

Journal of Ecology Special Feature: “The plant ecology of Nature-based Solutions for people, biodiversity and climate”

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Summary

1. Integrated solutions to the climate and biodiversity crises – together with other global sustainability challenges – include the identification, design and implementation of Nature-based Solutions (NbS). Living organisms mediate biogeochemical cycles and greenhouse gas (GHG) fluxes from land and sea, and provide NbS to both climate change mitigation and adaptation. Plants, as the primary producers in ecosystems, lie at the heart of NbS.

2. Plant ecology provides the foundation for developing and evaluating NbS based on an understanding of the ecological processes that underlie ecosystem service flow to people. In this Special Feature, we provide a collection of mini-reviews that presents concise and focused analysis of the plant ecology of NbS. The mini-reviews highlight key insights, challenges, and opportunities for future research.

3. The development of NbS that target specific ecosystem functions (e.g. carbon storage), or aim at increasing ecosystem resilience against perturbations (e.g. those associated with climate change), requires unification of ecological theory from areas such as biodiversity-ecosystem function, plant-animal interactions, resilience and functional traits of organisms.

4. *Synthesis*

Plant ecology and NbS research are complementary. Plant ecology can inform the design and management of effective NbS, and provide insights for the creation of novel ecosystems that provide NbS; while learning from the implementation of NbS can progress theory. To deploy NbS at the speed and scale needed to mitigate and adapt to climate change, we must rapidly integrate ecological concepts into the design of NbS. At the same time, the design and deployment of NbS in different ecological contexts provides an unprecedented opportunity to learn how performances of individual NbS sites can be explained in an integrated way, leading to the development of general concepts. Ultimately, a mechanistic understanding of how plants and their functional traits contribute to ecosystem function and service provision is critical for the design, verification of benefits from, and avoidance of adverse effects of, NbS.

Key-words: Global change ecology, Plant-climate interactions, Multi-trophic interactions, Natural climate solution, biodiversity, ecosystem function and services, ecological theory, ecosystem-based approach, applied ecology

Introduction

“In short - our world needs climate action on all fronts — everything, everywhere, all at once” António Guterres, United Nations Secretary-General (Gutierrez, 2023)

Solutions to slow down, stop, and ultimately reverse climate change – together with solutions that address unsustainable use of land and water bodies – are urgently needed at local and global scales to enable people and nature to thrive on a changing planet (Diaz et al., 2015; IPBES, 2019). Acceleration of climate action is required to meet the ambitions of the Paris agreement (United Nations, 2015), and biodiversity protection and restoration are needed to meet the commitments of the Kunming-Montreal Global Biodiversity Framework (Convention on Biological Diversity, 2022). However, the climate and biodiversity crises are intimately linked and cannot be tackled in isolation (InterAcademy Partnership, 2021; Pörtner et al., 2021). Integrated solutions to the climate and biodiversity crises (Gorman et al., 2023), together with other global sustainability challenges, include the identification, design and implementation of Nature-based Solutions.

“Nature-based Solution” is an umbrella term which includes many existing applications of ecology (Cohen-Shacham et al., 2016; Seddon et al., 2020). All definitions of NbS include the concept of actions in natural and managed ecosystems to provide solutions to global challenges like climate change, while benefitting people and protecting and restoring biodiversity. NbS are fundamentally about how people interact with biodiversity, both as ecosystem managers and beneficiaries of the ecosystem services provided (Fig 1). People are central to the NbS concept, as both stewards and beneficiaries (Standish & Parkhurst, 2024). However, as the primary producers in ecosystems and the dominant life form on earth (Bar-On et al., 2018), plants lie at the heart of NbS, and plant ecology, by extension, lies at the heart of understanding how and why NbS work.

Plants provide solutions to both climate change mitigation and adaptation; they regulate biogeochemical cycles, greenhouse gas (GHG) fluxes and the Earth system, and mediate the effects of climate on the functioning and resilience of ecosystems. There is a long history of the application of plant ecology to various domains relevant to NbS including ecosystem-based approaches, agroecology, forestry, restoration, conservation, and population ecology for pest control. Plant ecology can provide the foundation for developing and evaluating NbS based on an understanding of the ecological processes that underlie ecosystem service flow to people. What distinguishes NbS from more general

applications of ecology is that NbS address a societal challenge that benefits both people and biodiversity (Fig. 1). The deep connections of plants to other living and non-living components of ecosystems, and with human systems, underpin NbS.

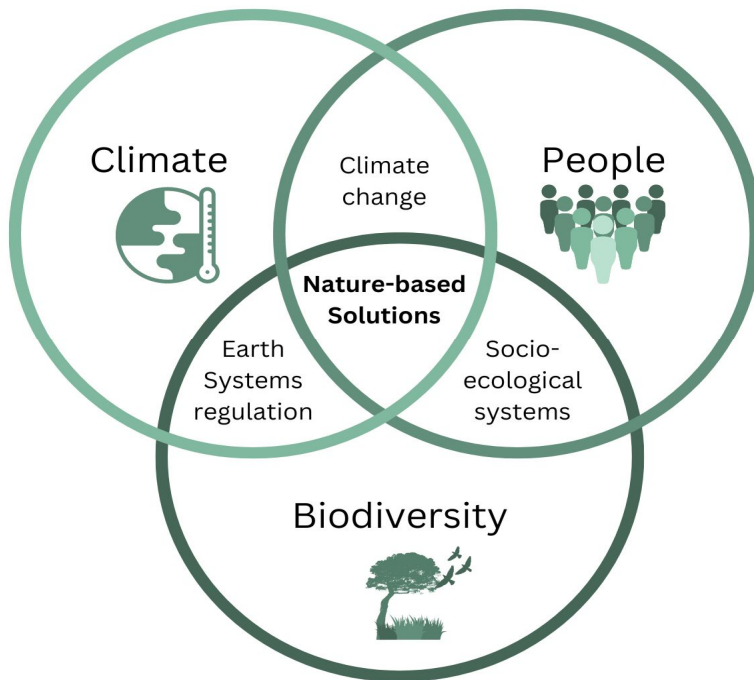


Figure 1. Nature-based Solutions are at the intersection of climate, biodiversity and social systems. Successful NbS solve an important problem (e.g. climate change mitigation or adaptation) while providing benefits to people and to biodiversity.

Here we provide a collection of nine mini-reviews that presents focused analysis of the plant ecology of NbS and highlights key insights, challenges, and opportunities for future research. As illustrated in our overview below, the mini-reviews cover a wide range of domains in which NbS are deployed: from multi-species pastures and grasslands to forests and coastal wetland systems (Fig 2). In this editorial, we identify three overarching themes, together with general challenges and opportunities that, we hope, will lead to new directions in both plant ecology research and the further development of NbS.

Three key themes connecting plant ecology and NbS

1. NbS enable development, and tests, of plant ecology theory

For decades, ecologists have worked to understand the ecological mechanisms that govern plant community assembly, structure and functions (Ali, 2023; Lortie et al., 2004) and that drive plant community resistance and resilience to perturbations (Smith & Boers, 2023). Similarly, the use of plant communities for food, shelter, fuel, medicine and coastal protection has long stimulated research in plant ecology. As highlighted in this Special Feature, the convergence of theoretical, empirical, observational and applied plant ecology has led to the development of ecological theories and concepts that have been tested through observation of plant community responses to natural disturbances (Lovelock et al., 2024), or through the manipulation of plant community diversity and composition (Finn et al., 2024) and the simulation of biotic and abiotic perturbations. NbS have emerged by making use of these theories and concepts, thereby helping to protect, restore and assemble more resilient plant communities (Chausson et al., 2020; Malhi et al., 2020; Standish & Parkhurst, 2024) (Fig. 2). The development of NbS that target specific ecosystem functions (e.g. carbon storage), or aim to increase ecosystem resilience (Standish & Parkhurst, 2024), requires unification of multiple ecological theories. This is leading to the development of existing or new ecological theories in a more applied context (e.g., forestry, agriculture). As illustrated by this collection of mini-reviews, biodiversity-ecosystem function relationships (Finn et al., 2024), trait-based approaches (Ramachandran et al., 2024; Standish & Parkhurst, 2024; Wright & Francia, 2024) and plant-herbivore interactions (Borer & Risch, 2024) are active areas of plant ecology research with profound implications for the design, implementation, and functioning of NbS.

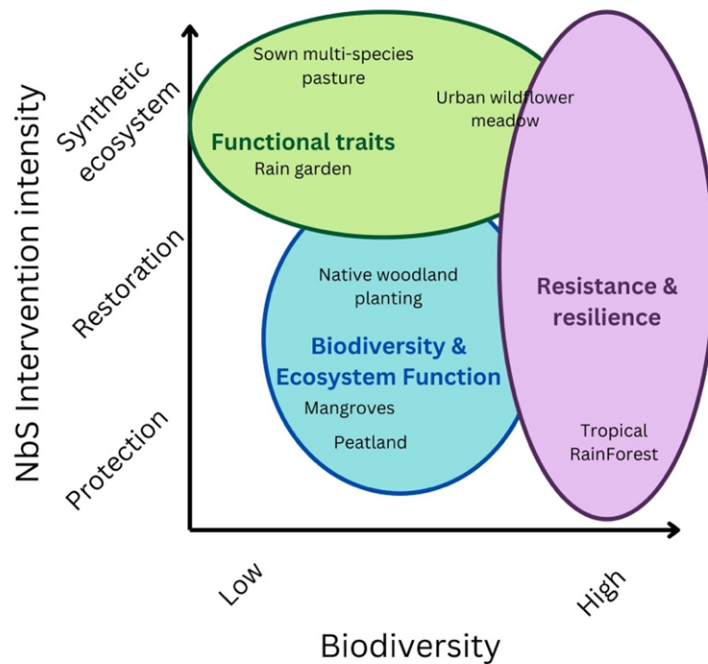


Figure 2. Contributions of plant ecology to Nature-based Solutions across the intervention and biodiversity axes. NbS can be categorised as different intensities of interventions, from protection of existing ecosystems to restoration of degraded ecosystems, through to the assembly of synthetic ecosystems. The biodiversity- axis also varies within NbS from relatively low biodiversity (e.g., synthetic multi-species swards in agroecosystems, or urban rain gardens (Ishimatsu et al., 2017)) to those involving high biodiversity (e.g., high diversity forests for carbon storage). Different areas of plant ecology (coloured ellipses) can be applied within the biodiversity-intervention intensity space. Three areas are highlighted here, but are not exclusive or confined to particular areas of intervention intensity-biodiversity space: functional traits, biodiversity and ecosystem function, and resistance and resilience.

The design of pasture systems to maximise productivity for food production, while providing benefits for biodiversity, is a Nature-based Solution. Learning from the design of managed productive grasslands communities, in their mini-review, Finn *et al.* (2024) applied a Diversity-Interactions model that uses a multiple regression modeling framework to separately quantify the effects of species identity, species proportions and interspecific interactions on plant productivity in a designed pasture community. They conclude that plant species richness does not necessarily improve productivity beyond a small number

of species and that the complementarity between different plant functional groups (e.g., grass-legumes) can have stronger impacts than species richness. Their approach helps to validate, and identify limitations to, the complementarity hypothesis of the biodiversity-ecosystem function relationship.

Trait-based ecology links plant traits with emergent functions at the population, community and ecosystem scales. Wright and Francia (2024) provide a trait-based framework that can be used to assess the influence of traits on microclimate temperature and humidity under vegetation. Described in their mini-review, this framework includes two classes of plant traits, *i.e.* the sensible heat flux traits related to the physical structures of the plants (e.g., leaf area index, canopy height) that can increase or decrease the rate of heat exchange between the atmosphere and vegetation, and the latent heat flux traits (e.g., stomatal density, rooting depth, transpiration rate) that can modify the microclimate through evaporative cooling. While they identify important plant traits that can have a cooling effect, such as high canopy, high stomatal conductance, high albedo or deep rooting, they also emphasize gaps in knowledge for the impact of plant traits on microclimate and propose new avenues for the development of ecological theories. For example, investigating the relative importance of latent *versus* sensible heat flux traits on microclimate effects could shed light on important mechanisms underlying ecological resilience to climate change.

In their mini-review, Borer and Risch (2024) summarize the role that vertebrate and invertebrate herbivores can play in NbS, especially for the maintenance of grassland biodiversity and carbon storage. They identify multiple gaps in ecological research and emphasize the need to better understand the role of invertebrate diversity and interactions on plants and larger herbivores, especially due to the recent, widespread, and rapid declines in invertebrate populations (Wagner et al., 2021). Furthermore, they suggest considering the interacting role of grazing type and intensity with spatial, climatic and edaphic conditions in future plant-herbivore interactions research to identify management practices (*e.g.*, grazing intensity) that are best suited to site conditions.

2. Plant ecology informs the design and implementation of NbS and helps avoid unintended consequences

NbS provide ecosystem services to people. There are clear links between the characteristics of the ecosystem, the traits of plants within that ecosystem, and the supply of ecosystem services. Moreover, failure to include ecological knowledge in the design of NbS can lead to poor functionality (Lovelock et

al., 2024) and unintended consequences – for instance in the case of tree planting for climate mitigation, which can have negative impacts on native biodiversity and ecosystem functioning when done inappropriately (Moyano et al., 2024). Therefore, a mechanistic understanding of how plants and their functional traits contribute to function and service provision is critical for the design of, verification of benefits from, and avoidance of adverse effects of, NbS. As exemplified in this Special Feature, current knowledge on the impact of some plant functional traits on microclimate can be used to create plant communities that are more resistant and resilient to climate change (Wright & Francia, 2024). Similarly, knowledge on forest canopy attributes that determine the microclimate experienced by organisms in the understory can also mitigate impacts of global change (Verheyen et al., 2024).

There is now strong empirical and theoretical support that plant functional traits mechanistically underpin the ecosystem services that NbS aim to enhance. Yet, as emphasized by Ramachandran et al. (2024), functional traits are rarely considered in the design of NbS. These authors highlight the rich literature that has identified linkages between traits and ecosystem services and provide a framework for applying trait-based approaches in the design of different types of NbS with differing management objectives. They also outline a research agenda for greater integration between functional traits and NbS; for instance, the need for improved understanding of the trait compositions that best confer resilience of ecosystem services to perturbations, which could inform species selection and interventions. Trait-based approaches are also considered by Rafferty and Cosma (2024), who argue that incorporating knowledge on the traits of keystone plants and pollinators into the design of NbS could enhance the resilience of pollination services under future climate change.

Ecological resilience, or the capacity of an ecosystem to tolerate disturbance without switching to a different state (*sensu* Holling (1973)), is important for the persistence of ecosystem services provided by NbS under future global change. While there are examples of ecological resilience being used in the NbS literature, it is generally limited, especially for resilience mechanisms that operate at the genetic and landscape levels of biological organisation (Moyano et al., 2024; Standish & Parkhurst, 2024). Nevertheless, Standish & Parkhurst (2024) identify several ecological resilience mechanisms, including both stress tolerance and recovery potential, from the wider literature that can inform the design and implementation of NbS. These include the incorporation of a sufficient range of species' responses (i.e., response diversity) in NbS, this is important for maintaining ecosystem function in the face of disturbances (Mori et al., 2013) and ensuring connectivity and modularity in the landscape, which contributes to landscape-scale ecosystem resilience (Oliver et al., 2015). Moreover, the temporal scale

over which NbS are expected to operate is important, but rarely considered; as stressed by Standish and Parkhurst (2024), “quick fixes” may not be resilient or persistent in the longer term.

The sustained function of NbS also depends on species interactions with herbivores, pollinators and microbes. There is extensive literature on the impact of herbivores, such as wild and domestic livestock and invertebrates, on plant diversity and on the impact of herbivory on soil carbon storage (Borer & Risch, 2024). Knowledge on the impact of livestock management on ecosystem processes can inform the design of grazing systems that promote ecosystem service multifunctionality and the sustainability of NbS (Borer & Risch, 2024). Also highlighted in this Special Feature is a general lack of recognition for the utility of considering species interactions in NbS literature, and very few papers consider pollination, with the exception of agro-ecosystem solutions. However, as Rafferty and Cosma (2024) point out, conserving and restoring species interactions is critical for NbS. The stable provision of pollination services will contribute to the long-term success of NbS under future climate change.

3. Plant ecology can inform synthetic NbS

Some NbS are so different from anything that has been previously observed in nature that they fall into the category of ‘synthetic ecosystems’. A subset of novel (or non-analogue) ecosystems (Hobbs et al., 2006), a synthetic ecosystem is intentionally created by humans and often combines biodiversity with technology to result in an ecosystem with little to no historical precedent (reviewed in Hammond *et al.* (2023)). Synthetic ecosystems, therefore, move past restoration, management, and reclamation, into the territory of creating novel ecosystems that are explicitly designed for human benefit, through the provision of ecosystem services (Palmer et al., 2004; Ross et al., 2015). An historic example is ‘The Three Sisters’, a polyculture of squash, beans, and corn that increases the yields of all three crops when grown together compared to when they are grown separately (Zhang et al., 2014). Some modern examples include multispecies wastewater treatment plants (Todd et al., 2003) and algae cultivators that interface with computers (Blersch et al., 2013).

This Special Feature highlights three examples of how plant ecology can inform these synthetic ecosystems to create NbS. Finn et al. (2024) show how synthetic plant communities can enhance ecosystem services or productivity. They use the Diversity-Interactions modeling framework to determine the optimal abundance and identity of plant species to maximize NbS in productive grasslands (grasslands that are typically of relatively low diversity and are intensively managed to

maximize particular ecosystem services, such as food for grazers or livestock, carbon sequestration, or biodiversity maintenance). Rafferty & Cosma (2024) highlight the extent to which pollination mutualisms have yet to be included in synthetic NbS. Specifically, they demonstrate how phylogenetic signal can be used to design species mixes and to engineer redundancy for traits that are phylogenetically conserved (e.g., several related species could be used to provide a similar service). Keystone species (and their interactions) that contribute the most to biodiversity, stability, and function would be good candidates to prioritize in NbS aiming to create synthetic plant and pollinator communities that maximize ecosystem function (plant reproduction) and services (pollination). Their approach is applicable beyond plant-pollinator interactions. Finally, Verheyen et al. (2024) demonstrate how tree canopies can be managed for NbS pertaining to processes that occur underneath the canopy and organisms that live under the canopy, including humans. Different management interventions, like altering species composition and vertical and horizontal canopy structure, can influence tree canopy attributes that subsequently affect ecosystem processes and services. Indeed, Guo et al., (2022) point out that size-related trait variation in horizontal and vertical ecosystem dimensions contributes to ecosystem multifunctionality. For example, the identity, spatial configuration and canopy density of urban trees can be optimized to improve air quality. Plant ecology has much to offer when designing synthetic plant communities for NbS.

Key challenges and opportunities for integrating plant ecology into NbS

As a collection, and building on the wider literature, the mini-reviews in this Special Feature reveal some generalities that should apply broadly to NbS. Intensive production systems often focus on monocultures but usually at the cost of high inputs of fertilisers, herbicides, and pesticides, and with loss of long-term soil health and the risk of disease and pest outbreaks. Diversification provides an effective NbS if practical limitations around cultivation and scale of production can be overcome. However, diversification must be done with consideration of which species and mixtures are most appropriate for delivering a particular ecosystem outcome. Diverse systems are often more productive and stable than low diversity systems (Craven et al., 2018; Hautier et al., 2018; Hooper et al., 2005), albeit dependent on context (Dee et al., 2023). Diversification also has implications for ecosystem resilience but the mechanisms underlying diversity effects on resilience (both stress tolerance or resistance effects and recovery), are rarely reported in NbS literature (Standish & Parkhurst, 2024). Explicit consideration of resilience is needed to design NbS that will persist through changing conditions.

One of the key challenges for integrating plant ecology into NbS is the high degree of context dependency in ecological systems (Catford et al., 2022; Dee et al., 2023). There are few ecological generalities that apply across all ecosystems and locations. Instead, NbS, developed using general ecological concepts, need to be tailored to local systems and situations (e.g. Molloy et al., (2024)). Controversy surrounding regenerative agriculture and afforestation as NbS highlight the importance of ecological context. “Right tree, right place”, as the guide for afforestation efforts to sequester carbon and avoid unintended consequences, such as soil carbon loss, explicitly calls out the need for sensitivity to context when assessing impacts (Moyano et al., 2024). Yet our understanding of the role of plant-soil interactions, as a driver of soil carbon sequestration and stabilization, is far from complete and is crucial for ensuring the effectiveness of NbS aimed at climate mitigation. The current interest in ‘regenerative agriculture’ and related concepts (European Academies Science Advisory Council, 2022) aims to develop agricultural systems, and particularly livestock production systems, that are better for biodiversity and soil health. However, whether regenerative agriculture can be done at a scale that reduces greenhouse gas emissions, while also being productive and economically viable, is unclear. The evidence base for regenerative livestock systems will involve complex lifecycle analyses that consider local to landscape scale impacts on biodiversity, greenhouse gas emissions and soil carbon sequestration within the livestock supply chain.

Some forestry efforts have been unsuccessful due to an emphasis on which timber species were economically or environmentally successful in other contexts rather than on consideration of what species are appropriate for the local ecological conditions. There is potential for better outcomes from more careful consideration of matching of species to location. Increasingly, given ongoing climate change, strategies for restoration (especially for long lived organisms like trees) need to account for the likely future changes in climate when selecting species. Designing for future climates, and climate variation through time, will involve a wide range of species traits including persistent traits of the organism (e.g., architecture, leaf traits) and traits that are only evident at certain times (e.g., reproductive traits of trees). The optimal forest structure and composition for mitigation of extreme droughts depends on the relative importance of different drivers of drought stress (Verheyen et al., 2024). A better understanding of the mechanistic drivers of plant responses to climatic stressors, and their relative importance, trade-offs and synergies, is urgently needed so that site specific advice for locally effective solutions can be provided (Verheyen et al., 2024).

Ultimately, NbS involve a complex compromise between plant ecology theory and the management system setting (e.g. agronomic and forestry systems often prioritise high yields with the lowest number of species as possible), within the social context of stakeholder preferences and economic forces. In other cases, protection or restoration of natural (or semi-natural) systems provide solutions. For example, coastal mangrove forests are of high value for disaster risk reduction (Lovelock et al., 2024), and restoration of peatlands can reduce GHG emissions and sequester carbon (Renou-Wilson et al., 2019). In all cases given the complexity of the problem, the interaction of social, economic and ecological systems (Farrell et al., 2024) and the need to understand the context dependence of solutions, embedding plant ecology within transdisciplinary research systems will be needed.

Conclusions

Learning from the implementation of NbS can enable the development of plant ecology theory, while plant ecology can inform the design and management of successful NbS, and provide insights for new synthetic ecosystems delivering NbS. To deploy NbS at the speed and at the scale needed, we must integrate plant ecological concepts rapidly and meaningfully into the design and implementation of NbS. At the same time, the design and deployment of NbS in many different ecological contexts provides an unprecedented opportunity to learn how local performance can be integrated with, and lead to the further development of, general concepts. Ultimately, a mechanistic understanding of how plants and their functional traits contribute to ecosystem function and service provision is critical for the design, verification of benefits, and avoidance of adverse effects of NbS.

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Author contributions

All authors conceived the ideas, commissioned mini-reviews, analysed the literature, contributed critically to the drafts and gave final approval for publication. YMB led the writing of the manuscript.

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