# ECOGRAPHY

## Forum

# Future restoration should enhance ecological complexity and emergent properties at multiple scales

James M. Bullock, Elisa Fuentes-Montemayor, Ben McCarthy, Kirsty Park, Rosie S. Hails, Ben A. Woodcock, Kevin Watts, Ron Corstanje and Jim Harris

J. M. Bullock (https://orcid.org/0000-0003-0529-4020) ✉ (jmbul@ceh.ac.uk) and B. A. Woodcock, UK Centre for Ecology and Hydrology, Wallingford, UK. – E. Fuentes-Montemayor, Scotland's Rural College, Craibstone Estate, Bucksburn, Aberdeen, UK. – B. McCarthy and R. S. Hails, National Trust, Heelis, Kemble Drive, Swindon, UK. – K. Park and K. Watts, Biological and Environmental Sciences, Univ. of Stirling, Stirling, UK. KW also at: Forest Research, Alice Holt Lodge, Farnham, UK. – R. Corstanje and J. Harris, School of Water, Energy and Environment, Cranfield Univ., Cranfield, UK.

Ecological restoration has a paradigm of re-establishing 'indigenous reference' communities. One resulting concern is that focussing on target communities may not necessarily create systems which function at a high level or are resilient in the face of ongoing global change. Ecological complexity – defined here, based on theory, as the number of components in a system and the number of connections among them – provides a complementary aim, which can be measured directly and has several advantages. Ecological complexity encompasses key ecosystem variables including structural heterogeneity, trophic interactions and functional diversity. Ecological complexity can also be assessed at the landscape scale, with metrics including β diversity, heterogeneity among habitat patches and connectivity. Thus, complexity applies, and can be measured, at multiple scales. Importantly, complexity is linked to system emergent properties, e.g. ecosystem functions and resilience, and there is evidence that both are enhanced by complexity. We suggest that restoration ecology should consider a new paradigm to restore complexity at multiple scales, in particular of individual ecosystems and across landscapes. A complexity approach can make use of certain current restoration methods but also encompass newer concepts such as rewilding. Indeed, a complexity goal might in many cases best be achieved by interventionist restoration methods. Incorporating complexity into restoration policies could be quite straightforward. Related aims such as enhancing ecosystem services and ecological resilience are to the fore in initiatives such as the Sustainable Development Goals and the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services. Implementation in policy and practice will need the development of complexity metrics that can be applied at both local and regional scales. Ultimately, the adoption of an ecological complexity paradigm will be based on an acceptance that the ongoing and unprecedented global environmental change requires new ways of doing restoration that is fit for the future.

Keywords: connectivity, conservation, ecosystem functions, ecosystem services, landscape, resilience, UN Decade on Ecosystem Restoration

1

*"It is interesting to contemplate a tangled bank, clothed with many plants of many kinds, with birds singing on the bushes, with various insects flitting about, and with worms crawling through the damp earth, and to reflect that these elaborately constructed forms, so different from each other, and dependent upon each other in so complex a manner, have all been produced by laws acting around us", Charles Darwin: On the Origin of Species By Means of Natural Selection.*

## Introduction

There is an increasing global imperative to restore degraded ecosystems to tackle the biodiversity and climate crises. Ecological restoration is being operationalised through a range of international and national initiatives, including the UN Decade on Ecosystem Restoration, the Bonn Challenge, the English Nature Recovery Network (Isaac et al. 2018), the Everglades Restoration Plan (ERP 2021) and Gondwana Link (GL 2021). An increasing reliance on restoration is also reflected by the emergence of no net loss and net gain principles for biodiversity during infrastructure developments (Bull and Brownlie 2017). The current paradigm for restoration focuses on the re-establishment of 'indigenous reference' ecosystems and the species, communities and features defining them (Gann et al. 2019). This conceptualisation has been dubbed the 'carbon copy' approach by Hilderbrand et al. (2005), which is predicated on the assumption that ecosystems develop somewhat predictably towards specified end points. These targets are often defined through conservation goals for rare or threatened habitats (Gann et al. 2019).

The 'carbon copy' approach to ecosystem restoration is debated (Murcia et al. 2014, Higgs et al. 2018). It can be difficult and sometimes impossible to re-create ecosystems that resemble reference sites, as these reference ecosystems often developed in a different time, environment and climate (Lira et al. 2019, Watts et al. 2020). This approach also assumes that these historically determined indigenous reference systems will be resilient to the unprecedented challenges from global change that face us in the near future, while ongoing and predicted biodiversity declines would suggest this is not the case (Tittensor et al. 2014, Trisos et al. 2020). Indeed, conservation is recognising the need to move away from the traditional focus of attempting to preserve ecosystems as they once were, towards actions to facilitate their adaptation (e.g. species range shifts) and transformation (e.g. change in communities) in response to inevitable change while still maintaining their character, functions and services (Oliver et al. 2015a, Gardner and Bullock 2021, Peterson St-Laurent et al. 2021).

In contrast to the carbon-copy concept, the 'field of dreams' approach focuses on restoring the physical conditions of the target ecosystem, with the idea that the biotic composition will then self-assemble in a predictable fashion towards the desired end point (Hilderbrand et al. 2005). This includes approaches such as stripping topsoil or planting trees, often at a large scale (Harvey et al. 2017) and is often

the basis of simple, quantifiable restoration targets. Such targets include the area of woodland to be planted, exemplified by the Bonn Challenge commitment to restore up to 350 million hectares of global degraded and deforested lands by 2030 (Verdone and Seidl 2017), or the number of trees to be planted, such as the one trillion trees campaign launched by the World Economic Forum (2020). Although appealing, simple and quantifiable, there is limited evidence to show that these schemes are successful in terms of achieving the anticipated ecosystem assembly. Indeed, there have been notable problems with this approach, such as the mass tree planting in Northern India, which has not led to an increase in forest cover (Coleman et al. 2021).

Landscape-scale restoration has been subject to less theorising than ecosystem (i.e. local, site-based) restoration, but the implied approach is generally for restoration of a set of similar ecosystems across a landscape (Menz et al. 2013, Aronson et al. 2017). This conceptualisation is very much based on the need for habitat patches to support meta-populations and meta-communities (Perring et al. 2015). However, restoration success is not simply the sum of site-based restoration activities (i.e. creating more of the same), and an alternative is to attempt to restore the interactions and functionality of the landscape as a whole. This wider approach to restoration, emphasising ecological functionality, underpins the (IUCN 2021) principles of 'forest landscape restoration'.

These considerations motivate us to suggest that restoration needs to be re-interpreted, recognising that there has been a systemic loss of ecological complexity (e.g. species, trophic structure, connectivity; Box 1) in ecosystems and landscapes over the world (Gámez-Virués et al. 2015, Johnson et al. 2017). This has led to an undermining of their functionality and capacity to support key ecosystem processes as well as their ability to remain resilient under future environmental change (Oliver et al. 2015b, Fanin et al. 2018). While this does not exclude the 'carbon copy' or 'field of dreams' approaches, we suggest the focus of restoration needs to encompass ecosystem functioning at all spatial scales and interactions between these scales and ensure these functions are resilient to future global change. Indeed, the principles and standards of the Society for Ecological Restoration (Gann et al. 2019) suggest that reference ecosystems should be chosen taking account of ecological complexity, although they lack clarity about how this might work in practice or how complex references can be identified. Rather than aiming to recreate reference systems (as proxies of ecosystem complexity) or restoring the physical conditions of the target ecosystem (and assuming complexity will develop), we propose that the focus should be directly on achieving complexity. To achieve complex restored ecosystems, we propose that restoration policy and practice need to have a systems-based approach, that emphasises the development of ecologically complex systems. In this paper, we make the case that restoration should aim to achieve multi-scale complexity and the enhancement of emergent properties such as ecosystem functions

**Box 1. Defining ecological complexity**

Complexity is a commonly cited concept in ecology but one which suffers from a variety of definitions and consequent ambiguity in its use and application. A further issue is the conflation of complexity with emergent properties. An emergent property is a characteristic of a system which cannot be explained entirely by its individual components (Mayr 1982) and results from an interacting set of variables (Gilbert and Henry 2015). For example, ecosystem functions or resilience to perturbations can be considered as emergent properties which may increase with higher complexity but are not themselves a measure of complexity (Parrott 2010). Here, we consider earlier definitions of complexity and aim to consolidate these into a pragmatic and practicable definition, which applies to restoration at multiple scales.

Anand et al. (2010) and Parrott (2010) consider a variety of definitions for complexity that are related to the temporal dynamics, spatial organisation or structure of a system. Spatial measures of complexity discussed include Shannon entropy, dispersion and fractal dimension. Structural complexity measures describe the organization and relationships between components of a system with a focus on network (e.g. food web) structure. Moreno-Mateos et al. (2020) use the definition: 'The amount of ecological information required to describe a metric or attribute of an ecosystem'. They relate this to the structure of interaction networks, ecosystem functioning and ecosystem stability.

The preceding definitions are multifarious. Levin (1998) lists among the attributes of 'complex adaptive systems': diversity (such as number of species or functional groups) and flows (such as, of energy, nutrients, information). This characterisation provides a good basis for defining complexity.

1) Number. Pimm (1984) relates complexity to species number and evenness. Landscape complexity is often represented as the number of habitat types present (Chaplin-Kramer et al. 2011). One can extend this concept to measures of structural heterogeneity (Zellweger et al. 2013) if one considers this as counting the number or diversity of structure classes in a system (Parrott 2010).
2) Connections. Complexity has also been defined in terms of interactions and flows, which we subsume here under the term 'connections'. MacArthur (1955), in his famous study of complexity and stability, considers complexity of a food web in terms of the number of pathways for energy to reach a consumer. Pimm (1984) also relates complexity to the number of species interactions. Filotas et al. (2014) conceptualise complex systems in which 'heterogeneous entities' interact locally to form ecosystems, which also themselves interact with other ecosystems across a landscape.

Our resulting definition of ecological complexity is simple, applicable at multiple scales and relates clearly to empirical measurement: the number of components in a system and the number of connections among them. Components can include, e.g. species, height classes, functional groups and habitats. Connections can include species interactions, energy flows among species or connectivity among habitat patches. Figure 1 and 2 depict this complexity concept, showing how it is relevant to real ecosystems and applicable at multiple scales.

and resilience at nested spatial scales. To support this argument, we first describe the conceptual basis for considering ecosystem and landscape complexity and emergent properties, how one can assess and achieve complexity in the field and finally how an ecological complexity framing might be implemented in policy. In making this case we note that while the complexity approach may use some of the same restoration actions or measures of outcomes as are currently used, the overall aim of restoration and thus the interpretation of these measures are fundamentally different.

## Ecological complexity and emergent properties

Our suggested re-framing of restoration in terms of enhancing complexity and emergent properties requires clear definitions and conceptual evaluation of these terms. We define ecological complexity and emergent properties in Box 1 and visualise what ecological complexity looks like in Fig. 1, 2. Emergent properties that are most relevant to restoration

comprise the range and level of functions supported (i.e. the flow of energy and materials through an ecosystem or landscape (Manning et al. 2018)) and the resilience (the ability of a system to either resist, or recover rapidly from, a perturbation (Oliver et al. 2015a)) of these functions to environmental pressures. Other emergent properties of ecological systems include stability and self-organisation (Ponge 2005), but we focus on functions and resilience here. This approach to restoration involves moving degraded (low ecological complexity) systems towards a state of high ecological complexity (restored) (Fig. 1, 2).

In general, research suggests that emergent properties increase with ecological complexity, albeit not necessarily in a linear fashion. In the following, we briefly summarise knowledge on these relationships, acknowledging that this remains a greatly debated topic (Duffy et al. 2017). At the ecosystem scale, the increase in multiple types of ecosystem function with higher species, functional group or phylogenetic richness is commonly reported at different trophic levels (Flynn et al. 2011, Gagic et al. 2015, Creamer et al. 2016). In general, these relationships are typically non-linear,
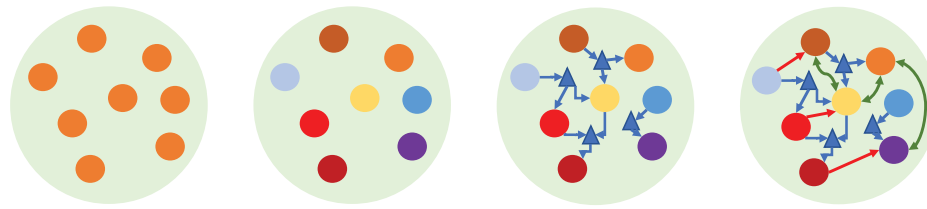
| Components: | Homogeneous | Diverse | Diverse | Diverse |
|---|---|---|---|---|
| Connections: | None | None | Direct or indirect | Direct, indirect & diverse |
| Ecological complexity: | None | Low | Moderate | High |
| Emergent properties: | None | Weak | Moderate | Strong |

**Legend:** ● Species; →▲→ Indirect connection e.g. exuded resource; →→ Direct connection e.g. predation; ↘↗ Direct connection e.g. symbiosis-mutualism.

Figure 1. A conceptual diagram depicting increasing degrees of ecological complexity within a system. As the number of components and connections increases so does complexity (Box 1). As complexity increases, so do emergent properties such as ecosystem functioning and resilience. In this case, an ecosystem is depicted, and the progression from left to right could be a restoration trajectory, but the same principles apply at multiple scales (Fig. 2).

with attenuating effects of increasing richness at higher levels (Cardinale et al. 2012). Furthermore, richness metrics have been related to increased multifunctionality (i.e. higher overall levels of multiple functions (Manning et al. 2018)), which shows less attenuation than single functions at higher richness levels due to complementarity effects (Lefcheck et al. 2015). A greater density of species interactions might also be expected to enhance the flow of energy and materials (i.e. functioning) within an ecosystem (Hines et al. 2015, Schleuning et al. 2015). Resilience of ecosystem functions is also enhanced by increased richness (Oliver et al. 2015a), due to redundancy. Indeed, resilience of ecosystem functions may be enhanced by a re-configuration of the community in the face of perturbations, with the result that complexity may be maintained even when taxonomic composition has changed (Oliver et al. 2015a). Highly connected nested networks tend to be more resilient (Oliver et al. 2015a). However, the topology of the interaction web is critical, as more compartmentalised interaction webs tend to be more resilient to perturbations (Hines et al. 2015).

At the landscape scale, greater patchiness and heterogeneity (and thus ecological complexity, according to our definition, Fig. 2) have been related to increased functioning. A greater variety of land/water uses and habitats, each of which is associated with particular functions, will lead to higher landscape multifunctionality than in simpler landscapes (Manning et al. 2018). There is also more specific evidence that higher β diversity across a landscape leads to higher multifunctionality as different species support different functions (Creamer et al. 2016, van der Plas et al. 2016). Higher landscape connectivity (complexity via more connections among patches) has been linked to greater multifunctionality (Manning et al. 2018) and resilience of metacommunities and ecosystem functions through rescue effects and spatial insurance (Oliver et al. 2015a). By contrast, if β diversity drives the levels of functions across a landscape,

theory suggests that higher connectivity may actually lead to decreases in β diversity and, so, functioning (Gonzalez et al. 2020). Thus, the precise impact of landscape connectivity on emergent properties is not yet clear.

## Measuring ecological complexity during restoration

For this re-conceptualisation to have practical value, we must be able to measure ecological complexity at the scale of individual sites as well as across landscapes. Conventional measures of restoration success, such as the presence of indicator species, species composition or similarity to target habitats, are unlikely to provide holistic insights into complexity or emergent properties. For practitioners and policymakers, this is a significant issue as indicator species and simple proxy measures are regularly used to monitor the efficacy of management decisions, justify the cost-benefit of restoration schemes and predict the net landscape-scale benefits of these endeavours (Hooper et al. 2021, Montanarella and Panagos 2021).

Measures or indices of complexity are limited by the practicalities of monitoring systems. For example, different sampling techniques typically target different taxa. However, there are a number of approaches that may provide insights into ecosystem and/or landscape complexity during restoration. To gain a holistic measure of complexity, it is important that multiple complexity measures are used in combination. Here we give some examples of such measures, some of which are used in some restoration studies. We emphasise that the difference in our approach is not in the measures per se but in their use to assess complexity during restoration rather than, say, to compare to reference sites. 1) Architectural/habitat complexity represents a measure of the three-dimensional niche space within a system that will have additive impacts on system
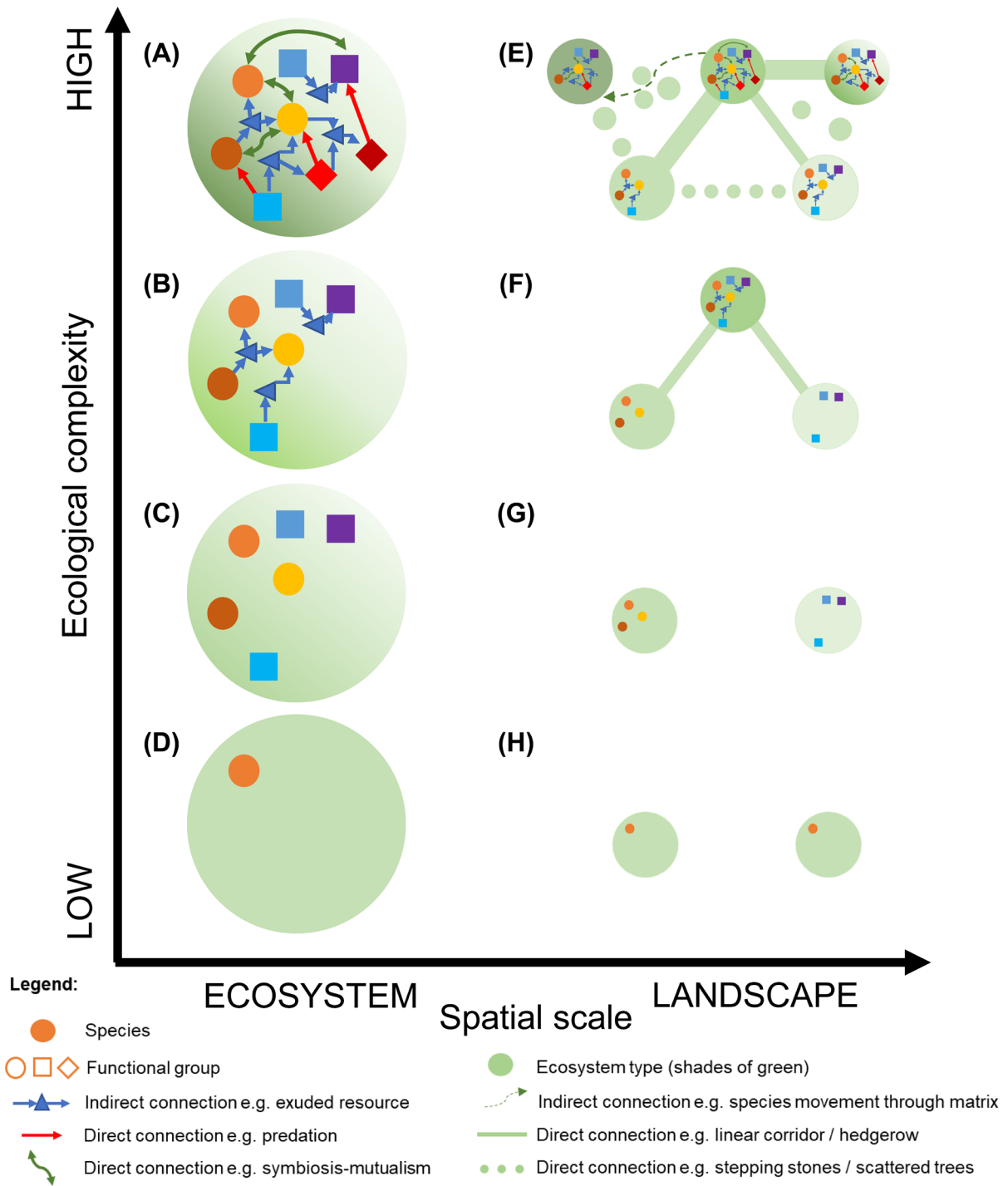
Figure 2. A conceptual diagram of ecological complexity across spatial scales. Locally within an ecosystem or habitat patch (A–D) and across a landscape (E–H). Ecological complexity advances up the y-axis. For example, (A) shows a complex ecosystem (Fig. 1) with high species richness, varied functional groups and many species interactions; whilst (D) shows an ecosystem with very low complexity, comprising low species richness, minimal functional groups and no species interactions. (E) shows a complex landscape with high (within and between) habitat/ecosystem diversity, high β and γ species diversity, varied functional groups, many species interactions and high connectivity between patches; whilst (H) shows a simple landscape with low habitat/ecosystem diversity, a depauperate regional species pool (i.e. low β and γ species diversity), few functional groups and species interactions and limited connectivity between patches.

complexity across increasing spatial scales (Torres-Pulliza et al. 2020). Measurements of architectural complexity can be done at local scales using direct quantification of vertical physical structures (Woodcock et al. 2007) or at ecosystem or landscape scales using active (e.g. LiDAR) or passive (e.g. optical hyperspectral imagery) remote sensing from aircraft or satellite sources (Camarretta et al. 2020). Hyperspectral imagery has also been used to quantify fractal dimensions across the entire spectrum of remotely sensed data to quantify habitat structure at landscape scales (Qiu et al. 1999). In coral reef systems, new approaches have been developed to link spatial and ecosystem-level complexity through aggregated descriptors of structures recorded at different spatial scales (e.g. height, rugosity and fractal dimensions) (Torres-Pulliza et al. 2020). 2) Species richness assessment might be aided by using environmental DNA (eDNA) and metabarcoding approaches, thus avoiding some of the taxonomic constraints of more traditional approaches (Fernandes et al. 2019, Foster et al. 2020). These approaches do not provide a panacea however, and Ruppert et al. (2019) listed several caveats and drawbacks. While local species or functional richness (α diversity) can be assessed at the site scale, landscape-scale complexity can be assessed in terms of β and λ diversity. 3) Food web complexity typically involves observing feeding relationships (e.g. pollinators and flowers or rearing parasitoids from hosts) (Pocock et al. 2012), although increasingly, DNA metabarcoding and eDNA provide a way to quantify dietary associations between species (Staudacher et al. 2016, Shutt et al. 2020). Even where such data are not available, food webs can be inferred from species inventories at local scales (Woodcock et al. 2012b). At large scales, species distribution data can be used to calculate landscape or regional scale food web complexity (Redhead et al. 2018). 4) Soil microbial community complexity can be studied with approaches including shotgun sequencing, which allows gene lists to be functionally annotated to infer biological processes, molecular functions and cellular components (Huerta-Cepas et al. 2017, Nurk et al. 2017). These approaches could be expanded with sufficient sampling to derive landscape-scale measures of the complexity of microbial communities (Griffiths et al. 2011). 5) Soundscape complexity can be quantified using full-spectrum acoustic recorders to detect shifts in faunal communities (Burivalova et al. 2019), allowing inferences about changes in multiple taxonomic communities and higher-order interactions reflecting diversity and behaviour (e.g. change in bird calls).

While we focus here on quantifying ecological complexity, it is important to measure emergent properties to understand if and how complexity supports these processes. Ecosystem functions have been assessed using a wide range of methodologies that quantify properties such as soil functions (e.g. nutrient cycling, microbial biomass, organic matter or mycorrhizal colonisation (Fry et al. 2018)), litter decomposition rates (Ferreira et al. 2020), above-ground biomass (Camarretta et al. 2020) or predation and pollination rates (Woodcock et al. 2016). Over larger scales, the impact of restoration on ecosystem functions might be measured using approaches including eddy covariance to derive carbon and water fluxes (Li et al. 2021) or remote sensing to assess gross primary productivity (Camarretta et al. 2020, Chen et al. 2021). Resilience in the provision of these ecosystem functions can also be assessed. At small scales, this may be done by direct experimental manipulations using targeted perturbations, for example by simulating droughts (Fry et al. 2018). Analysis of ecosystem functions over larger scales (or aggregation point measurement data from multiple sites) provides an opportunity to assess system resilience resulting from landscape-scale restoration by directly observing changes in annual delivery of these processes (Redhead et al. 2020).

Box 2 describes how restoration might be focussed to achieve enhanced ecological complexity at local and landscape scales. Measures such as those described here could be used to assess progress towards complexity. Indeed, in operationalising the complexity concept, an adaptive management approach could be employed (Ebberts et al. 2018, Camarretta et al. 2020). This would involve checking progress in the development of complexity at relevant scales, using a range of measures to encompass the holistic nature of complexity, and modifying restoration interventions if and when progress is stalled or slow.

## How might a complexity framing inform restoration policy?

Increasing evidence of environmental degradation (IPBES 2018), and the lack of success in combatting this degradation (Secretariat of the Convention on Biological Diversity 2020), have contributed to a reframing of nature conservation in terms of value to humans (IPBES 2019). Expressing the benefits provided by nature in terms of human well-being is anticipated to ensure inclusion of nature more broadly in decision-making processes. A complexity paradigm directly addresses these benefits to people, as ecological complexity is expected to enhance ecosystem functions and their resilience at multiple scales. Restoration of ecosystem functions directly underpins enhancement of ecosystem services (Rey Benayas et al. 2009, Rey Benayas and Bullock 2012), as well as their resilience (Oliver et al. 2015a).

Legislation and policy typically remain targeted on rare or threatened species and associated habitats; for example, the Habitats and Birds Directives of the European Union or the USA Endangered Species Act. Even more recent legislative and policy developments such as no net loss and net gain focus on offsetting biodiversity losses that occur because of human developments (Bull and Brownlie 2017). While conventional targets to restore a preferred habitat might deliver increased complexity, functioning and resilience, this should not be assumed. Indeed, given many of these communities are characterised by rarities with narrow environmental tolerances, they may well represent some of the assemblages least likely to be resilient in the face of environmental change despite their socio-political resonance (Oliver et al. 2016, Enquist et al. 2019). For example, range-edge populations of butterflies are highly sensitive to changes in the weather

## Box 2. Achieving ecological complexity during restoration

What might restoring for ecological complexity look like and how might it differ from current approaches?

### Different aims, similar methods?

Restoring for ecological complexity may involve many of the same activities as for traditional restoration, although it will not typically involve management targeted at particular species. Even so, where key species important for re-establishing processes are missing (e.g. grazers, predators) or acting as hubs for trophic interactions (e.g. keystone species), reintroductions might be employed.

### Different evaluation

What does differ is how restoration is evaluated and deciding what success looks like. Martin et al. (2013) found that restoring tropical forests achieved tree species numbers (a measure of complexity) comparable to intact forests after ca 50 years, and carbon pools (an ecosystem function) after 80 years, but species composition was not close to resembling intact reference forests even after 100 years. In floodplain meadows, restoration of plant community functional structure was far faster than that of species similarity to target ancient grasslands (Woodcock et al. 2011). Viewing through the lens of reference communities, these outcomes might not be seen as successful, whilst there is room for optimism if restoring for complexity.

### Influential factors for restoring complexity

1) *Time* is often cited as the most important factor in achieving restoration in general and complexity specifically (Crouzeilles et al. 2016, Moreno-Mateos et al. 2020). However, the development of ecological complexity and emergent properties is generally non-linear with time (Woodcock et al. 2012a, Martin et al. 2013), and time alone may not be sufficient without additional actions. So, if one is no longer concerned with achieving a specific target composition, how might one speed up the enhancement of complexity? Several factors have been related to speeding up success for traditional restoration, and we list some of these that are likely to be important in enhancing complexity.

2) *The initial state or level of degradation* is important for traditional restoration, with more degraded sites typically taking longer to restore, particularly if that initial state is physically and/or chemically adverse (Klimkowska et al. 2010, Crouzeilles et al. 2016). Indeed, a complexity approach may be useful where these conditions constrain the restoration of a target community.

3) *Restoration initiation*, depending on the system, includes the establishment of physical attributes in hydrological systems (Palmer et al. 2014), the plant species sown (Fry et al. 2018), choosing between natural colonisation and planting trees (Reid et al. 2018) or undertaking soil amendments (Martins et al. 2021). A complexity approach could involve applying a range of methods over a landscape, selecting functional groups that enhance species interactions at the site level (Fry et al. 2018) and avoiding more difficult approaches if the aim is no longer to establish a reference system.

4) *Management* throughout a restoration programme can range from the more 'hands-off' approach of rewilding to highly interventionist (du Toit and Pettorelli 2019). It is clear that management is a key factor driving the development of restored systems (Guiden et al. 2021). Depending on the system, management can involve cutting herbaceous vegetation, thinning woodlands, introducing deadwood, introduction or exclusion of grazers, dredging of river channels, fire management, etc.

### The scale of restoration

Restoration management, particularly that governed by policy guidelines and/or achieving reference ecosystems, may tend towards highly prescribed approaches. Such prescription may lead to a homogeneity of restored ecosystems across landscapes. Complexity at landscape scales may be better supported by less fixed end points, including an emphasis on allowing more natural trajectories of community assembly. This includes greater consideration of landscape context and configuration to support connectivity (Fig. 2).

---

(Mills et al. 2017). Socio-political choices may therefore need to be made about the extent to which investment in ecological restoration seeks to prioritise particular species and habitats of cultural value or instead on alternative ecosystems that are more able to provide a variety of ecosystem services and are resilient under global change (Harris et al. 2006,

Gardner and Bullock 2021). A cost-benefit analysis could be undertaken whereby the resources needed to support traditional conservation goals (e.g. replicating an indigenous habitat type) are weighed against the creation of more cost-effective and resilient but non-standard communities, which nevertheless support ecological complexity and emergent

properties. The restoration of indigenous target communities and the associated costs or risks may be justified in some cases. In many others, such target-driven restoration may simply be unnecessary where the goals are more diverse, e.g. general augmentation of biodiversity, carbon sequestration or water resource protection. Ultimately, the decisions depend on priorities defined at national and international levels, but a presumption that certain communities will always be better needs to be challenged.

Environmental policies have rarely considered landscape-scale restoration, but there is increasing interest. The push for 'Forest Landscape Restoration' is leading to the development of landscape-focussed policies (Slobodian et al. 2020). A complexity framing could be valuable here, by addressing connectedness alongside the number and quality of habitat patches, the three measures that underpin the ability of systems to deliver ecosystem services (Mace et al. 2015). The reference ecosystem approach may in fact conflict with a landscape complexity aim as it could lead to a homogeneity of ecosystems across a landscape, because all have been restored towards the same target (Pywell et al. 2003). This problem may be exacerbated by the tendency of government schemes, such as agri-environmental funding, to have strict guidelines for restoration actions and targets (de Snoo et al. 2013), potentially leading to similar restoration activities by different actors (e.g. farmers) in a landscape and even at wider scales. A complexity aim could therefore be supported by policies that encourage planning for a variety of outcomes across landscapes. These might allow for more idiosyncratic local outcomes determined by spatial context and priority effects or more directed planning of local restorations to create landscape-scale variety. Connectivity, for example using corridors or stepping stones, would be critical to pursuing a complexity agenda and is enshrined in the ideas for a Nature Recovery Network in England (Isaac et al. 2018).

Rewilding is attracting huge interest in the policy and public arenas (Pettorelli et al. 2018) and could be one approach to enhancing complexity. Rewilding seeks to restore lost interactions between animals and plants, enabling natural processes to return and so restore ecosystem functioning (Svenning 2020). Complexity is cited as an aim for rewilding (Fernández et al. 2017, Perino et al. 2019), although it is not clear whether rewilding in itself necessarily achieves complexity. Trophic rewilding represents a specific approach, whereby the introduction of large predators or herbivores hopefully drives the development of complex interaction networks and provides niches for a variety of species (Bakker and Svenning 2018). However, some approaches to rewilding, such as natural regeneration, are not guaranteed to restore complexity due to high variability in outcomes (Reid et al. 2018). While complexity might be achieved by rewilding, high complexity, functioning and resilience can also be achieved by highly interventionist restoration approaches (Churchill et al. 2013, Jacobs et al. 2015). Thus, rewilding can be seen as sitting within a wider, complexity, framing of restoration, and we suggest that the ideas developed in this paper could be applied to relate rewilding actions more explicitly to a complexity framing.

Ultimately, incorporating complexity concepts into policy may not be too onerous. Related concepts such as ecosystem services and ecological resilience are already embedded in major initiatives such as the Sustainable Development Goals and the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services. Designing indicators and targets for complexity to help develop and assess policy will need research and co-design with policymakers; rewilding faces similar issues (Pettorelli et al. 2018). Metrics of complexity are therefore needed at both local (ecosystem) and regional (landscape) scales; for example, landscape connectivity indicators have been developed (JNCC 2019). It may, in fact, be more straightforward to develop indicators for emergent properties, such as ecosystem services (Maes et al. 2016) or ecological resilience (Ferrier et al. 2020). In due course, the development of such indicators and targets may facilitate the comparison of restoration outcomes across very different sites and landscapes and so aid assessment of success.

## Conclusions

To summarise, developing our understanding of ecological complexity, and the emergent properties associated with complex systems, will provide a complementary strategy to conventional restoration approaches. Advances can be made and consensus built if restoration policy and practice are grounded in the socio-cultural context, yet emphasise ecological processes over community composition, with pragmatic goals that are flexible in setting objectives to restore ecosystems and secure public benefits in a changing world. Our argument also emphasises the need for research to understand better how ecological complexity develops in ecosystems and across landscapes, what are the key drivers of complexity, the degree to which different aspects of complexity co-vary across scales and how these aspects of complexity link mechanistically to a variety of ecosystem functions and their resilience to ongoing environmental change.

## Author contributions

**Elisa Fuentes-Montemayor, Ben McCarthy, Kirsty Park, Rosie S. Hails, Ben A. Woodcock** and **Kevin Watts** contributed equally to this publication. **James** M. **Bullock**: Conceptualization (equal); Funding acquisition (equal); Writing – original draft (lead); Writing – review and editing (lead). **Elisa Fuentes-Montemayor**: Conceptualization (equal); Writing – original draft (equal); Writing – review and editing (equal). **Ben McCarthy**: Conceptualization

(equal); Writing – original draft (equal); Writing – review and editing (equal). **Kirsty Park**: Conceptualization (equal); Funding acquisition (equal); Writing – original draft (equal); Writing – review and editing (equal). **Rosie S. Hails**: Conceptualization (equal); Funding acquisition (equal); Writing – original draft (equal); Writing – review and editing (equal). **Ben A. Woodcock**: Conceptualization (equal); Writing – original draft (equal); Writing – review and editing (equal). **Kevin Watts**: Conceptualization (equal); Writing – original draft (equal); Writing – review and editing (equal). **Ron Corstanje**: Conceptualization (equal); Writing – review and editing (supporting). **Jim Harris**: Conceptualization (equal); Funding acquisition (lead); Writing – original draft (equal); Writing – review and editing (equal).

### Transparent Peer Review

### Data availability statement

No new data were created or analyzed in this study.

## References

Anand, M. et al. 2010. Ecological systems as complex systems: challenges for an emerging science. – Diversity 2: 395–410.

Aronson, J. et al. 2017. Conceptual frameworks and references for landscape-scale restoration: reflecting back and looking forward. – Ann. Mo. Bot. Gard. 102: 188–200.

Bakker, E. S. and Svenning, J.-C. 2018. Trophic rewilding: impact on ecosystems under global change. – Phil. Trans. R. Soc. B 373: 20170432.

Bull, J. W. and Brownlie, S. 2017. The transition from no net loss to a net gain of biodiversity is far from trivial. – Oryx 51: 53–59.

Burivalova, Z. et al. 2019. The sound of a tropical forest. – Science 363: 28–29.

Camarretta, N. et al. 2020. Monitoring forest structure to guide adaptive management of forest restoration: a review of remote sensing approaches. – New For. 51: 573–596.

Cardinale, B. J. et al. 2012. Biodiversity loss and its impact on humanity. – Nature 486: 59–67.

Chaplin-Kramer, R. et al. 2011. A meta-analysis of crop pest and natural enemy response to landscape complexity. – Ecol. Lett. 14: 922–932.

Chen, S. et al. 2021. Detecting drought-induced GPP spatiotemporal variabilities with sun-induced chlorophyll fluorescence during the 2009/2010 droughts in China. – Ecol. Indic. 121: 107092.

Churchill, D. J. et al. 2013. Restoring forest resilience: from reference spatial patterns to silvicultural prescriptions and monitoring. – For. Ecol. Manage. 291: 442–457.

Coleman, E. A. et al. 2021. Limited effects of tree planting on forest canopy cover and rural livelihoods in northern India. – Nat. Sustain. 4: 997–1004.

Creamer, R. E. et al. 2016. Ecological network analysis reveals the inter-connection between soil biodiversity and ecosystem function as affected by land use across Europe. – Appl. Soil Ecol. 97: 112–124.

Crouzeilles, R. et al. 2016. A global meta-analysis on the ecological drivers of forest restoration success. – Nat. Commun. 7: 11666.

de Snoo, G. R. et al. 2013. Toward effective nature conservation on farmland: making farmers matter. – Conserv. Lett. 6: 66–72.

du Toit, J. T. and Pettorelli, N. 2019. The differences between rewilding and restoring an ecologically degraded landscape. – J. Appl. Ecol. 56: 2467–2471.

Duffy, J. E. et al. 2017. Biodiversity effects in the wild are common and as strong as key drivers of productivity. – Nature 549: 261–264.

Ebberts, B. D. et al. 2018. Estuary ecosystem restoration: implementing and institutionalizing adaptive management. – Restor. Ecol. 26: 360–369.

Enquist, B. J. et al. 2019. The commonness of rarity: global and future distribution of rarity across land plants. – Sci. Adv. 5: eaaz0414.

ERP 2021. – <www.evergladesrestoration.gov/>.

Fanin, N. et al. 2018. Consistent effects of biodiversity loss on multifunctionality across contrasting ecosystems. – Nat. Ecol. Evol. 2: 269.

Fernandes, K. et al. 2019. Invertebrate DNA metabarcoding reveals changes in communities across mine site restoration chronosequences. – Restor. Ecol. 27: 1177–1186.

Fernández, N. et al. 2017. Rewilding: a call for boosting ecological complexity in conservation. – Conserv. Lett. 10: 276–278.

Ferreira, V. et al. 2020. Organic matter decomposition and ecosystem metabolism as tools to assess the functional integrity of streams and rivers – a systematic review. – Water 12: 3523.

Ferrier, S. et al. 2020. A globally applicable indicator of the capacity of terrestrial ecosystems to retain biological diversity under climate change: the bioclimatic ecosystem resilience index. – Ecol. Indic. 117: 106554.

Filotas, E. et al. 2014. Viewing forests through the lens of complex systems science. – Ecosphere 5: art1.

Flynn, D. F. B. et al. 2011. Functional and phylogenetic diversity as predictors of biodiversity–ecosystem–function relationships. – Ecology 92: 1573–1581.

Foster, N. R. et al. 2020. A muddy time capsule: using sediment environmental DNA for the long-term monitoring of coastal vegetated ecosystems. – Mar. Freshwater Res. 71: 869–876.

Fry, E. L. et al. 2018. Soil multifunctionality and drought resistance are determined by plant structural traits in restoring grassland. – Ecology 99: 2260–2271.

Gagic, V. et al. 2015. Functional identity and diversity of animals predict ecosystem functioning better than species-based indices. – Proc. R. Soc. B 282: 8.

Gámez-Virués, S. et al. 2015. Landscape simplification filters species traits and drives biotic homogenization. – Nat. Commun. 6: 8568.

Gann, G. D. et al. 2019. International principles and standards for the practice of ecological restoration. Second edition. – Restor. Ecol. 27: S1–S46.

Gardner, C. J. and Bullock, J. M. 2021. In the climate emergency, conservation must become survival ecology. – Front. Conserv. Sci. 2: 659912.

Gilbert, J. A. and Henry, C. 2015. Predicting ecosystem emergent properties at multiple scales. – Environ. Microbiol. Rep. 7: 20–22.

GL 2021. – <https://gondwanalink.org/>.

Gonzalez, A. et al. 2020. Scaling-up biodiversity–ecosystem functioning research. – Ecol. Lett. 23: 757–776.

Griffiths, R. I. et al. 2011. The bacterial biogeography of British soils. – Environ. Microbiol. 13: 1642–1654.

Guiden, P. W. et al. 2021. Effects of management outweigh effects of plant diversity on restored animal communities in tallgrass prairies. – Proc. Natl Acad. Sci. USA 118: e2015421118.

Harris, J. A. et al. 2006. Ecological restoration and global climate change. – Restor. Ecol. 14: 170–176.

Harvey, J. W. et al. 2017. Role of a naturally varying flow regime in Everglades restoration. – Restor. Ecol. 25: S27–S38.

Higgs, E. S. et al. 2018. Keep ecological restoration open and flexible. – Nat. Ecol. Evol. 2: 580–580.

Hilderbrand, R. et al. 2005. The myths of restoration ecology. – Ecol. Soc. 10: 19.

Hines, J. et al. 2015. Chapter Four – Towards an integration of biodiversity–ecosystem functioning and food web theory to evaluate relationships between multiple ecosystem services. – In: Woodward, G. and Bohan, D. A. (eds), Adv. Ecol. Res. Academic Press, pp. 161–199.

Hooper, T. et al. 2021. Developing policy and practice for marine net gain. – J. Environ. Manage. 277: 111387.

Huerta-Cepas, J. et al. 2017. Fast genome-wide functional annotation through orthology assignment by eggNOG-mapper. – Mol. Biol. Evol. 34: 2115–2122.

IPBES 2018. The IPBES assessment report on land degradation and restoration (edited by Montanarella, L. et al.). – Secretariat of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services, Bonn, Germany. 744 p.

IPBES 2019. Global assessment report on biodiversity and ecosystem services of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (edited by Brondizio, E. S. et al.). – IPBES secretariat, Bonn, Germany. 1148 p.

Isaac, N. J. B. et al. 2018. Defining and delivering resilient ecological networks: nature conservation in England. – J. Appl. Ecol. 55: 2537–2543.

IUCN 2021. – <www.iucn.org/theme/forests/our-work/forest-landscape-restoration>.

Jacobs, D. F. et al. 2015. Restoring forests: what constitutes success in the twenty-first century? – New For. 46: 601–614.

JNCC 2019. Habitat connectivity. – <https://jncc.gov.uk/our-work/ukbi-c2-habitat-connectivity/>.

Johnson, C. N. et al. 2017. Biodiversity losses and conservation responses in the Anthropocene. – Science 356: 270–274.

Klimkowska, A. et al. 2010. Prospects for fen meadow restoration on severely degraded fens. – Perspect. Plant Ecol. Evol. Syst. 12: 245–255.

Lefcheck, J. S. et al. 2015. Biodiversity enhances ecosystem multifunctionality across trophic levels and habitats. – Nat. Commun. 6: 7.

Levin, S. A. 1998. Ecosystems and the biosphere as complex adaptive systems. – Ecosystems 1: 431–436.

Li, Y. et al. 2021. Assessing MODIS carbon and water fluxes in grasslands and shrublands in semiarid regions using eddy covariance tower data. – Int. J. Remote Sens. 42: 595–616.

Lira, P. K. et al. 2019. Temporal lag in ecological responses to landscape change: where are we now? – Curr. Landscape Ecol. Rep. 4: 70–82.

MacArthur, R. 1955. Fluctuations of animal populations and a measure of community stability. – Ecology 36: 533–536.

Mace, G. M. et al. 2015. Towards a risk register for natural capital. – J. Appl. Ecol. 52: 641–653.

Maes, J. et al. 2016. An indicator framework for assessing ecosystem services in support of the EU Biodiversity Strategy to 2020. – Ecosyst. Serv. 17: 14–23.

Manning, P. et al. 2018. Redefining ecosystem multifunctionality. – Nat. Ecol. Evol. 2: 427–436.

Martin, P. A. et al. 2013. Carbon pools recover more quickly than plant biodiversity in tropical secondary forests. – Proc. R. Soc. B 280: 8.

Martins, W. B. R. et al. 2021. Ecosystem restoration after bauxite mining: favorable indicators for technosols construction and soil management using liming and subsoiling. – New For. 52: 971–994.

Mayr, E. 1982. The growth of biological thought. – The Belknap Press.

Menz, M. H. M. et al. 2013. Hurdles and opportunities for landscape-scale restoration. – Science 339: 526–527.

Mills, S. C. et al. 2017. European butterfly populations vary in sensitivity to weather across their geographical ranges. – Global Ecol. Biogeogr. 26: 1374–1385.

Montanarella, L. and Panagos, P. 2021. The relevance of sustainable soil management within the European Green Deal. – Land Use Policy 100: 104950.

Moreno-Mateos, D. et al. 2020. The long-term restoration of ecosystem complexity. – Nat. Ecol. Evol. 4: 676–685.

Murcia, C. et al. 2014. A critique of the 'novel ecosystem' concept. – Trends Ecol. Evol. 29: 548–553.

Nurk, S. et al. 2017. metaSPAdes: a new versatile metagenomic assembler. – Genome Res. 27: 824–834.

Oliver, T. H. et al. 2015a. Biodiversity and resilience of ecosystem functions. – Trends Ecol. Evol. 30: 673–684.

Oliver, T. H. et al. 2015b. Declining resilience of ecosystem functions under biodiversity loss. – Nat. Commun. 6: 8.

Oliver, T. H. et al. 2016. Are existing biodiversity conservation strategies appropriate in a changing climate? – Biol. Conserv. 193: 17–26.

Palmer, M. A. et al. 2014. From ecosystems to ecosystem services: stream restoration as ecological engineering. – Ecol. Eng. 65: 62–70.

Parrott, L. 2010. Measuring ecological complexity. – Ecol. Indic. 10: 1069–1076.

Perino, A. et al. 2019. Rewilding complex ecosystems. – Science 364: 5570.

Perring, M. P. et al. 2015. Advances in restoration ecology: rising to the challenges of the coming decades. – Ecosphere 6: 25.

Peterson St-Laurent, G. et al. 2021. R–R–T (resistance–resilience–transformation) typology reveals differential conservation approaches across ecosystems and time. – Commun. Biol. 4: 39.

Pettorelli, N. et al. 2018. Making rewilding fit for policy. – J. Appl. Ecol. 55: 1114–1125.

Pimm, S. L. 1984. The complexity and stability of ecosystems. – Nature 307: 321–326.

Pocock, M. J. O. et al. 2012. The robustness and restoration of a network of ecological networks. – Science 335: 973–977.

Ponge, J. F. 2005. Emergent properties from organisms to ecosystems: towards a realistic approach. – Biol. Rev. 80: 403–411.

Pywell, R. F. et al. 2003. Plant traits as predictors of performance in ecological restoration. – J. Appl. Ecol. 40: 65–77.

Qiu, H.-I. et al. 1999. Fractal characterization of hyperspectral imagery. – Photogrammet. Eng. Remote Sens. 65: 63–71.

Redhead, J. W. et al. 2018. Potential landscape-scale pollinator networks across Great Britain: structure, stability and influence of agricultural land cover. – Ecol. Lett. 21: 1821–1832.

Redhead, J. W. et al. 2020. The influence of landscape composition and configuration on crop yield resilience. – J. Appl. Ecol. 57: 2180–2190.

Reid, J. L. et al. 2018. Positive site selection bias in meta-analyses comparing natural regeneration to active forest restoration. – Sci. Adv. 4: eaas9143.

Rey Benayas, J. and Bullock, J. 2012. Restoration of biodiversity and ecosystem services on agricultural land. – Ecosystems 15: 883–899.

Rey Benayas, J. M. et al. 2009. Enhancement of biodiversity and ecosystem services by ecological restoration: a meta-analysis. – Science 325: 1121–1124.

Ruppert, K. M. et al. 2019. Past, present and future perspectives of environmental DNA (eDNA) metabarcoding: a systematic review in methods, monitoring and applications of global eDNA. – Global Ecol. Conserv. 17: e00547.

Schleuning, M. et al. 2015. Predicting ecosystem functions from biodiversity and mutualistic networks: an extension of trait-based concepts to plant–animal interactions. – Ecography 38: 380–392.

Secretariat of the Convention on Biological Diversity 2020. Global Biodiversity Outlook 5, Summary for Policy Makers. Montréal.

Shutt, J. D. et al. 2020. Gradients in richness and turnover of a forest passerine's diet prior to breeding: a mixed model approach applied to faecal metabarcoding data. – Mol. Ecol. 29: 1199–1213.

Slobodian, L. et al. 2020. Policies that support forest landscape restoration: What they look like and how they work. – Gland, Switzerland: IUCN.

Staudacher, K. et al. 2016. Diagnostic PCR assays to unravel food web interactions in cereal crops with focus on biological control of aphids. – J. Pest Sci. 89: 281–293.

Svenning, J.-C. 2020. Rewilding should be central to global restoration efforts. – One Earth 3: 657–660.

Tittensor, D. P. et al. 2014. A mid-term analysis of progress toward international biodiversity targets. – Science 346: 241–244.

Torres-Pulliza, D. et al. 2020. A geometric basis for surface habitat complexity and biodiversity. – Nat. Ecol. Evol. 4: 1495–1501.

Trisos, C. H. et al. 2020. The projected timing of abrupt ecological disruption from climate change. – Nature 580: 496–501.

van der Plas, F. et al. 2016. Biotic homogenization can decrease landscape-scale forest multifunctionality. – Proc. Natl Acad. Sci. USA 113: 3557–3562.

Verdone, M. and Seidl, A. 2017. Time, space, place and the Bonn Challenge global forest restoration target. – Restor. Ecol. 25: 903–911.

Watts, K. et al. 2020. Ecological time lags and the journey towards conservation success. – Nat. Ecol. Evol. 4: 304–311.

Woodcock, B. A. et al. 2007. The importance of sward architectural complexity in structuring predatory and phytophagous invertebrate assemblages. – Ecol. Entomol. 32: 302–311.

Woodcock, B. A. et al. 2011. Can long-term floodplain meadow recreation replicate species composition and functional characteristics of target grasslands? – J. Appl. Ecol. 48: 1070–1078.

Woodcock, B. A. et al. 2012a. Identifying time lags in the restoration of grassland butterfly communities: a multi-site assessment. – Biol. Conserv. 155: 50–58.

Woodcock, B. A. et al. 2012b. Limiting factors in the restoration of UK grassland beetle assemblages. – Biol. Conserv. 146: 136–143.

Woodcock, B. A. et al. 2016. Spill-over of pest control and pollination services into arable crops. – Agric. Ecosyst. Environ. 231: 15–23.

World Economic Forum 2020. – <www.1t.org/>.

Zellweger, F. et al. 2013. Remotely sensed forest structural complexity predicts multi species occurrence at the landscape scale. – For. Ecol. Manage. 307: 303–312.