Mathematical Perspectives on Rewilding

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Abstract

Achieving sustainable human-wildlife coexistence in well-functioning ecosystems is a vitally important and major challenge under global change. In response, rewilding is an emerging paradigm in ecosystem service provision through the re-establishment of natural ecological processes in self-sustaining ecosystems.

Effective prediction of ecological changes in rewilding projects requires tools integrating quantitative methods with social-economic dimensions and thinking. We consider the current state of such quantitative treatments, highlighting opportunities for harnessing mathematics and statistics. We present an emerging quantitative framework, encompassing four key areas of the rewilding process: design and planning, ecological modelling, metrics for assessment, and coupled social-ecological systems, informed by recent progress in mathematical, statistical, and ecological modelling. The adaptive cycle concept is used to integrate these four key areas. Dynamical systems modelling informed by empirical knowledge allows us to address trans-disciplinary feedbacks, nonlinearities, and anticipate the potential for emerging properties and critical transitions/regime shifts during rewilding, predicting the range and likelihood of alternative scenarios.

Our framework provides a possible foundation and new opportunities for a more robust quantitative and predictive methodology for rewilding. We argue that a project is more likely to achieve its goals, and in a more cost-effective way, if mathematical scientists are included from the beginning.

1 Introduction

Rewilding is an emerging, radical and sometimes controversial approach to renewing degraded ecosystems (Box 1 and references therein). Research into rewilding has advanced around conceptual frameworks (e.g., Holling & Gunderson, 2002; Du Toit & Pettorelli, 2019; Perino et al., 2019; Wang et al., 2025; see also Box 2), with recent calls to incorporate expert advice and scientific evidence (O'Connell & Prudhomme, 2024). Rewilding is now starting to develop a qualitative and quantitative evidence base (e.g., Hart et al., 2023; Selwyn et al., 2025). Mathematical and statistical concepts and applications must now be integrated as the field matures, maximising opportunities to synthesise and generalise relevant insights.

In this perspective, we report on initial discussions between rewilding practitioners, ecologists, statisticians and mathematicians that arose from a series of seminars and workshops held in 2024 (see Acknowledgements), highlighting how mathematical and statistical approaches can contribute to the rewilding agenda, through four broad themes: planning and design, ecological modelling, metrics for assessment, and coupled social-ecological systems. There is considerable overlap across these themes, given the inherently trans-disciplinary nature and methods associated with rewilding (Box 2).

We propose a planning cycle (Figure 1) suited to the development and monitoring of a rewilding project, exploring how mathematical and statistical modelling can improve rewilding success. Designing a rewilding project requires scenario generation and uncertainty quantification, e.g., predicting ways to restore one or more ecosystem services. Although mathematical modelling provides a rigorous set of analytical tools, well-used in ecology to

Box 1: What is rewilding?

Here, we adopt Pettorelli et al. (2018) proposed definition of rewilding:

> 'The reorganisation of biota and ecosystem processes to set an identified social-ecological system on a preferred trajectory, leading to the self-sustaining provision of ecosystem services with minimal ongoing management.'

While there is not necessarily a sharp line between rewilding and restoration, here are some of the typical differences:

- Restoring generally means taking the landscape back to a particular historical baseline, managing habitats for resident and increasingly rare species; rewilding acknowledges environmental and other anthropogenic pressures are causing such significant changes that novel ecosystems must be allowed to emerge;
- Accordingly, (re)introduction or translocation of new species based on their traits (rather than historical precedent) to re-establish ecosystem function are more accepted in rewilding. In restoration, translocations would be based on historical species compositions;
- Willingness to accept novel species assemblies leads to less predictability of the rewilded system, greater risk, and new modelling challenges;
- There may be less room for people in a restored landscape, while paradoxically there may also be a need for greater long-term management commitment. The rewilding definition explicitly works with social-ecological systems, recognising people as part of nature, while at the same time preferring (human) interventions that can be reduced over time as ecological processes are re-established.

See Pettorelli et al. (2018), Pettorelli et al. (2019), Jepson & Blythe (2021), and Svenning et al. (2024) for in-depth discussion and Du Toit & Pettorelli (2019) and Mutillod et al. (2024) for the differences between rewilding and more traditional ecological restoration; the case for new conservation paradigms is also made forcefully in Gardner & Bullock (2021).

understand how processes create structure (patterns) and function in ecosystems, it is becoming more apparent that detailed simulation models are needed to capture the full complexity of such systems. However, modelling in general forces us to make our assumptions explicit—e.g., by identifying and quantifying the interactions between species that are likely to occur after a rewilding intervention—and is key to quantifying possible outcomes and uncertainties emerging from such interventions. These outcomes could include predicting which species are likely to thrive, decline, be attracted to the rewilded area, or be driven out. Translating theoretical insights from mathematical models (see Table 1) to practical guidance also requires the integration of empirical data via statistical modelling and inference.

A crucial step towards more successful management of rewilding projects is the explicit acknowledgment of the dynamic feedbacks between the complex dynamics of both the natural world and human behaviour, e.g. public opinion and decision-making in the context of multiple stakeholders with competing priorities. For example, considering how rewilding projects interact with adjacent agricultural land-use through changes in the presence, abundance, and functions provided by natural pests and beneficial species, these projects will impact public engagement and opinions and, thereby, may more effectively drive policy change (Kline et al., 2017). Social-ecological modelling approaches provide a useful framework to uncover subtle and often unexpected effects emerging from complex social-ecological systems (Liu et al., 2007; Alberti et al., 2011), in particular the potential for tipping points, regime shifts, long transients and other outcomes associated with non-linear dynamics that may impact rewilding success (Biggs et al., 2018; Maes et al., 2024a).

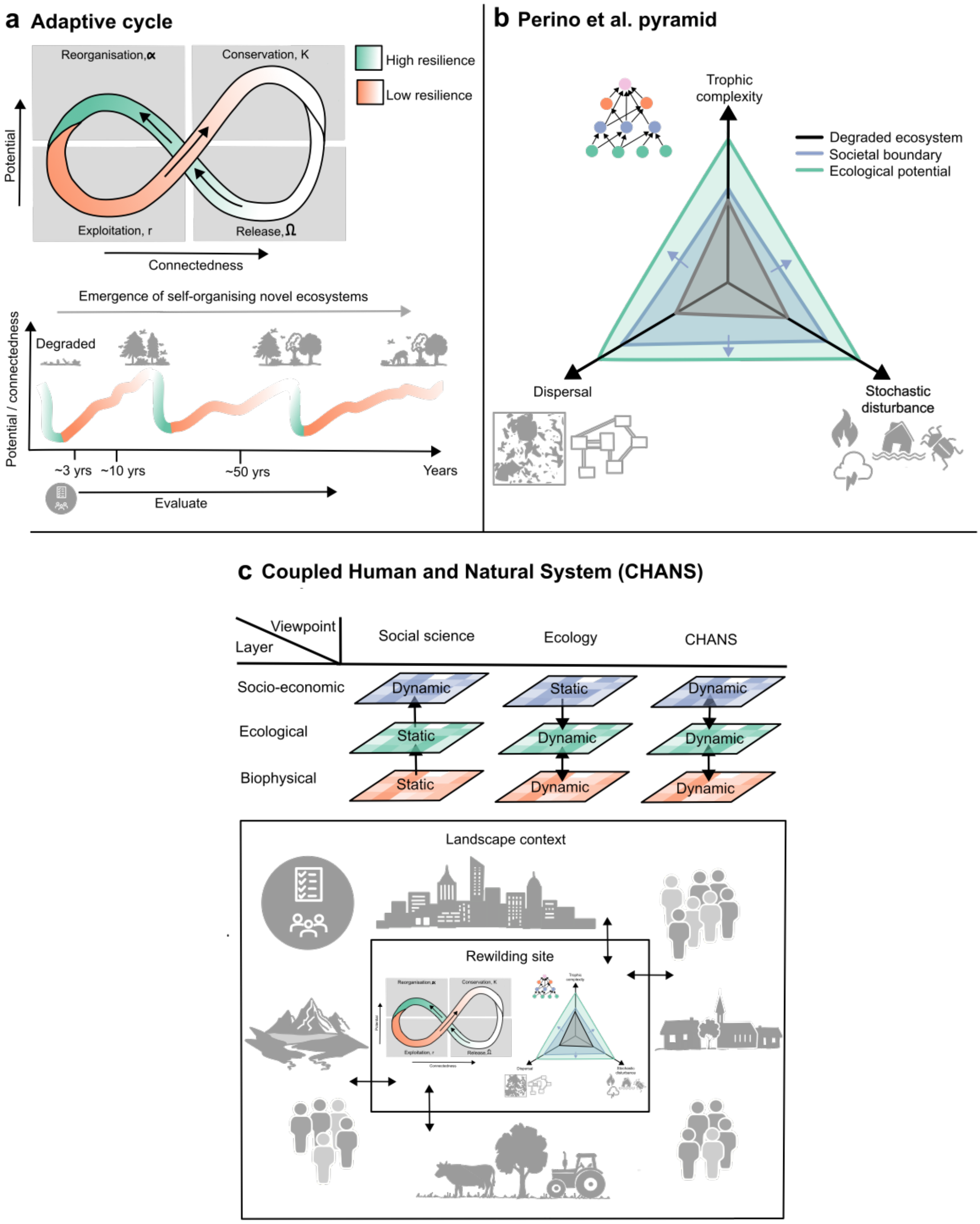
An established methodology for monitoring and measuring the success of a rewilding project emerges from a rewilding definition explicitly based on ecosystem service delivery by providing a link to the large literature on natural capital and valuation of ecosystem services (Costanza et al., 1997; Daily, 1997; Kareiva et al., 2011; Braat & De Groot, 2012). A multi-dimensional view of success accounts for the various priorities held by different stakeholders, related to the emerging concepts of ecosystem function and service multifunctionality (Hector & Bagchi, 2007; Byrnes et al., 2014; Manning et al., 2018). However, rather than prescribing a particular set of metrics to be used for rewilding quantification, we advocate a tailored approach unique to each project. We aim to provide a framework helping rewilding researchers identify the best metrics for their objectives, as well as pointing to challenges that mathematicians and statisticians are well placed to address.

As rewilding matures with the accumulation and synthesis of relevant data and concepts within and across disciplines, we believe it is timely to build on this growing evidence base and invite researchers from empirical ecology and environmental sciences, to mathematics, statistics, social sciences and the humanities, to collaborate and contribute to the rewilding agenda.

2 Planning, design, and assessment

Rewilding initiatives are particularly challenging given the complex mix of stakeholders, their contrasting priorities, and the substantial spatial, temporal and cross-biological scales of rewilding questions and approaches. For example, the Rewilding Europe Initiative identified a minimum period of 20 years to obtain meaningful results (Rewilding Europe, 2021). However, the planning stage rarely involves mathematical modellers, with modelling often only done after the experimental or data gathering stages (if ever), which is too late to have a positive impact. Our aim here is to highlight where principles and aims of rewilding can be informed by mathematical and statistical modelling to plan, design, and assess rewilding projects (Figure 1).

Box 2: Conceptual frameworks for rewilding



A variety of conceptual frameworks have been proposed to help us engage with the ecological processes underpinning rewilding projects. **a, Adaptive cycle.** The adaptive cycle metaphor conceptualises how ecosystems continually cycle through phases of exploitation, conservation, release, and reorganisation. The conceptual space is characterised by *potential, connectedness and resilience.*

Box 2 continued

a, Adaptive cycle continued. Connectedness refers to the links between components and or processes in the system, with high connectedness indicating a system strongly affected by external variability, since connectedness allows easy propagation of external disturbance through the ecosystem. **Potential** represents the broad range of options for future ecosystem behaviour in response to change, determined by the accumulated biomass and nutrients available for organisms to interact with through exploitation or synergy. Finally, **resilience** is the degree of disturbance a system can buffer without undergoing a regime shift or transition to a new attractor. This property is low at the front of the loop (the fore-loop, orange shading) and high at the back of the loop (back-loop, green shading). For example, a climax community can be regarded as having approached the K-phase of conservation, functionally rich and therefore with high potential, but the high connectedness and interdependencies of species in the ecosystem can make it potentially vulnerable to the cascading effects of extreme external disturbance such as a fire or flood, giving the ecosystem low resilience. The low resilience comes from the presence of keystone species, where only a few species are able to produce a particular ecosystem service and the loss of such species cannot be compensated for by the remaining members of the ecological community (e.g., beavers play the role of keystone species in riparian ecosystems (Biggs et al., 2012; Sundstrom & Allen, 2019)). In a food web context, keystone species enable the transport of nutrients between trophic levels, so that removing them would likely result in extinction cascades.

b, Rewilding assessed by ecosystem state: The extent to which an ecosystem is self-organising, complex and robust to future disturbances can be characterised by three processes: **trophic complexity** (increases with the number of components and connections between them), **dispersal** (increases with increased landscape connectivity) and **stochastic disturbance** (increases as ecosystems are released from natural disturbance suppression and from controlled anthropogenic disturbances) (Perino et al., 2019). Promoting these three properties enhances ecosystem resilience and rewilding aims to shift the boundaries constraining these properties via a range of endeavours, from humans retreating from a location (passive rewilding) to reintroductions (e.g., of large herbivores) and restoration of natural flood regimes to facilitate the return of trophic complexity and habitat connectivity (active wilding).

c, CHANS: Coupled Human and Natural Systems (CHANS) modelling treats both the human and ecological system as coupled and dynamically varying on timescales that prevent easy decoupling. This recognises that human behaviour and decision making (e.g., through suppressing natural disturbance, or farmland abandonment) has a strong influence on the trajectories of natural systems, but also *vice versa* with natural systems highly integrated in social systems (e.g., opportunities for nature based economies or increased human-wildlife conflicts). In a rewilding system both the human and natural system are highly complex.

Ecological modelling can help understand the maximum potential of a landscape in terms of ecosystem services, based on its typology, history, and location within the wider landscape. By embedding this with stakeholder perspectives (see Section 5), such models can offer a powerful tool to evaluate trade-offs and set rewilding targets. Species distribution modelling (Elith & Leathwick, 2009; Lawler et al., 2011), and other habitat suitability and spatial planning analyses may be valuable to identify key areas enabling the most valuable or cost-effective rewilding projects, whilst models of opinion dynamics and decision-making (Hegselmann & Krause, 2002; Epstein, 2018; Helfmann et al., 2023; Vortkamp & Hilker, 2023; Petrovskii et al., 2025a), reveal the sensitivity of the corresponding social-ecological system to different factors (Cariboni et al., 2007; Banos-Gonzalez et al., 2018) and can be used to suggest an optimal solution (Law & Morton, 2013; Verhagen et al., 2018; Knight et al., 2024). The ecological benefits of rewilding ideally trigger reinforcing beneficial feedback loops in both ecosystem services and public opinion. However, the same interconnected complex systems can also give rise to detrimental feedback cycles. Mathematical modelling of nonlinear dynamics can help understand possible scenarios and long-term outcomes.

Mathematical models of ecological dynamics (see Section 3) can be used as a 'virtual laboratory' for exploring rewilding ideas in a way that is faster, cheaper, and without the potential negative consequences of real-life experiments. Modelling can be used to predict ecosystem responses to different interventions, revealing the subtle, often counter-intuitive, effects that can emerge from complex, highly nonlinear species interactions, in particular possible tipping points and regime shifts (Biggs et al., 2018; Vignal et al., 2023; Maes et al., 2024b), and ecosystems dominated by human-caused ecological novelty (Svenning et al., 2024). Modelling can help predict emerging properties, such as species coexistence, as well as understanding changes in dynamic ecosystem processes towards—ideally—self-sustaining natural systems. Reliable predictions also require further mathematical modelling to account for, estimate and quantify uncertainties inherent in highly complex systems (Berger & Smith, 2019; Volodina & Challenor, 2021).

Due to these uncertainties, the observed trajectory may deviate from the most likely path. Quantitative information about the current ecosystem state and the observed direction of change is therefore needed at all stages (Figure 1), so that any unanticipated or undesirable changes can be detected as early as possible and potential actions evaluated within the social-ecological context of the system and its overall aims. This requires continuous monitoring, data collection, and analysis. Monitoring methodology of a rewilding site can be optimised by use of bespoke statistical design (Smith et al., 2011). When indirect observations (including remote sensing, LiDAR and eDNA) are used, care should be taken to establish a clear link between the proxy measurement and the desired information, through strong theoretical or evidence-based underpinning (e.g., Schulte to Bühne et al., 2022). This is another area where mathematical and statistical analysis is necessary in developing consistent and scalable methodologies (Wong et al., 2024). Adaptive protocols should be used (Månsson et al., 2023), informed by consideration of appropriate metrics at different stages of the project (see Section 4) and directly fed into the mathematical models to update the predicted dynamics. In conclusion, rewilding projects are complex and uncertain; stakeholders need to take decisions at all points over long timescales. Ecological modelling (Section 3) can provide key insights and quantitative information for robust decision making at all stages of the project, from planning to strategy, implementation, and evaluation (Figure 1).

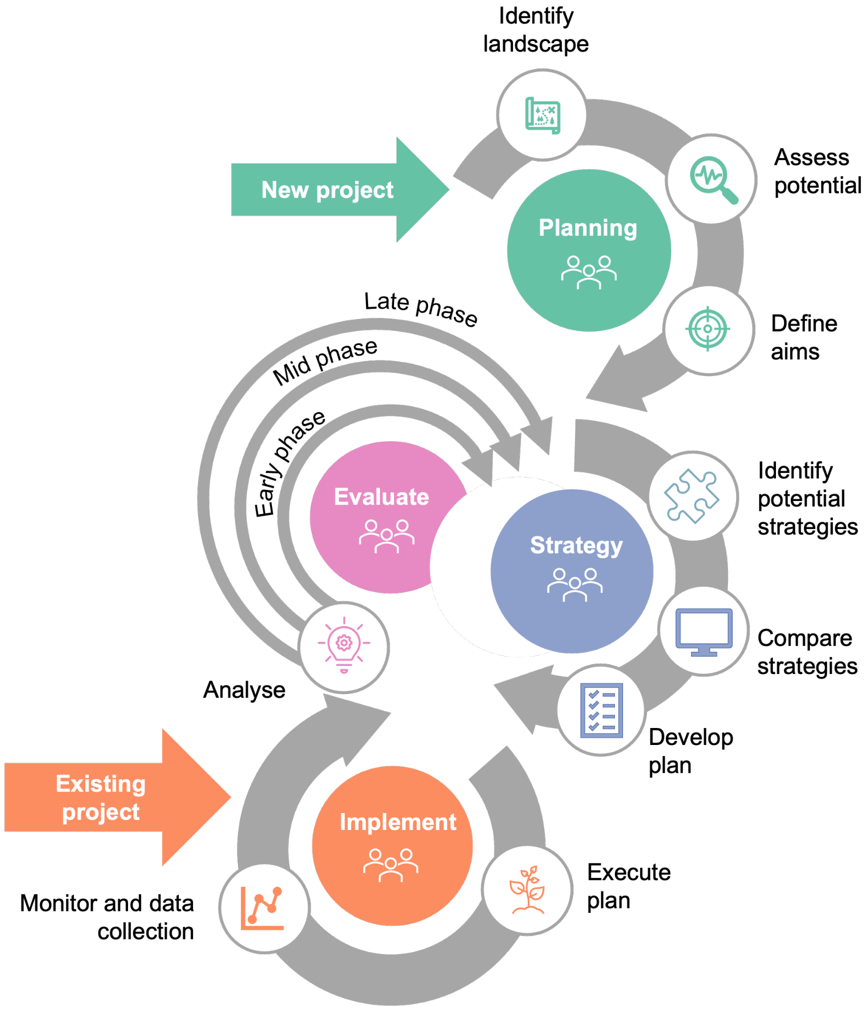


Figure 1: **Schematic for a rewilding project cycle.** New projects will start with an initial planning phase, identifying appropriate sites and evaluating the potential of sites. Aims of the project should be constructed in collaboration across all stakeholder groups to ensure comprehensive understanding of potential impacts. Identification and comparison of different rewilding strategies is then undertaken, with a planned pathway developed to align the proposed aims of the project with the most effective way of realising the ambitions. Implementation of the plan is closely accompanied by monitoring and evaluation of the ecosystem state. Evaluation at different phases of the project in response to analysis of the monitoring and data collection is essential to ensure that aims and strategies can be revisited and predicted outcomes evaluated against observations being made. Existing rewilding projects may enter this project cycle at the evaluation stage, using the approach to update strategy. At each core element of the project cycle (Planning, Strategy, Implementation and Evaluation) mathematics can play a key role, providing stakeholders with insight to ensure robust decision-making at all points within a project.

3 Ecological modelling

In this section, we discuss how ecological modelling may be applied to rewilding, with a focus on ecosystem states, dynamics, and application to systems that are adaptively responding to anthropogenic and other stressors. We summarise eight (primary or focal) processes or levels of analysis of relevance to rewilding (Table 1). These studies represent examples of mathematical modelling approaches that range from the 'easily translatable to rewilding problems' to the more 'inspirational in terms of their formulation'. The table is indicative of the range of mathematical and numerical tools (kinds of equations and methods of analysis) that have previously addressed issues relevant to rewilding.

3.1 Bridging rewilding concepts and ecological theory

Ecological and ecosystem modelling have a wealth of methods that can be adapted to the multi-scale and multi-dimensional complexities of rewilding (Table 1). Important differences arise that suggest a shift in thinking when applying these methods to rewilding. These can be broadly categorised as: (i) a focus on self-sustaining delivery of prioritised ecosystem service(s), contrasting with restoration and conservation approaches which tend to emphasise a specific species or habitat target (Du Toit & Pettorelli, 2019), (ii) a shift in focus away from the individual species-level to functional groups, (iii) a need to develop predictions that incorporate the continual disturbance associated with natural turnover and anthropogenic pressures, recognising that the ecological communities currently supported in a site may change in the future (Martes et al., 2024), (iv) a wider social-ecological context (e.g., multiple stakeholder priorities and opinions) that influences the prioritisation of particular ecosystem services provided by rewilded systems through positive and/or negative dynamical feedbacks (discussed in Section 5).

The adaptive cycle (Holling & Gunderson, 2002) has been proposed as a conceptual framework relevant to rewilding (Du Toit & Pettorelli, 2019), capturing the continual disturbance and recovery inherent in ecosystems that are episodically perturbed (fire, extreme weather, herbivore eruptions, etc.). These multiple disturbances, and the various stages of an ecosystem's response to them—through phases of exploitation, conservation, release, and reorganisation—result in a landscape characterised by continual change across space and time, which can be conceptually classified using three properties: potential, connectedness and resilience (Box 2(a)).

Rewilding aims to take advantage of ecosystems' reorganising potential to facilitate the flow through the adaptive cycle with minimal further intervention. A system's response diversity ('the diversity of responses to environmental change among species contributing to the same ecosystem function' (Elmqvist et al., 2003)) determines the range of potential trajectories of ecosystem reorganisation following disturbance, during the adaptive cycle's α-phase. High response diversity supports future ecosystem function under a range of environmental fluctuations (Walker et al., 2023). Response diversity is a crucial property of resilient and adaptive systems. From a trophic point of view, this is related to prey switching (Gasparini & Castelt, 1997), omnivory (Bridier et al., 2021) and mixotrophy (Mitra et al., 2014). Response diversity of a degraded system is contained within its residual abiotic and biotic diversity, together with spatial spillovers of diversity from the surrounding landscape (Bradfer-Lawrence et al., 2025). Importantly, response diversity can be augmented through management (Ross & Sasaki, 2024). In the face of uncertainty, ecological modelling can provide stakeholders with projections about the range of potential ecosystem trajectories and their relative probabilities. However, the response diversity concept still lacks a rigorous mathematical foundation (Ross & Sasaki, 2024), highlighting the need for further theoretical development and its formal

Table 1: Process models: general references and selected type-annotated studies relevant to rewilding

Primary process*	Application	Study+	Model⋆	Space†	Time‡	Primary analyses#
1. Movement	Seed dispersal (wind)	1a	PDE	Hom	Aut	Proj
	Seed dispersal (animal)	1b	IBM	Pix	Aut	Proj, Sens
	Animal dispersal	1c	Sim	Hom, Pix	N-aut	Proj
	Home range creation	1d	PDE	Hom	Aut	Stab
	Pollination services	1e	Sim	Pix	N-aut	Stab, Opt
2. Population Growth	Rewilding plants	2a	Mat, Stoc	Hom	Aut	Proj, Sens
	Rewilding herbivores	2b	Mat, Stoc	Hom	Aut	Proj
	Rewilding carnivores	2c	Sim, Stoc	Pat, Pix	N-aut	Proj
	Habitat enrichment	2d	ODE	Hom	Aut	Stab
	Reforestation	2e	T-S	Hom	Aut	Proj
	Patchy environment	2f	Stoc	Pat	N-aut	Stab
	Invasion	2g	T-S	Hom	Disc	Proj
3. Competition	Grass-tree balance	3a	Mat, Stoc	Hom	N-aut	Proj, Sens
	Browser-grazer balance	3b	Sim	Hom	N-aut	Proj
	Multispecies coexistence	3c	ODE	Hom	Aut	Stab
	Extinction cascades	3d	ODE	Hom	Aut	Stab
4. Consumer-resource	Herbivore-veg balance	4a	ODE	Hom	Aut	Proj, Sens
	Predator-prey balance	4b	ODE	Hom	Aut	Stab
	Predator-prey spatial	4c	IBM, MF	Pix	Aut	Proj
	Host-parasite dynamics	4d	ODE	Hom	Aut	Proj, Stab
	Decomposition	4e	ODE	Hom	Aut	Proj
	Multiconsumer	4f	PDE	Dist	Aut	Stab
	Multispecies (density)	4g	ODE	Hom	Aut	Form
	Multispecies (biomass)	4h	ODE	Hom	Mem	Form
5. Tritrophic	Food chain stability	5a	ODE	Hom	Aut	Stab
	Food chain exploitation	5b	Stoc	Hom	Aut	Opt, Stab
	Biological control	5c	ODE	Hom	N-aut	Stab
	Spatially explicit	5d	IBM	Pix	Disc	Stab
6. Foodweb	Food chain comparison	6a	ODE	Hom	Aut	Form, Stab
	Consumer networks	6b	ODE	Hom	N-aut	Stat
	Scavenger impacts	6c	ODE	Hom	N-aut	Stat
	Link indiv & pop states	6d	IBM	Pat, Pix	N-aut, Mem	Form
	Extinctions	6e	ODE	Hom	Aut	Stab
7. Ecosystem	Niche models	7a	Stat	Pix	Aut	Proj
	Emergent structure	7b	IBM	Pix	N-aut	Proj, Stab
	Trophic mass balance	7c	Sim	Pix	Disc, N-aut	Proj
8. Humans in-the-mix	Landuse simulator	8a	ABM, Sim	Pat, Pix	Disc, N-aut	Proj, Opt
	Coupled human-natural	8b	ABM, Sim	Pix	Disc, N-aut	Proj, Opt

⋆**Type:** ABM/IBM=agent/individual-based, ODE =Ordinary diff. eqn., PDE=partial diff. eqn., Mat=Matrix projection, Sim=Simulation, Stat=Statistical (not dynamic), Stoc=Stochastic, T-S=time series

†**Space:** Dist=distributional, Hom=homogeneous, Pat=patches; Pix=pixelated

†**Time:** Aut=autonomous (time-independent params.), Disc=discrete, Mem=memory (time delays, integro-diff), N-aut=non-autonomous (time-dependent drivers)

#**Analysis:** Form=formulation, Proj=projection (prediction), Sens=sensitivity, Stab=stability, Opt=optimisation

*__General references:__ (by process number) **1:** Schupp et al., 2010; Morales & Morán López, 2022; **2:** (Moorcroft et al., 2001; Ovaskainen & Hanski, 2004; Le et al., 2012; Newman et al., 2014; Lewis et al., 2016); **3:** Barabás et al., 2018 ; **4:** Fortin et al., 2015; White et al., 2018; Diz-Pita & Otero-Espinar, 2021; **6:** Amarasekare, 2008; **7:** Kearney & Porter, 2009;

+**Studies:** 1a: Katul et al., 2005 ; 1b: Will & Tackenberg, 2008; 1c: Vuilleumier & Metzger, 2006; 1d: Moorcroft et al., 1999 ; 1e: Häussler et al., 2017; 1f: Kot et al., 1996; 2a: Crone et al., 2011; 2b: Gaillard et al., 1998; 2c. Gantchoff et al., 2022; 2d: Gurney & Lawton, 1996; 2e: Fox et al., 2001; 2f: Evans et al., 2013 ; 3a: Baxter & Getz, 2005; 3b: Donaldson et al., 2022; 3c: Saavedra et al., 2017; 3d: Lundberg et al., 2000; 4a: Månsson & Lundberg, 2006 ; 4b: Sáez & González-Olivares, 1999; 4c: Surendran et al., 2020; 4d: Tompkins et al., 2002 ; 4e: (Todd-Brown et al., 2012) ;4f: He et al., 2023; 4g: Lafferty et al., 2015; 4h: Getz, 2011; 5a: Hastings & Powell, 1991; 5b: Liu & Bai, 2016 ; 5c: Gutierrez et al., 1994; 5d: Charnell, 2008; 6a: Pahl-Wostl, 1997 ; 6b: Boit et al., 2012; 6c: Mellard et al., 2021; 6d: Getz, 2013 ; 6e: Fowler, 2013 ; 7a Escobar, 2020; 7b: Harfoot et al., 2014 ; 7c: Christensen & Walters, 2004 ; 8a: Le et al., 2008 ; 8b: Synes et al., 2019 integration into mathematical models.

Ecosystems generally transition through the back-loop of the adaptive cycle very rapidly while the fore-loop transitions are much slower (Box 2). Transitions from the α- to r-phase typically occur over one or two seasons (e.g., food webs reassembling and biomass growing following a major disturbance such as a flood or pest outbreak), and the r- to K-phase transition takes many years (e.g., the gradual accumulation of nutrients and trophic complexity). We therefore focus our attention on how modelling could shed light on the fore-loop phase transitions. We use the language of a terrestrial ecosystem, but the ideas apply more generally (e.g., in the marine realm, Brooker et al., 2025).

3.2 Ecosystem recovery from initial distrubance/degredation

As a first step to identifying potential trajectories of a rewilding site, it is instructive to make an account of achievable ecosystem states. Keith et al. (2022) proposed a typology of ecosystems in terms of resources, ambient environment, disturbance regimes, biotic interactions and human activity. In parallel, mapping the residual diversity (the remnant vegetation, seed banks and animals that survived a disturbance event) along with the arrival of endemic or exotic species during the α-phase offers new opportunities for predictive modelling. These features, when aggregated appropriately, help determine the initial response diversity of an ecosystem.

Organic matter decomposition models (e.g., Moorhead & Sinsabaugh, 2006) may also play a role in understanding the initial transition from the α-phase to the r-phase, at least in a terrestrial setting. In particular, mechanistic modelling of soil biological processes can predict the resource dynamics following ecosystem collapse. The α-phase is characterised by 'leakiness', of both resources and biomass (Holling & Gunderson, 2002). This may involve lateral spread of above-ground dead matter, or the loss of mineralised nutrients into groundwater in the absence of viable plant roots to retain them and support microbial consumers (Chapin III et al., 2011; Runyan & D'Odorico, 2012). We propose combining deterministic plant-microbe-nutrient models (which can produce realistic estimates of the leak stabilisation time and hence the approximate duration of an initial α-phase) with the concept of response diversity. Community assembly theory can then be applied to determine which biota from the diverse pool of potential colonists are more likely to occupy the area and survive the initial reorganisation phase (Chase, 2003; HilleRisLambers et al., 2012). Some of the 'historical accidents' (Holling & Gunderson, 2002) caused by new species introductions may be preserved in the model end-state, yielding a new ecosystem type.

3.3 Dynamics of ecosystem self-organisation

Once an initial community has been assembled, dynamic ecosystem models can be adapted to forecast the self-organisation and temporal evolution of the ecosystem. Because rewilding prioritises ecological processes over specific species compositions, a coarse-grained approach, such as modelling functional types rather than individual species, is often more appropriate and allows communities to be assessed in terms of their capacity to promote a self-sustaining complex ecosystem. Coarse-graining by functional type has been successfully applied in large-scale vegetation modelling (e.g., Joint UK Land and Environment Simulator (JULES), Harper et al. (2016)), which classifies all plant species globally into as few as nine functional types. For rewilding, extending the list of functional types to include other taxonomic ranks is desirable. General ecosystem models such as the Madingley model (Harfoot et al., 2014) attempt to do this, and have been used to assess potential recovery of trophic structure in response to active rewilding strategies (Hoeks et al., 2023). These methods are currently typically aimed at continental or national scales and would need adaptation to work at smaller spatial scales. At small spatial scales, agent-based modelling has also been trialled (Neil et al., 2025), allowing for the representation of individual-level interactions and heterogeneity. Regardless of approach, the identification of appropriate functional groupings is critical (Streit & Bellwood, 2023). For example, maintaining a diverse range of responses to disturbance across functional groups is essential for minimising the need for human intervention and ensuring long term ecosystem self-regulation (Walker et al., 2023).

Interactions between functional groups can be modelled and classified as either inhibition or promotion of biomass growth (e.g., competition and mutualism) or as transfers of biomass (e.g., predation, Geary et al. (2020), and Figure 2). The biomass transformation web (BTW) formulation (Getz, 2011) provides a useful framework with two advantages over traditional compartmental modelling. First, it explicitly tracks and recycles dead biomass into system resources, properly capturing scavenging and decomposition processes, which are crucial when studying degraded ecosystems and are important parts of nutrient cycling/ecosystem processes. Second, it includes a memory variable to keep track of stress and the cumulative impact of past favourable or unfavourable conditions on the growth and sustainability of ecosystem components. Thus, this framework facilitates predicting the evolution of the biomass distribution among functional groups (the biomass signature), and hence of a coarse-grained community type. Such predictions can be validated against empirical data, making the approach well-suited to applied monitoring in rewilding contexts.

One of the many challenges of taking a coarse-graining approach to dynamical ecosystem modelling lies in the parameterisation of the models and their integration with data (Larsen et al., 2016), which is often available at the species level. For example, it is not trivial to estimate the reproductive rate of a functional group when its constituent species have markedly different reproductive rates. Additionally, the number and definition of functional groups, and the allocation of species into these groups, will vary across rewilding sites. As a result, the parameters determining the interactions between functional groups, which may implicitly attempt to aggregate over the underlying species-level parameters, may also vary significantly between systems. This variability complicates both model calibration and the transferability of models across sites.

To estimate parameter values at the level of functional groups, modellers can draw on ecological metabolic theory, which quantifies how metabolic rates scale with body size and temperature (Brown et al., 2004; Loeuille & Loreau, 2005; Kearney et al., 2021). Even when adopting such approaches, aggregating species into functional groups requires that uncertainty due to variation in body sizes within a functional group be combined with uncertainty in the metabolic rate estimates, and propagated through to predictions at the level of the rewilding site. Accurate quantification of these uncertainties may require a combination of large numbers of model runs to capture parameter uncertainty, and ensemble modelling approaches to reflect structural model uncertainty (Vollert et al., 2024)

3.4 Interacting adaptive cycles and landscape recovery

So far, we have limited our considerations to conceptualising the landscape within a single adaptive cycle. Starting with a degraded landscape, an appropriate set of functional types is assembled, which then interact to drive the site through this cycle. However, natural disturbances mean that the cycle is continually repeated—and not always from the same starting point.

During that process, a panarchy of adaptive cycles will emerge (Figure 3) , as heterogeneity develops across the landscape. Each of these weakly connected adaptive cycles may operate asynchronously and semi-independently, self-organising into a mosaic of ecosystem patches

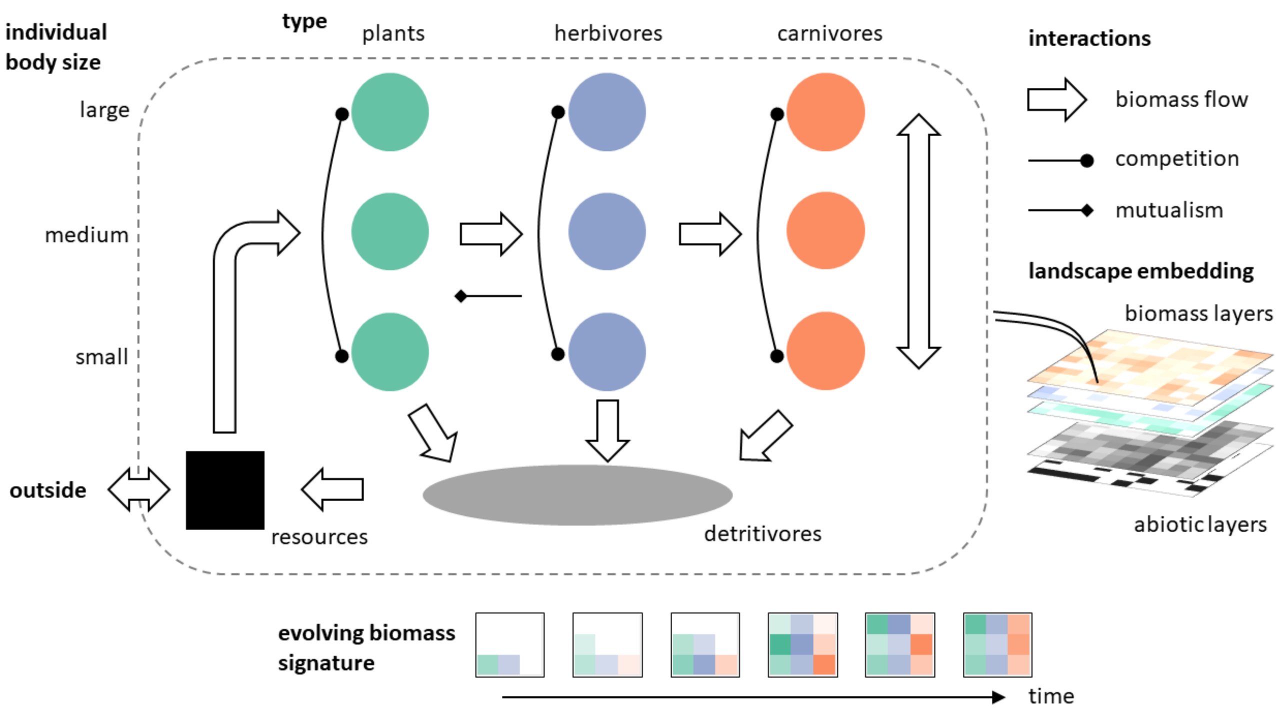


Figure 2: **Schematic of a model for terrestrial community dynamics at a functional group resolution. Core panel:** The core process modelled is biomass transfer between functional groups. This occurs by consumption of biomass (e.g., predation) and decomposition of dead biomass (returning to a resource pool). Note small carnivores can consume the biomass of (deceased) larger carnivores by scavenging. Competition, or mutualism, between functional groups would degrade, or enhance, biomass conversion. Note that competition will also emerge naturally from consumption; it is included explicitly to capture trait-based effects such as shading. The importance of mutualism varies considerably between communities. Critical mutualistic interactions would need to be identified and included; we illustrate this with a mutualist interaction between small plants and herbivores, e.g. pollination. Species are assigned to functional groups using suitable characteristics, in this case trophic position and individual body size. **Landscape embedding:** A spatial approximation for a rewilded area could be constructed by discretising the landscape into grid cells with varying abiotic properties. The community dynamics model could then be solved in each grid cell accounting for between-cell dispersal by each functional group. **Evolving biomass signature:** The community composition would be characterised in terms of its total biomass and its distribution between functional groups. Here we assume that plant, herbivore, and carnivore biomass in each size category could be monitored. The distribution of biomass between these nine functional groups is represented by colour saturation in a grid corresponding to the core panel (*cf.* to the density distributions in Figure 3).

that contributes to ecological stability and resilience across the entire rewilded landscape. Indeed, a resilient ecosystem is one in which its component parts occupy a diversity of states at any one time, so that a disturbance collapsing one part of the system does not result in systemic collapse.

The selective extinction of certain kinds of organisms can dramatically reduce ecosystem stability. For example, top predators, generally depending on a much larger area, are more sensitive to habitat fragmentation (Komonen et al., 2000). This also means that rewilding can be disproportionately more successful in larger (or well-connected) areas than at smaller spatial scales. Oostvaardersplassen in the Netherlands provides a paradigmatic example: an approximately 60 km^2 landscape of drained seabed initially developed into a relatively homogeneous expanse of grassland and shrubs (Jepson & Blythe, 2021). Introducing large herbivores acted as a disturbance regime, triggering the emergence of a more heterogenous landscape of grassy meadows, clumps of trees, ponds, streams, etc., each with its own dynamic behaviour (Marris, 2009). The modelling approaches we prescribe can be applied in a similar fashion at either the landscape scale (e.g., for the system driven by large herbivore disturbance), the patch scale (e.g., for the meadows grazed by geese), or even finer scale (e.g., ponds, individual decomposing trees, or deer carcasses). Modellers can draw from the extensive existing literature on spatially structured modelling, to partition the landscape of interest into smaller patches, each represented by a chosen model, such as the BTW biomass model (Getz, 2011), with dispersal between these patches. The appropriate number, size and connectance of patches will depend on a range of ecological and practical considerations, including the spatial extent of the rewilding project, the intrinsic and desired degree of landscape heterogeneity, the number of functional groups considered, and computational resources.

4 Rewilding metrics

A well-designed rewilding project will have long-term goals that can be measured, defined in terms of the delivery of an agreed bundle of ecosystem services. These goals should be established in advance through collaboration with relevant stakeholder groups (Section 2). Defining goals in terms of ecosystem services has several advantages: there is a general agreement on the definition of the concept, and a vast literature on their quantification and valuation (Daily, 1997; Costanza et al., 1997; Kareiva et al., 2011; Braat & De Groot, 2012; *cf.* also Table 2).

However, it is important to respect the different biological, temporal and spatial scales involved in a rewilding project. Detailed measurement of ecosystem services may be inappropriate in the early stages, specifically during the α- and r-phase of the adaptive cycle, Box 2(a), as the long-term behaviour of a complex ecosystem cannot be reliably inferred from its initial development (Hastings et al., 2018; Abbott et al., 2024). The most appropriate measure of success in the 3–10 years following a species (re)introduction or translocation might simply be an (annual) assessment of whether the species remains present and is establishing a viable population. At later stages, as key ecological processes and functions underlying ecosystem service delivery begin to take shape, the emphasis should shift towards identifying indicators of healthy ecosystem development, and conversely to pick up potential early warning signs of undesirable regime shifts. Thus, it becomes appropriate to monitor ecosystem properties such as connectivity, demography, genetics, phenology, dispersal, (Box 2(b)) and ecosystem dynamics (stability, density dependence, alternative stable states). Many early warning indicators are based on the statistical analysis of time series, emphasising the importance of regular, long-term data collection—ideally spanning multiple generations of the

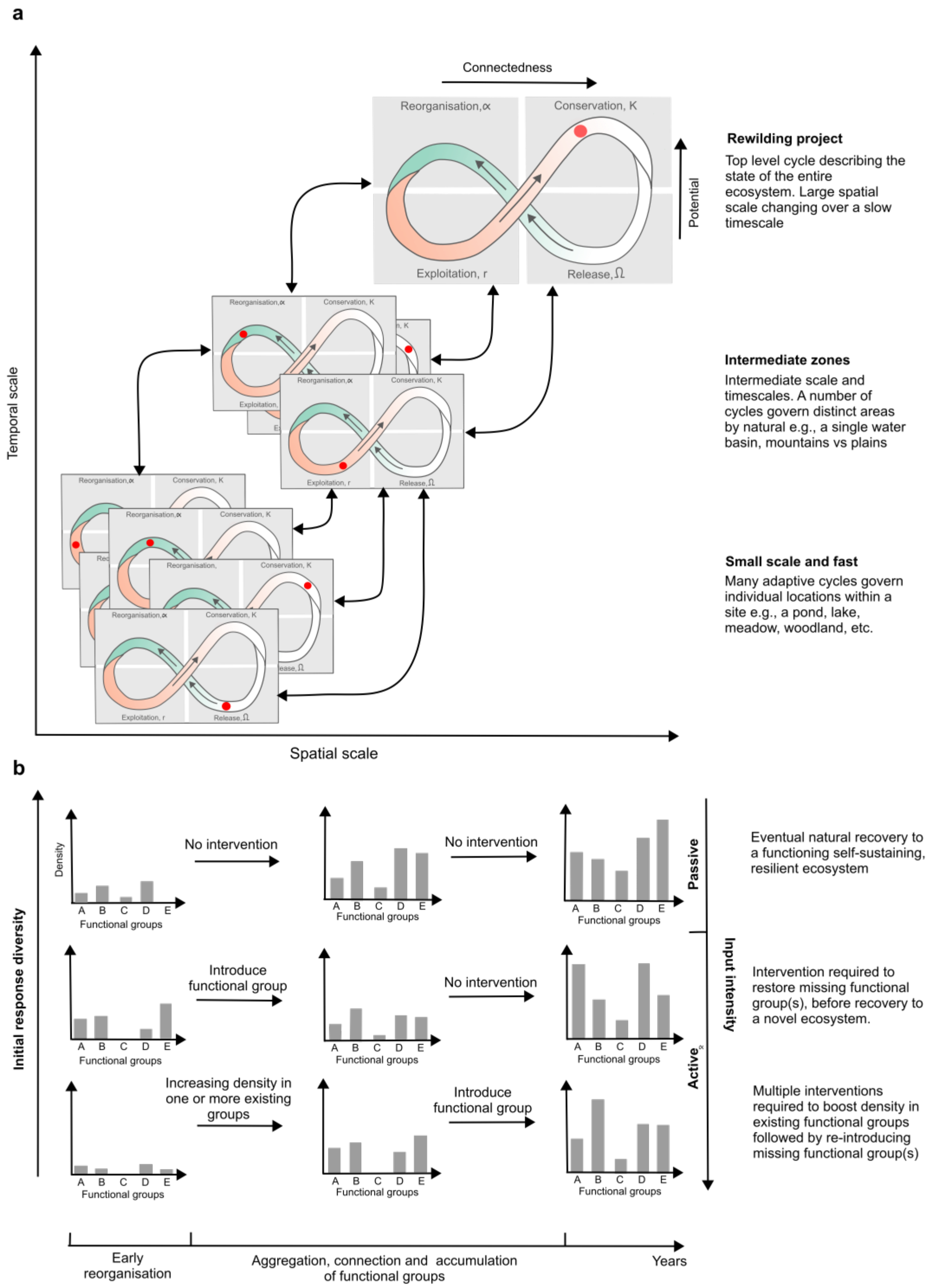


Figure 3: **Rewilding across spatial and temporal scales through the conceptual lens of panarchy. a** Illustration of variation in community state depending on choice of temporal and spatial resolution. The landscape scale meta-community is composed of communities for distinct habitat types. These communities are further divided into sub-communities which are influenced by the properties of a specific site and interact with neighbouring sub-communities. Each sub-community can be at a different stage (red dot) of its own adaptive cycle and are combined to obtain the state of a community. Similarly the state of the meta-community is a combination of the states of the communities. **b** Illustrative community trajectories for different initial community compositions/response diversities and levels of intervention. Densities of five notional functional groups are represented in the bar charts (*cf.* biomass signatures). When all functional groups are present in an initial degraded community, it can recover with minimal intervention (first row). If a functional group is missing in the initial community, it may be possible to (re-)introduce suitable species and leave a new ecosystem to emerge (middle row). In very degraded communities, it may be necessary to first (re-)introduce species in extant functional groups to restore community robustness, before (re-)introducing absent functional groups (final row).

focal organisms and functions (Scheffer et al., 2012; Dakos et al., 2024). After this, in the late r- to K-phase of the adaptive cycle, the focus shifts towards quantifying the delivery of ecosystem services, with metrics related to these services (Table 2) becoming the primary indicators of project success.

In practice, temporal scales will overlap, and monitoring schemes will need to recognise this. For example, if water purification is an objective, simple checks on water clarity and appearance of indicator species can be performed early on, supplemented by quantitative estimates in the later stages of the project. In the next subsections, we discuss recent approaches to measurement in rewilding and the future opportunities and challenges of monitoring and measuring success.

4.1 Linking metrics to conceptual frameworks

Perino et al. (2019) proposed quantifying rewilding success and the extent to which an ecosystem becomes self-organising and robust to future disturbances by measuring three processes: trophic complexity, dispersal and stochastic disturbance (Box 2(b)).

Trophic (or food web) complexity—a classic concept in ecology (Paine, 1966; Paine, 1969)—has been (loosely) defined as species richness within or across trophic levels (Jabiol et al., 2013) and/or functional groups (Anujan et al., 2021). In practice, however, trophic levels can be difficult to delineate, and hence assess quantitatively in real multispecies systems, as consumers do not always fall within discrete trophic levels (e.g., due to cannibalism, intraguild predation, omnivory, ontogenetic niche shifts, etc.). An upper limit of three to four effective trophic levels has been suggested based on a suite of complexity metrics that account for the power-law relationships inherent to trophic transfers (Ulanowicz et al., 2014). Measures of trophic richness may also be constructed from biodiversity measures incorporating a suitable similarity matrix (Leinster & Cobbold, 2012). Ecological network analysis offers a well-developed methodology to quantify macroscopic systems-indicators to compare (Baird et al., 1991) or monitor (Ulanowicz, 1996) the macroscopic structure of ecological systems. A network approach combining a resource-consumer-function tensor (a multi-dimensional array) with phyto-centric and function-centric embedding through multilayer ecological and bipartite networks has recently been developed (Hervías-Parejo et al., 2024). This framework is general enough to apply to ecosystems encompassing multiple ecological functions, which will likely prove to be useful in rewilding contexts.

Stochastic/Natural disturbances can initially be quantified by their frequency and magnitude. For example, Gilljam et al. (2019) show how numerous terrestrial animal populations are affected by common environmental drivers (temperature, precipitation, etc.), with differing temporal autocorrelation structures. Further insight can be gained from estimating the variance and trends of these environmental variables over time and space—and how these translate into corresponding distributions (and their statistical moments) of demographic rates through (potentially non-linear) species-environment functional responses. In other situations, the frequency, or simply the presence or absence, of extreme or catastrophic environmental events may be useful metrics for rewilding scenarios.

Dispersal can be defined as the movement of individuals across continuous space, or as transfers among discrete habitat patches, with different metrics applicable depending on the spatial scale and landscape structure. For example, rates of spread/net-squared displacement are relevant for individuals moving across spatially continuous habitats, while multiple structural and functional connectivity metrics already exist for conservation planning across discrete habitat patches/protected areas (Keeley et al., 2021), with a recommendation to focus on functional metrics where possible. Mathematical models in landscape ecology help identify landscape elements (patches and corridors) that are critically important for maintaining connectivity (Pereira et al., 2017).

4.2 An evidence base for rewilding

Hart et al. (2023) reviewed 22 studies of European rewilding projects and almost half (10/22) assessed the abundance of focal species and/or species richness. Calculating biodiversity metrics (e.g., beta-diversity) using these basic data was rare. Five of the twenty two studies measured plant cover, often as a percentage, and using remote sensing technologies such as satellite imagery or LiDAR. Only one study made use of eDNA, to quantify the diet of focal herbivores. Two studies went beyond abundance-based quantitative methods, assessing performance of focal species through indicators such as plant productivity and bird nesting behaviour. Five studies used qualitative approaches to understand the values and narratives of stakeholders and local communities, but only one study mixed narrative and abundance-based approaches.

These findings perhaps reflect the challenges of collecting relevant quantitative information early in the life cycle of rewilding projects—at the beginning of the fore-loop, the r-phase of the adaptive cycle. They also point at opportunities for developing monitoring strategies appropriate to the rewilding timeline.

4.3 Ecosystem resilience, service delivery and measurement

Resilience is a concept closely associated with rewilding, and frequently appearing in definitions of the practice (Du Toit & Pettorelli, 2019; Carver et al., 2021). Yet, its measurement and quantification are challenging (see, however Yi & Jackson (2021) and Dakos & Kéfi (2022)). The review of Selwyn et al. (2025) assessed the resilience (engineering, ecological and social-ecological) of a number of rewilding projects, using a general framework (Lloret et al., 2024). Their results provide important empirical support for the hypothesis that rewilding (*sensu* Perino et al. (2019)) tends to increase ecosystem resilience.

The establishment of sustainable ecosystem service delivery will take time: at least twenty years for a terrestrial ecosystem and this temporal scale should be assessed on a case-by-case basis (Rewilding Europe, 2021). Thus, we argue for long-term monitoring programmes that evolve alongside the system, adapting as the system runs from the α- through the r- to the K-phase of the adaptive cycle (Box 2(a)). Possible metrics for ecosystem services relevant in rewilding are given in Table 2.

The key concept of *biodiversity* is not an ecosystem service (though it underlies services such as provision of genetic resources, soil formation, and pollination services). The 'multi-layered relationship' between biodiversity and ecosystem services is discussed in (Mace et al., 2012). Nonetheless, assessments of species abundance and biodiversity should be included in the monitoring of a rewilding project, possibly using a similarity matrix (Leinster & Cobbold, 2012) to count 'trait biodiversity', in line with the coarse-graining approach discussed in Section 3. It is crucial to focus on functional diversity, instead of biodiversity *per se*, by quantifying redundancy both within and between functional groups. The former is more related to reliability (Naeem & Li, 1997) and insurance (Loreau et al., 2003), while the latter quantifies functional redundancy (Luczkovich et al., 2003) and functional diversity (Lin et al., 2022). In an extreme case, a functional group can be composed of a single species that is irreplaceable and solely responsible for an ecological function. These are keystone species (defined as single-species functional groups (Bond, 1994)).

Much of the work on ecosystem service assessment (e.g., Kareiva et al. (2011)) focuses on measuring an individual ecosystem service in isolation. While our definition does not state this explicitly, a rewilding project will generally aim to deliver a number (or bundle) of ecosystem services simultaneously. It may therefore be preferable to adopt metrics that capture ecosystem multifunctionality, in which case care must be taken to avoid over-counting (Manning et al., 2018).

5 Rewilding projects as social-ecological systems

Our definition of rewilding from Pettorelli et al. (2018) (see Box 1) recognises rewilding as a process applicable to social-ecological systems. Thus, we must incorporate human interactions in our models. The importance of such interactions can be seen from the simple example of a species facing extinction. This situation may affect human behaviour and result in a conservation campaign that will avert the immediate extinction threat. Ignoring the social-ecological aspects of this simple system would likely lead to unreliable predictions of extinction times.

More generally, human decision-making and public support play a key role in the dynamics of a rewilded ecosystem and are, in turn, affected by environmental change. This reciprocal relationship is a key issue broadly affecting conservation and natural resource management, where environmental problems are embedded in highly complex and uncertain social-ecological systems characterised by strong links and multiple interactions (reviewed in Schlüter et al. (2012); Figure 4). Acknowledging this feedback effect when modelling is crucial, resulting in more realistic scenario generation, with great potential to assist decision making and planning (Farahbakhsh et al., 2022; Bialozyt et al., 2025; Khodaparast et al., 2025). Furthermore, rewilding decisions must be taken within a wider landscape context, requiring methods to optimise decisions in complex, shared, multifunctional landscapes (Cole et al., 2023). While ecological engineering and management tools are improving over time, limitations are still strong (e.g. as encountered during assisted migration in forestry (Williams & Dumroese, 2013)).

5.1 Coupled human and natural systems (CHANS) framework

Coupled Human and Natural Systems (CHANS) modelling provides a framework for the study of the two-way feedbacks in social-ecological systems (Box 2(c)). In essence, a CHANS framework must incorporate the following three components:

- **i. Ecosystem dynamics**: modelling the relevant ecological and/or environmental processes at play;
- **ii. Social dynamics**: modelling the relevant aspects of human behaviour, societal processes (e.g. health, education, culture, etc.), social learning, social norms, economic and political considerations;
- **iii. Coupling**: modelling the information flow and driving influences between the ecosystem and social dynamics components: these include environmental change in response to human actions and, in turn, human response to environmental change, so that both the environment and human behaviour are seen as dynamic (as opposed to pure ecosystem models in which the background social environment is fixed).

A CHANS model is therefore essential to understanding “the impacts of social interventions and their potential to avoid catastrophic environmental events” (Farahbakhsh et al., 2022). This is particularly true over the longer timescales relevant to rewilding, where it is unrealistic to treat human interactions with the ecosystem as fixed. A CHANS model may

Table 2: **Examples of ecosystem services related to Rewilding** adapted from Costanza et al. (2017). There is widespread agreement on the main headings and minor differences of detail in the illustrative examples (Costanza et al., 1997; Daily, 1997; World Resources Institute et al., 2003; Sukhdev et al., 2010). See also Selwyn et al. (2025), Table 2 for related information. In the last column we have given indicative measures or methods for the assessment and quantification of the given ecosystem services. Detailed methods for mapping and measuring many, but not all of these ecosystem services, in both biophysical and monetary values have also been proposed (Kareiva et al., 2011). Although not an ecosystem service, *biodiversity* is a crucial indicator of ecosystem health and is an important tool in measuring and monitoring any rewilding project (Kareiva et al., 2011, Ch. 13; Leinster & Cobbold, 2012).

Ecosystem service	**Illustrative examples**	**Possible metrics**
Provisioning	Food production	Quantity normalised by area (g/m^2)
	(Fresh) water	Water clarity/turbidity (Formazin Nephelometric Units (FNU) or Nephelometric Turbidity Units (NTU)), indicator species (presence/absence)
	Raw materials	Quantity extracted (e.g., gravel) normalised by area (g/m^2)
	Genetic resources	Biodiversity; similarity sensitive diversity measures of different pheno-/genotypes, e.g., ${}^qD^{\mathbf{Z}}(\mathbf{p})$ (Leinster & Cobbold, 2012)
Regulating and habitat	Gas/pollution regulation	Concentration of nitrogen oxides in air (volume), NO_x g/m^3 (or ppm) or CO_2 concentration in air or water (ppm)
	Water regulation	Long-term monitoring of extreme events (flood/drought); flow rates (m^3/s)
	Erosion control	Soil loss rates (km^{-2}/yr)
	Pollination	Insect biodiversity/key insect species (individuals/m^2)/plant biodiversity (${}^qD^{\mathbf{Z}}(\mathbf{p})$)
	Biological control	Reduction in pest species (individuals/m^2)
Supporting and habitat	Nutrient cycling	Rate of nitrogen fixation (nmol/L/hr)
	Refugia	Nurseries for fisheries (individuals/m^2 or m^3)
	Soil formation	Soil volume created (m^3/s)
	Water cycling	Evaporation/transpiration (mm/s), residence times (s or yr)
	Primary production	g/m^2/yr
Cultural	Recreation	Biodiversity
	Cultural	Green spaces, providing areas for safe play, shade (reduced temperatures, °C) and reduction in noise pollution (e.g., in parks, graveyards, dB)
	Spiritual or religious enrichment	Quality of life indicators (e.g., ONS Measures of national well-being dashboard: Quality of life in the UK)
	Cultural heritage	Participation, satisfaction (%)
	Recreation and tourism	Number of participants/visitors/users (per 100k) per year (individuals/yr)
	Aesthetic experience	% agreement with statement

predict effects that would not be seen otherwise, such as shocks, hysteresis, memory effects and other types of unexpected tipping points and regime shifts (Liu et al., 2007; Suzuki & Iwasa, 2008; Figueiredo & Pereira, 2011; Sugiarto et al., 2015; Henderson et al., 2016; Synes et al., 2019).

CHANS models are needed to understand how social-ecological coupling affects the dynamics in time-varying environmental conditions typical in rewilding. Further, they are indispensable when it comes to addressing the effects of microscale human decision-making (Schlüter et al., 2012). This includes the incorporation of indigenous knowledge into conservation and resource management decisions (Jessen et al., 2022). Despite this potential for CHANS models to be applied to rewilding projects when considered in their full complexity as social-ecological systems, considerable work is required to describe such systems (Box 2(c)) within their landscape-scale ecosystem context and in terms of their multi-faceted human-human and human-environment couplings (Figure 4).

While incorporating social-ecological coupling (component iii) in a CHANS model may yield qualitatively different predictions from modelling the ecosystem (component i) alone, it greatly increases model complexity. This leads to a trade-off between more realistic but more computationally intensive and data-demanding models versus simpler, more tractable ones (Getz et al., 2018). For CHANS modelling to be meaningfully applied to rewilding decision making, this trade-off will typically require the incorporation of the needs of the most relevant (human) stakeholders as well as the identification of the most significant elements of the ecosystem.

One of the important but subtle ways in which the environment impacts human dynamics is by producing changes in *opinion*. The dynamic nature of public opinion may be of critical importance: for example, the public perception of a natural resource crisis and flood risk has played a key role in Switzerland transitioning from net deforestation to net reforestation in the twentieth century (Mather & Fairbairn, 2000). On the other hand, despite its many successes in increased biodiversity, adverse public opinion in the face of grazer mortality in Oostvaardersplassen led to management policies that were perceived as more humane but took away from the 'pure' rewilding ethos of the project as conceived in the late 1980s (Jepson & Blythe, 2021).

5.2 Rewilding in multifunctional landscapes

Balancing the benefits and risks of rewilding in a multifunctional landscape with a significant agricultural component is an important but complex subject. Trade-offs in land allocation (for example between intensive agriculture and wider ecosystem service provision (Mikolajczak et al., 2022)) can be analyzed through the concept of multifunctional landscapes (Cole et al., 2023) and decisions informed by insights from multi-objective mathematical optimisation (Knight et al., 2024). There is potential to use such techniques to reach a consensus reflecting both human-centric perspectives and, for example, biodiversity (Petrovskii et al., 2025b).

The provision of ecosystem services by a rewilding project will benefit the human communities that are part of the multifunctional landscape. Such benefits should feed into a virtuous circle in which the value of rewilding is recognised and further investments made. However some rewilding actions, particularly the (re)introduction of large mammals, especially predators, may carry real costs and turn public opinion against such projects (Pettorelli et al., 2019).

At a smaller scale, the increased biodiversity associated with a rewilding project will bring a range of species, some of which are pests, others beneficial (Emden, 1964; Cleveland et al., 2006; Yang et al., 2019). The balance of costs and benefits needs to be assessed in each case through monitoring and modelling studies to inform public opinion and contribute to the design and ongoing monitoring of the project.

5.3 Rewilding and public opinion

When it comes to interactions with public opinion, rewilding projects face challenges that are typical of other types of conservation projects and more generally of problems around climate change mitigation (Bauer et al., 2009). Thus findings from those fields can be reinterpreted and used in the rewilding context. But rewilding has its own specific features, providing new opportunities for social-ecological modelling.

In the field of climate change, CHANS models have been developed that incorporate *personal experience and perception of risk* and these are highly relevant to rewilding problems. Studies have been conducted to understand both how to change minds about climate change and how to favour the transition from awareness to behavioural change (Većkalov et al., 2024). As a result, the scientific community's approach to communication of climate-change issues has undergone a significant transformation as it has become clear that negative messages around extinction, increasing temperatures etc., are ineffective, leaving people overwhelmed and without any options for positive action (Jepson & Blythe, 2021). By contrast, more personal messages, relating to impacts on everyday life, have been found to be more effective (Soliman, 2024; Većkalov et al., 2024).

Beckage et al. (2018) provide an example of CHANS modelling to couple a climate model for CO_2 emissions with a social model for perception of risk and personal experience based on planned behaviour theory. In this coupled model, increasing the levels of CO_2 emissions produce higher global temperatures, triggering more frequent extreme events. The frequency of extreme events drives behavioural change, decreasing GHG emissions. Analogous studies geared towards rewilding seem to be lacking at present. Public preferences about rewilding interventions have generally been gauged by surveys (Mikolajczak et al., 2022; Hart et al., 2023) and discrete-choice experiments (Dunn-Capper et al., 2024).

CHANS modelling of public opinion and perception of rewilding projects in relation to the current biodiversity crises is ripe for development, an important point being that successful rewilding projects often have *positive* messages for example around biodiversity gain and nature recovery, where climate change messaging is generally very negative (Tree & Burrell, 2023). Of course a balanced view must be presented of the potential negative opinions and on-the-ground consequences (encroachment of agricultural areas and human population centres) of reintroduction of large herbivores or carnivores (Lecuyer et al., 2022). One possibility is further to mathematise and reinterpret Ostrom's works, devoted to understanding the effect of graduated punishment in enforcing social norms (Ostrom, 2000; Kinzig et al., 2013) into models that put more emphasis on reward (Lee & Iwasa, 2013). An objective of constructing CHANS models of rewilded social-ecological systems would be to balance the positive and negative perceptions and to understand how they are impacted by possible rewilding interventions. In particular, rewilding requires governments, investors and the public to adopt a future-focused mindset. Studies on "future thinking" (Oyserman & Horowitz, 2023), where a felt image of the future is employed to aid behaviour modification in the present (for example in the context of financial planning, where they have informed the design of interactive tools to help plan personal finances), could then be brought to bear in rewilding.

Changes in opinion and behaviour are also affected by *legislation and social norms*, processes relevant to rewilding. CHANS modelling in this direction has included the integration of ecological models with opinion formation models of various types (Bak-Coleman et al., 2021), ranging from classical agent-based models for consensus formation and the impact of the spread of fake news (Franceschi & Pareschi, 2022), to models that describe the relationship between cooperation, enforcement of legislation (Sugiarto et al., 2015) and social welfare.

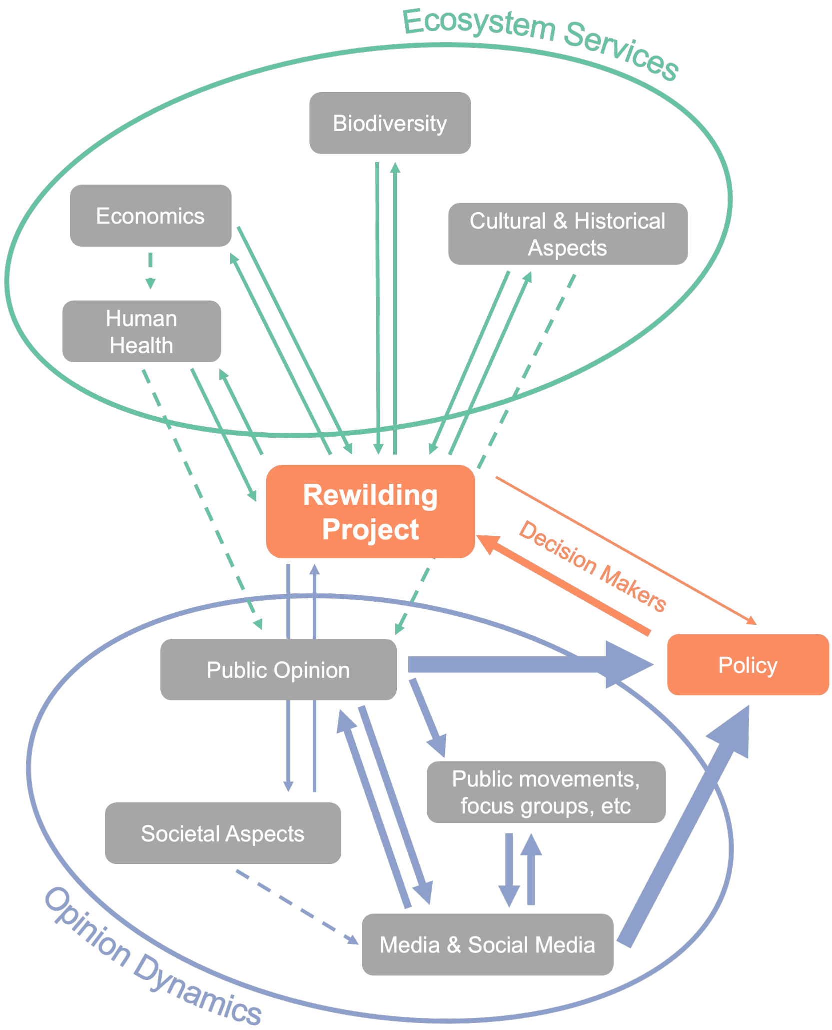


Figure 4: **A conceptual flowchart of interactions and influences (arrows) between different social-ecological components of a rewilding project.** Public opinion plays a central role both in the stage of the project planning and design (as embraced by the lower circle) and in the perception of its success, i.e. whether the expected improvements of the ecosystem services have been achieved (embraced by the upper circle). Models of opinion dynamics (e.g. (Milli, 2021; Helfmann et al., 2023)) and mathematical methods of optimisation (Law & Morton, 2013; Knight et al., 2024) can be used to find a consensus among different stakeholders, social groups and general public.

For example, recent interdisciplinary modelling work has highlighted that incentives based on peer punishment may increase cooperation but can be detrimental for welfare, while peer reward may lead to an increase in social welfare (Han et al., 2024).

In many such models, specifying interaction rules among agents of the social dynamics remains a difficulty, but this is true also of agent-based models for ecological systems. While more effort should go into understanding realistic forms for such interaction kernels, for example by further integration of such models with empirical studies (Bak-Coleman et al., 2021), alternative frameworks are available. For instance, generalised modelling, a type of dynamical systems model which does not require detailed specification of causal relationships between system variables, has been successfully employed to obtain insightful qualitative understanding in a CHANS model for Baltic sea cod abundance (Lade et al., 2015) and such approaches could also be adapted for rewilding problems.

6 Discussion and conclusions

Rewilding offers an increasingly popular and impactful approach to the restoration of degraded ecosystems, with the potential to enhance biodiversity and ecosystem services on which all life on Earth depends. Indeed, it has been argued that a rewilding approach may often be the most viable for ecosystem service restoration. Perhaps for this reason, rewilding projects can now be seen across an increasing range of spatial scales and ecosystem types. (Du Toit & Pettorelli, 2019; Perino et al., 2019; Pettorelli et al., 2019; Hart et al., 2023; Tree & Burrell, 2023)).

We have highlighted the exciting opportunities to improve the efficiency and scientific foundations of rewilding programmes incorporating some of the many mathematical methods and ecological models which have been developed and applied in related ecological research. Thus, we endeavour to bridge the gap between rewilding practice and theoretical and mathematical ecology.

We argue that mathematical methods and models, alongside data analysis and statistical inference, can crucially improve a rewilding project at all stages, from planning and design, through implementation, monitoring and assessment (Figure 1). Mathematical models are particularly important at the initial planning stage of a rewilding project and at early stages of its implementation where considerable uncertainties about the the set of likely ecological trajectories and social-ecological dynamics of a rewilding project across decadal timescales. Models of ecological dynamics of various complexity can generate a range of rewilding scenarios, addressing such challenges as (i) optimisation of the location of the rewilded area, (ii) prioritisation and refinement of project goals (stated in terms of ecosystem service delivery) and (iii) provision of robust advice to decision makers about the timing, location and nature of required rewilding interventions. Dynamical ecological models, combined with suitable monitoring protocols, can also help with the prediction of possible tipping points (Scheffer et al., 2012; Biggs et al., 2018) and long transients (Francis et al., 2021). Such information is critically important in a large-scale rewilding project for the avoidance or minimisation of undesirable consequences (including project failure (Duffy, 2010; Muhumuza & Balkwill, 2013; Catalano et al., 2019; Dasgupta, 2019)).

Public opinion, stakeholder preferences and the social-economic context of any ecological system, can fundamentally affect the feasibility and success of a rewilding project (Hertel & Luther, 2023)—an issue shared widely with any conservation project. The social dimension is ubiquitous at all stages of a rewilding project, stakeholder consensus being essential not only to get a project underway, but also for its long-term viability. Models of opinion dynamics and optimisation methods can be instrumental in helping to achieve such consensus.

Rewilding creates a new paradigm for the application of dynamical ecological models. In spite of their long and successful history of deciphering ecosystem dynamics, such models are sometimes criticised as being too schematic—never explicitly accounting for all species in the ecosystem and so neglecting potentially important ecological interactions (Levins, 1966; Getz et al., 2018). However, rewilding focuses on functional groups rather than individual species, giving a principled way of simplifying the modelling. Indeed, it suggests a 'coarse-graining' approach with variables representing functional groups (or sometimes similar species of the same taxonomic level) with the potential for significant model simplification. A functional group approach should be balanced against the use of few-species models that place a focus on the important role of key megafauna and ecosystem engineers that may have a disproportionate role in driving ecosystem change.

Creation of consensus, set-up, design, implementation and monitoring of a rewilding project are some of the many facets requiring an interdisciplinary team: we argue that the project is more likely to achieve its goals, and in a more cost-effective way, if mathematical scientists are included from the beginning (DeAngelis et al., 2021). We end on an evangelical note and hope that our perspective stimulates future collaborations among practitioners, social scientists, theoretical ecologists, mathematicians and statisticians with the aim of helping rewilding realise its full potential for resilient social-ecological systems around the world.

Statement of authorship

Authors apart from the lead corresponding author are listed alphabetically. All authors participated in the production of the manuscript starting from the ICMS workshop in Edinburgh in June 2024. All authors contributed ideas either then or subsequently. LB, CAC, MSF, RMcR, NBP and SP worked on several iterations of the text, coordinated by MO and MAS, with further contributions in the final stages from WMG, FJ and JTdT. The boxes, tables and figures were created as follows: Figure 1, RSMcR; Figure 2, DJB; Figure 3, DAE and CAC; Figure 4, SP and RMcR; Box 2, CAC; Table 1, MSF and WMG; Table 2, MSF and MAS. All authors agreed to its submission to Ecology Letters.

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