon</i>	Huds.	2	<a href="#">link</a>

<i>Juncus</i>	Willd.	<a href="#">1link</a>
<i>balticus</i>		
<i>Silene cretica</i>	L.	C-
<i>Androsace</i>	L.	<a href="#">1link</a>
<i>septentrionalis</i>		
<i>Orobanche</i>	Baumg.	3-
<i>lutea</i>		
<i>Carex curvula</i>	All.	C-
<i>Traunsteinera</i> (L.) Rchb.		3-
<i>globosa</i>		
<i>Rubus</i>	Lef`evre & P.J. Mull."	2-
<i>cardiophyllus</i>		
<i>Malaxis</i>	(L.) Sw.	3-
<i>monophyllos</i>		
<i>Chamaecytisus</i> (L.) Link		<a href="#">3link</a>
<i>s supinus</i>		
<i>Hieracium</i>	R. Meissn. & Zahn	1-
<i>cinereiforme</i>		
<i>Carex limosa</i>	L.	<a href="#">2link</a>
<i>Geranium</i>	Ehrh.	1-
<i>divaricatum</i>		
<i>Gentianella</i>	(L.) Borner"	2-
<i>amarella</i>		
<i>Cyperus</i>	(L.) Link	1-
<i>michelianus</i>		
<i>Amaranthus</i>	L.	<a href="#">3link</a>
<i>blitum</i>		
<i>Taraxacum</i>	Soest	1-
<i>vindobonense</i>		
<i>Scheuchzeria</i>	L.	2-
<i>palustris</i>		
<i>Cryptogramma</i> (L.) Hook.		<a href="#">2link</a>
<i>a crispa</i>		
<i>Chenopodium</i>	L.	1-
<i>urbicum</i>		
<i>Apium</i>	L.	<a href="#">3link</a>
<i>graveolens</i>		
<i>Polygala</i>	F.W. Schultz	<a href="#">3link</a>
<i>calcareo</i>		
<i>Crataegus</i>	Gand.	2-
<i>rhypidophylla</i>		
<i>Scolochloa</i>	(Willd.) Link	<a href="#">3link</a>
<i>festucea</i>		

<i>Ranunculus</i>	Borch.-Kolb			1-
<i>basitruncatus</i>				
<i>Lathyrus</i>	Willd.			<a href="#">link</a>
<i>japonicus</i>				
<i>Ranunculus</i>	Haas			2-
<i>phragmiteti</i>				
<i>Sagina apetala</i>	Ard.	3	-	
<i>Bupleurum longifolium</i>	L.	3	<a href="#">link</a>	
<i>Carex pulicaris</i>	L.	2	-	
<i>Lathyrus hirsutus</i>	L.	3	<a href="#">link</a>	
<i>Chondrilla chondrilloides</i>	(Ard.) H. Karst.	1	-	
<i>Zostera noltei</i>	Hornem.	3	-	
<i>Lactuca quercina</i>	L.	2	-	
<i>Subularia aquatica</i>	L.	0	-	
<i>Asplenium fissum</i>	Willd.	2	-	
<i>Carex binervis</i>	Sm.	3	-	
<i>Iris spuria</i>	L.	2	<a href="#">link</a>	
<i>Genista germanica</i>	L.	3	<a href="#">link</a>	
<i>Epilobium nutans</i>	F.W. Schmidt	2	-	
<i>Nymphoides peltata</i>	(S.G. Gmel.) Kuntze	3	<a href="#">link</a>	
<i>Micropyrum tenellum</i>	(L.) Link	0	-	
<i>Hypochaeris maculata</i>	L.	2	-	
<i>Eriophorum latifolium</i>	Hoppe	3	<a href="#">link</a>	
<i>Anagallis minima</i>	(L.) E.H.L. Krause	2	-	
<i>Ranunculus sardous</i>	Crantz	3	-	
<i>Ranunculus recticaulis</i>	Horandl & Gutermann"	2	-	
<i>Taraxacum</i>	Hudziok	1	-	
<i>brandenburgicum</i>				
<i>Salvinia natans</i>	(L.) All.	2	<a href="#">link</a>	
<i>Lathyrus aphaca</i>	L.	3	<a href="#">link</a>	
<i>Diphasiastrum oellgaardii</i>	Stoor et al.	1	-	
<i>Juniperus sabina</i>	L.	3	<a href="#">link</a>	
<i>Asperula arvensis</i>	L.	0	<a href="#">link</a>	
<i>Carex bigelowii</i>	Schwein.	2	-	
<i>Adonis flammea</i>	Jacq.	1	-	
<i>Adonis vernalis</i>	L.	3	<a href="#">link</a>	
<i>Rhinanthus serotinus</i>	(Schonh.) Oborny"	3	<a href="#">link</a>	
<i>Artemisia scoparia</i>	Waldst. & Kit.	1	<a href="#">link</a>	
<i>Calendula arvensis</i>	(Vaillant) L.	1	<a href="#">link</a>	
<i>Juncus atratus</i>	Krock.	1	-	
<i>Fumana procumbens</i>	(Dunal) Gren.	2	<a href="#">link</a>	
<i>Coeloglossum viride</i>	(L.) Hartm.	2	<a href="#">link</a>	
<i>Schoenus ferrugineus</i>	L.	3	-	

<i>Rubus incarnatus</i>	P.J. Mull.´	3	-
<i>Phyteuma orbiculare</i>	L.	3	<a href="#">link</a>
<i>Veronica spuria</i>	L.	0	<a href="#">link</a>
<i>Hieracium cymiflorum</i>	N´ageli & Peter	2	-
<i>Carpesium cernuum</i>	L.	0	-
<i>Moneses uniflora</i>	(L.) A. Gray	2	-
<i>Saponaria ocymoides</i>	L.	2	<a href="#">link</a>
<i>Luzula congesta</i>	(Thuill.) Lej.	3	-
<i>Hieracium heterodoxum</i>	(Tausch) N´ageli & Peter	2	-
<i>Ranunculus haasii</i>	Soo´	1	-
<i>Taraxacum gelertii</i>	Raunk.	3	-
<i>Narcissus radiiflorus</i>	Salisb.	1	-
<i>Knautia gracilis</i>	Szabo´	2	-
<i>Botrychium multifidum</i>	(S.G. Gmel.) Rupr.	1	-
<i>Asperugo procumbens</i>	L.	2	-
<i>Arctostaphylos uva-ursi</i>	(L.) Spreng.	2	<a href="#">link</a>
<i>Onobrychis montana</i>	DC.	2	-
<i>Diphasiastrum alpinum</i>	(L.) Holub	2	-
<i>Ventenata dubia</i>	(Leers) Coss.	2	-
<i>Ranunculus mergenthaleri</i>	Borch.-Kolb	2	-
<i>Trifolium striatum</i>	L.	3	-

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## References

1. Preisinger, H. *et al.* Berichte des Botanischen Vereins zu Hamburg. (2000).
2. Eichenberg, D. *et al.* Widespread decline in Central European plant diversity across six decades. *Glob. Chang. Biol.* (2020).

## Curriculum Vitae

### EXPERIENCE

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- PhD** Oct 2019 - Present  
*Rewilding Europe & iDiv*  
*Netherlands & Germany*
- Ecological researcher** Feb 2018 – Sep 2018  
*Conservation of wild fauna lab*  
*UNAM, Mexico*
- Ecological consultant** Apr 2017 – Oct 2017  
*Jacobs solutions*  
*UK*
- Research field assistant** Jun 2015/16 – Aug 2015/2016  
*American Prairie*  
*USA*
- Ecological consultant** Sep 2015 – Sep 2017  
*David Dodds associates ltd*  
*Scotland*
- Co-founder & fundraiser** Oct 2013 – Jun 2015  
*Skills for Change*  
*Scotland*

### EDUCATION

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- M.Sc. University of Oxford** 2018 – 2019  
*Major: Biodiversity, Conservation and Management*  
*(Awarded 1<sup>st</sup> = GPA: 4.0/4.0)*
  - St Peter's College Dissertation award
  - BCM Dissertation Grant award
- B.Sc. (hons) University of Edinburgh** 2014 - 2017  
*Major: Ecological and Environmental Sciences (Awarded*  
*1<sup>st</sup> = GPA: 4.0/4.0)*
  - Elizabeth Sinclair Irvine Prize for most distinguished ecology and environmental science graduate



- R Stewart McDougall Prize for best honors dissertation in any of the School of Geosciences, Animal Science or Biosciences Programmes
- Media Prize for excellent contribution to the university

## **ADDITIONAL ACTIVITIES**

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### **Theatre actress**

**2021 - current**

- Voice actress at Buchfunk
- Else in “Fräulein Else” written by Arthur Schnitzler (Freie Ensemble Jedermensch)
- Natalia Stepanova in “The Proposal” written by Anton Chekhov (Neues Schauspiel)
- Rosalind in “As you like it” written by William Shakespeare (Neues Schauspiel)
- Christa in “Scab” written by Sheila Callaghan (Neues Schauspiel)

### **Scientific Theatre Coordinator (Neues Schauspiel)**

**2023**

### **Yoga teacher**

**2022 - current**

- Certified by Yoga Alliance Society (200 hours)

## **LIST OF PUBLICATIONS**

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### Published

1. Segar, J., et al. (2022). Divergent roles of herbivory in eutrophying forests. *Nature Communications*. 10.1038/s41467-022-35282-6
2. Segar, J., et al. (2022). Urban conservation gardening in the decade of restoration. *Nature Sustainability*, 1-8.
3. Segar, J., et al. (2021). Expert-based assessment of rewilding indicates progress at site-level, yet challenges for upscaling. *Ecography*, 4.
4. Segar, J., & Keane, A. (2020). Species and demographic responses to wildlife-friendly fencing on ungulate crossing success and behavior. *Conservation Science and Practice*, 2(10), e285.
5. Holz, H., Segar, J., et al. (2022). Assessing extinction risk across the geographic ranges of plant species in Europe. *Plants, People, Planet*, 4(3), 303-311.
6. Staude, I., Segar, J., et al. (2023). Prioritise grassland restoration to bend the curve of biodiversity loss. *Restoration Ecology*, 10.1111/rec.13931.

7. Pereira, H., et al. (2020). Ecological restoration in the EU post-2020 biodiversity strategy: The opportunities of rewilding European landscapes for nature and climate. Policy Brief, Rewilding Europe.

#### Under review

1. Munschek et al., Putting conservation gardening into practice. (*Under review at Scientific Reports*).

#### In prep

1. Callaghan et al., Urban green spaces and the role of biogeography. *In prep*.
2. Lefebvre et al., Global analysis of local plant diversity in the presence of invasive and non-invasive neophytes. *In prep*.

### **ACADEMIC ACTIVITIES & AWARDS DURING PHD**

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#### *Conferences & Invited talks*

- Poster presentation at International Conference for Sustainability (January 2021)
- Terranova Marie-Curie consortium conferences x7 (2019 – 2023)
- Symposium presentation for ForestREPlot consortium (October 2021)
- Presentation at iDiv annual conference (April 2022)
- Volunteering at GEOBON conference (July 2020)

#### *Field work*

- Field work in Peneda to assist on camera trap project x4 (2020 – 2022)

#### *Review*

- European journal of wildlife research x2
- Conservation letters
- Ecology and evolution

#### *Prizes*

- iDiv science communication prize 2022
- Best presentation at conference award (iDiv) 2022

#### *Supervising & mentoring*

- Official supervisor of Oxford University masters student Suzanne Lefebvre
  - Completed masters' thesis: *Local plant diversity in the presence of invasive and non-invasive neophytes: a global analysis*
- Advisor to three masters students
  - Sjoerd Blommestijn, Georg Messerer & Ilse van Ekris

### *Teaching & guest lectures*

- Teaching on Nature Conservation course x3 (2020 – 2022)
- Guest lecture at University College Dublin (December 2020)
- Guest lecture at Royal Society for the Protection of Birds (September 2021)
- Guest lecture at Netherlands College Helicon (October 2021)
- Guest lectures at Oxford for Biodiversity Conservation & Management masters program x2 (May 2020, 2021)
- Webinar(s) for European Rewilding Network members x2 (October 2021)
- Webinar for rewilding practitioner workshop (November 2021)

### *Outreach & consulting*

- Talk at Rewilding Europe (RE) public webinar (70 people)
- Scientific consultant for rewilding children's book for publishing house
- Interview in RE Annual Review
- Work and consulting for RE
- Featured on French national TV about bison reintroductions in Netherlands (Feb 2020)
- Trailer for TerraNova website
- Panel discussion for Europe's New Wild film
- Radio talk for MDR
- Voice dubbing for GrazeLife movie
- Presentation to UK government – Tony Juniper at Natural England
- BBC interview
- Deutsche Welle video interview
- Interview for MIT tech review

### *Workshops*

- Organised and ran 3 workshops between iDiv and Rewilding Europe practitioners

### *Courses as yDiv member*

- yDiv welcome week courses
- Spatial Ecology course
- GitLab course
- Data Visualisation course
- Rethinking Stats
- Common Agricultural Policy

## **Eigenständigkeitserklärung**

Hiermit erkläre ich, dass die Arbeit mit dem Titel "**Biodiversity-enhancing approaches to landscape abandonment and urbanization**" bisher weder bei der Naturwissenschaftlichen Fakultät I Biowissenschaften der Martin-Luther-Universität Halle-Wittenberg noch einer anderen wissenschaftlichen Einrichtung zum Zweck der Promotion vorgelegt wurde.

Ferner erkläre ich, dass ich die vorliegende Arbeit selbstständig und ohne fremde Hilfe verfasst sowie keine anderen als die angegebenen Quellen und Hilfsmittel benutzt habe. Die den Werken wörtlich oder inhaltlich entnommenen Stellen wurden als solche von mir kenntlich gemacht. Ich erkläre weiterhin, dass ich mich bisher noch nie um einen Doktorgrad beworben habe.

Leipzig, den 13.05.2023

Josiane Segar