

OPINION

Global environmental change effects on ecosystems: the importance of land-use legacies

MICHAEL P. PERRING^{1,2}, PIETER DE FRENNE^{1,3}, LANDER BAETEN¹, SYBRYN L. MAES¹, LEEN DEPAUW¹, HABEN BLONDEEL¹, MARÍA M. CARÓN⁴ and KRIS VERHEYEN¹

¹Forest & Nature Lab, Ghent University, BE-9090 Melle-Gontrode, Belgium, ²Ecosystem Restoration and Intervention Ecology Research Group, School of Plant Biology, The University of Western Australia, Crawley, WA 6009, Australia, ³Department of Plant Production, Ghent University, Proefhoevestraat 22, BE-9090 Melle, Belgium, ⁴Laboratorio de Investigaciones Botánicas (LABIBO), Facultad de Ciencias Naturales, Universidad Nacional de Salta-CONICET, Av. Bolivia 5150, 4400 Salta, Argentina

Abstract

One of the major challenges in ecology is to predict how multiple global environmental changes will affect future ecosystem patterns (e.g. plant community composition) and processes (e.g. nutrient cycling). Here, we highlight arguments for the necessary inclusion of land-use legacies in this endeavour. Alterations in resources and conditions engendered by previous land use, together with influences on plant community processes such as dispersal, selection, drift and speciation, have steered communities and ecosystem functions onto trajectories of change. These trajectories may be modulated by contemporary environmental changes such as climate warming and nitrogen deposition. We performed a literature review which suggests that these potential interactions have rarely been investigated. This crucial oversight is potentially due to an assumption that knowledge of the contemporary state allows accurate projection into the future. Lessons from other complex dynamic systems, and the recent recognition of the importance of previous conditions in explaining contemporary and future ecosystem properties, demand the testing of this assumption. Vegetation resurvey databases across gradients of land use and environmental change, complemented by rigorous experiments, offer a means to test for interactions between land-use legacies and multiple environmental changes. Implementing these tests in the context of a trait-based framework will allow biologists to synthesize compositional and functional ecosystem responses. This will further our understanding of the importance of land-use legacies in determining future ecosystem properties, and soundly inform conservation and restoration management actions.

Keywords: climate change, forest understorey, functional traits, historical ecology, land-use history, nitrogen deposition, ozone, response-and-effect framework

Received 6 August 2015; revised version received 17 October 2015 and accepted 27 October 2015

Introduction

Much current ecological research attempts to predict the future responses of ecosystems to multiple contemporary environmental changes, highlighting effects on ecosystem structure, composition and function (e.g. Luo *et al.*, 2008; Pereira *et al.*, 2010; Ehrlén & Morris, 2015). These investigations use fundamental ecological understanding in attempting to achieve accurate anticipatory and explanatory predictions (Ollinger *et al.*, 2002; Kearney & Porter, 2009; Adler *et al.*, 2013; Mouquet *et al.*, 2015) and to improve current and future management actions (Perring *et al.*, 2015). Importantly, when realized trajectories do not follow projections, or management outcomes fail to match expectations, we

have an opportunity to refine our conceptual understanding by considering other factors that may be important in influencing ecosystem properties. Here, we suggest that environmental change studies projecting future terrestrial ecosystem states and dynamics need to take account of the context dependency created by land-use legacies.

Our opinion article encompasses four main sections. We first provide a brief synopsis of contemporary land-use legacy effects on ecosystems while also noting separate research in contemporary environmental changes. Secondly, we contend, through reviewing available literature, that research projecting the effects of multiple environmental changes on future ecosystem properties rarely considers land-use legacies, especially in terms of plant community dynamics. This is surprising given the long-acknowledged importance of land-use legacies for explaining contemporary ecosystem structure and function (Peet & Christensen, 1980; Foster *et al.*, 2003;

Correspondence: Michael P. Perring, tel. +32 9 2649046 or +61 8 6488 4692, fax +32 9 2649092 or +61 8 6488 7461, e-mail: michael.perring@ugent.be or michael.perring@uwa.edu.au

Lunt & Spooner, 2005) and the increasing presence of secondary lands such as postagricultural forests on old fields (Cramer *et al.*, 2008; Hurtt *et al.*, 2011). Our third section explores why interactions between land-use legacies and environmental changes have rarely been emphasized, and outlines arguments and methods to test for such interactions. Finally, we discuss how a trait-based approach in conjunction with recent analytical advances provides the opportunity to synthesize land-use legacy and contemporary environmental change effects on community composition and ecosystem function in one framework.

Our intention is to highlight the importance of land-use legacies in modulating environmental change effects on ecosystems, so examples come from a range of systems. However, many of our ideas are illustrated using vegetation and soil properties from temperate forests across environmental and land-use gradients. Firstly, temperate forests cover 16% of the terrestrial land surface (Hansen *et al.*, 2010), and their understoreys typically exhibit slow dynamics, with current research foci including land-use legacies (Flinn & Vellend, 2005) and contemporary environmental change (De Frenne *et al.*, 2013b; Maes *et al.*, 2014). In addition, understoreys typically represent 80% of plant species richness in temperate forests (Gilliam, 2007) and have a disproportionately large effect on ecosystem functions such as nutrient cycling and tree regeneration (George & Bazzaz, 1999; Olsson & Falkengren-Gerup, 2003; Moore *et al.*, 2007). Hence, temperate forests, and especially their understoreys, provide an ideal system to illustrate our idea that there is a much needed requirement to synthesize the research areas of environmental change and land-use legacy, and reveal the interactive effects of these factors on ecosystem properties.

Land-use legacies and contemporary global environmental change: a brief synopsis

Land-use legacies are the abiotic and biotic properties found at a site due, at least in part, to the influence of land-use history (Foster *et al.*, 2003). Land-use history is the sometimes complex successive sequence of human uses that a site has undergone (Arce-Nazario, 2007; Ewers *et al.*, 2013). Legacy effects have the potential to comprise signatures of anthropogenic disturbances from, for example, fire management (Meunier *et al.*, 2014), timber harvesting or agricultural land use (Flinn & Vellend, 2005; Hermy & Verheyen, 2007). Legacies can be remarkably persistent, even after centuries or millennia of land abandonment (Dupouey *et al.*, 2002; Dambrine *et al.*, 2007; Freschet *et al.*, 2014).

In the decade since Foster *et al.* (2003) stressed the need to consider land-use legacy in explaining contem-

porary patterns and processes in ecology, further investigations have affirmed its broad-reaching impact. These effects are usually quantified by comparing sites to a reference state in the absence of known land-use history. Effects include changes to soil resources (i.e. properties consumed by organisms e.g. for plants: nutrients or water, Fraterrigo *et al.*, 2005; McLauchlan, 2006; Flinn & Marks, 2007; MacDonald *et al.*, 2012; Szitár *et al.*, 2014) and alterations to environmental conditions potentially influenced by organisms but not consumed, for example microclimatic temperature (Manning *et al.*, 2006a) and pH (Koerner *et al.*, 1997). Biotic changes occur in tandem with these abiotic alterations. Investigations have shown persistent differences in floral and faunal species composition (e.g. Mitchell *et al.*, 2002; Rhemtulla *et al.*, 2009; McEwan *et al.*, 2011; Ewers *et al.*, 2013), genetic effects (Vellend, 2004), altered recruitment and population dynamics (Flinn, 2007; Comita *et al.*, 2010; Navarro-González *et al.*, 2013) and varied growth (Baeten *et al.*, 2011) due to land-use legacies.

Importantly, these legacies do not just alter the contemporary *state* of the system. They alter system dynamics, and lead to ecosystems being on a *trajectory of change* whether that be in terms of community interactions or ecosystem process rates (Fraterrigo *et al.*, 2006). Herbaceous plant community change through time has been related to dispersal and establishment limitation due to legacy effects (Baeten *et al.*, 2010, 2015; Löhmus *et al.*, 2014). Across Europe, the compositional change in herbaceous understoreys is related to denser canopy cover as forest dynamics react to decreased forest management intensities compared to previously (Verheyen *et al.*, 2012). In a carefully considered integration of historical ecological data with a biogeochemical ecosystem model, Gimmi *et al.* (2013) showed that litter raking in the forests of the Alps led to a decline in soil carbon (C). These systems are currently acting as a C sink as ecosystem processes realign with the contemporary absence of litter raking.

Simultaneously with accruing evidence on the ecosystem effects of land-use legacies, there has been a burgeoning literature, through observational studies, experiments and modelling, on the likely impacts of global environmental changes on future ecosystem properties (e.g. Luo *et al.*, 2008; Perring *et al.*, 2008; Langley & Megonigal, 2010; De Frenne *et al.*, 2011; Jarvis *et al.*, 2013; Savage *et al.*, 2013; Hovenden *et al.*, 2014; Talhelm *et al.*, 2014). Environmental issues that have been tackled, initially with single factor studies but increasingly with multi-factor, and even multilevel, investigations (e.g. Bradford *et al.*, 2012), include climate change, enhanced nitrogen (N) deposition and rising concentrations of atmospheric ozone [O_3] and

carbon dioxide [CO₂]. Here, we contend that these environmental changes, by affecting resources and conditions, and the ecophysiology of and interactions between individuals and species, will modulate the trajectories of change in systems already affected by land-use legacies *that have themselves altered resources, conditions and community dynamics*. We argue that the potential for this modulation has been overlooked to date. This could have important consequences for the fundamental and applied learnings we draw from environmental change studies.

Land-use legacies and contemporary global environmental change: an overlooked interaction?

Our initial argument that any potential interaction has generally been overlooked is based on a literature review searching among global environmental changes (such as nitrogen deposition) and land-use legacies. We did not include search terms reflecting ecosystem responses to land-use legacies and global environmental change (such as habitat, forest or wildlife change), despite their potential to be considered as environmental changes in their own right. Such changes have been considered in ecosystem studies from a land-use legacy or environmental change context; our contention is that the interaction among land-use legacies and global environmental changes has rarely been considered.

In a Web of Science search on 18 October 2015, 126 papers (across all years and all databases) were associated with a topic keywords search of 'land use legac*' and 'climate change' (a more restricted subset (101) was found when including the hyphen in land-use). Altering 'climate change' to 'sul*' depos* or 'nitr* depos*' or 'ozone' or 'carbon dioxide' added an additional 2, 11, 1 and 4 unique papers to this list, respectively. In contrast, searches for keywords separately garnered 385 030 (carbon dioxide), 364 214 (climate change), 136 912 (ozone), 126 828 (nitr* depos*), 91 436 (sul* depos*) and 871 (land use legac*) records. Taking account of the figures alone suggests potential interactions either do not exist or are being overlooked, as well as suggesting land-use legacy has less appeal to researchers, and could potentially be considered as a factor of lesser importance in dictating ecosystem dynamics, than contemporary environmental changes. These figures may also reflect the difficulties in unearthing and synthesizing robust historical information.

Closer inspection of the titles and abstracts of the 144 papers that considered both land-use legacy and one or more environmental changes confirmed the impression that potential modulation of ecosystem

trajectories is being ignored. Only 53 papers were of ecological relevance (see also Holl *et al.*, 2003 for similar findings of irrelevant search results from a targeted literature search). Six papers *hypothesized* that an interaction between legacies and environmental change may be important for future ecosystem dynamics (Mayle *et al.*, 2007; Haugo *et al.*, 2010; Staland *et al.*, 2011; Garbarino *et al.*, 2013; Henne *et al.*, 2013; Gill, 2014). However, results generally demonstrated the importance of past land use for the contemporary ecosystem state, while discussions suggested a need to take account of environmental history when projecting the future. For instance, Garbarino *et al.* (2013) showed that settlement patterns were fundamentally important to explaining current Alpine forest stand structure and suggested that forest harvesting and cattle grazing in past centuries are critical for understanding how contemporary global change factors may influence future dynamics. Others raised the important issue of accurately identifying the relative influences of environmental history and climate change when predicting future ecosystem properties (Haugo *et al.*, 2010; Staland *et al.*, 2011). In the only experimental investigation of potential interactions between land-use legacy and environmental change of which we are aware, changes in soil nitrogen availability and temperature did not interact with historical grazing legacies to affect ecosystem processes of production and respiration in subalpine meadows of Utah (Gill, 2014).

Only a few model-based papers provide direct evidence that land-use legacies can interact with future environmental changes (Ollinger *et al.*, 2002; De Cáceres *et al.*, 2013; Halofsky *et al.*, 2013). For instance, Halofsky *et al.* (2013) showed that land-use legacy dampened climate change effects on future ecosystem composition and function. The presence or absence of land-use legacy also changed expected bird distributions when simulated under altered fire regimes due to climate change (De Cáceres *et al.*, 2013). Interactive effects of land-use history with elevated [CO₂] and [O₃], together with N deposition, were revealed for C dynamics of hardwood forests in north-eastern United States (Ollinger *et al.*, 2002). Although qualitative patterns in forest responses to environmental changes, following timber harvesting vs. agricultural use and subsequent reforestation, were similar, N limitations were weaker in timber harvest simulations and lower plant C:N led to more responsiveness to increased [CO₂] relative to N deposition (Ollinger *et al.*, 2002). There is thus limited evidence for interactive effects among contemporary environmental changes and land-use legacies, but a few studies highlight its potential importance.

Absence of evidence: evidence of absence?

The paucity of evidence for potential interactions between land-use legacies and contemporary global environmental changes could be for at least three reasons: (1) the interaction does not (or rarely) exist(s) so need not be considered; (2) a rationale that projecting the future only requires knowledge of the present *state* of a system, regardless of the extent to which the present state depends on land-use legacy; and (3) it is difficult to show that such an interaction exists *now* because we are looking into the future, hence why there is a preponderance of modelling studies. We will tackle each of these reasons in turn. This emphasizes that the absence of evidence highlighted from our review is not sufficient evidence to ignore a need to test for the interaction between land-use legacies and contemporary global changes when projecting the future.

Assumption that interactions between land-use legacies and global environmental change do not exist

To illustrate that interactions among land-use legacies and global environmental changes need considering, we use a thought experiment that combines multiple disparate lines of existing empirical evidence from currently forested landscapes in a tangible manner. Ideally, we would use a case study to illustrate our synthetic resurvey trait-based framework (presented later) and demonstrate the existence of an interaction. However, the data required are not yet available, although the resurvey approach, in the absence of land-use legacy information, has been successfully utilized (e.g. Baeten *et al.*, 2014; Bernhardt-Römermann *et al.*, 2015). Here, we aim to highlight arguments for why an interaction should be borne in mind and later discuss how this hypothesis could be tested.

Consider walking into two neighbouring forests with identical structure and composition of the overstorey tree layer, the same slope, aspect and topography, in the same climate space. The underlying bedrock is the same and their contiguous location means that any large-scale disturbances of the deep past, for example glaciation, occurred at the same time. Their shared position on other large-scale environmental gradients (e.g. N deposition) in conjunction with this shared deep past means the regional pool of species available to both sites is also identical. Projecting the future development of such systems in the light of environmental change typically involves modelling their response to, say, projected climate change and N deposition. However, in the next paragraphs we will demonstrate how not considering the past would seriously compromise the accuracy of these future projections.

Inaccuracy would occur because 300 years previously one system was cleared and ploughed for crops, while the other was cleared for pasture (Fig. 1). A hundred years later, changing socio-economic circumstances led to both systems being reforested, in this case via planting of the overstorey with the same species with subsequent identical management. However, the legacies of land use have left different understorey compositions (Fig. 1a) and markedly different C and phosphorus (P) stocks in the surface soil (Fig. 1b). In the case of cropping, all forest understorey species were lost and a ruderal flora was present in the system at reforestation with a concomitant marked decline in surface soil C and P stocks due to offtake through the crop, the absence of litter inputs and no inorganic fertilizer addition (Flinn & Marks, 2007) [this is contrary to contemporary agricultural land which upon abandonment tends to have high soil P legacies (MacDonald *et al.*, 2012)]. Meanwhile, the pasture system retained some typical forest flora and sowing of typical pasture species increased species diversity. Surface C stocks were maintained given continued litter inputs, while P was little changed due to the return of the majority of nutrients through manure (McLauchlan *et al.*, 2006).

These contrasting legacies mean that, even in the absence of further environmental changes, systems are on different trajectories of change, despite superficial similarity. The system that was previously pasture exhibited compositional turnover as the system became reforested, and light-demanding species were shaded out. However, shade-tolerant forest species that had been retained in the pasture, for instance, in microrefugia or (rarer) in the seedbank (Bossuyt & Hermy, 2001), increased in importance as forest grew, potentially limiting the opportunity for other species to recruit as they pre-empt space and other resources (Baeten *et al.*, 2010). In the formerly cropped site, viable propagules remaining in the seed bank, if present, may establish while dispersal from the surroundings allows the establishment of other species, potentially with priority effects determining the community (e.g. initial floristic composition: Egler, 1954). This could lead to increases or decreases in species diversity depending on biotic interactions. From a functional, ecosystem process, point-of-view, the previously cropped system will be aggrading C as it adjusts to greater above- and below-ground litter inputs (Hooker & Compton, 2003). However, growth, and consequent litter inputs, may be constrained by the shortage of P, while the former pasture maintains its C and P stocks.

Environmental changes will act on the legacies left by cropping and grazing. Intra- and interspecific interactions and ecophysiological characteristics will determine population and community responses to these

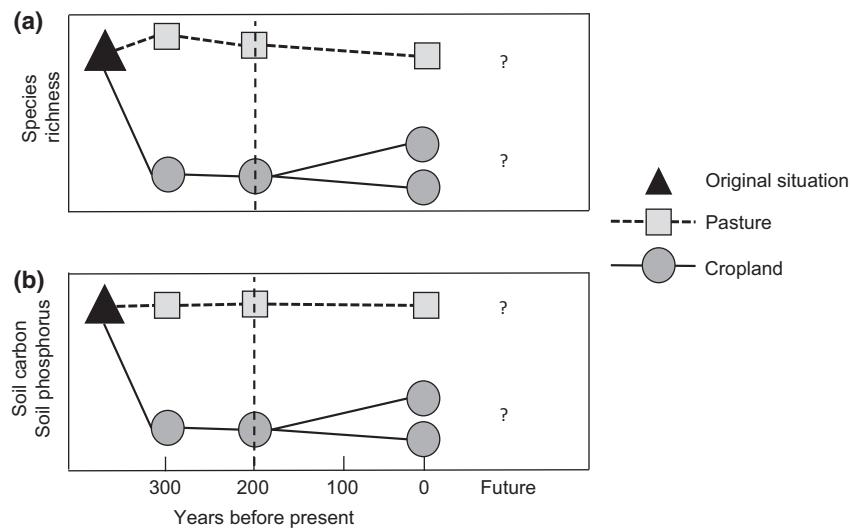


Fig. 1 A hypothetical example of how land-use legacies strongly affect ecosystem composition and function. Lands previously cleared for pasture as compared for cropping can exhibit different (a) compositional and (b) functional properties, all else being equal, and as explained further in the main text. Both panels suggest that ecosystems are on a trajectory of change, and contemporary environmental changes will interact with these land-use legacies, leading to an unknown future(s) (indicated by '?'), despite the systems being superficially similar following reforestation (vertical dashed line).

changes, in conjunction with further immigration of new species. Ecosystem processes will be directly altered by changed conditions, while also being indirectly altered through the compositional change (Suding *et al.*, 2008). In our example, the system that has a relatively stable pool of soil C will exhibit different dynamics to the system that is building soil C as it recovers from previous cropping due to the different P legacies. For instance, additional N may promote growth in the former pasture because the system still has sufficient P and growth is N limited, and thus inputs into the soil C pool will increase. In the previously cropped system, lacking in P, N addition may not enhance plant growth unless it also increases P availability through, for instance, the stimulation of phosphatase enzymes (Treseder & Vitousek, 2001). At the same time, N addition can have impacts on decomposition dynamics, which is also related to the availability of P (Cleveland *et al.*, 2006), and thus the direction of change in soil C is not obvious.

This hypothetical example clearly shows that it is important to consider interactions among land-use legacies and environmental change for both ecosystem composition and function. Taking soil C, projection of the direction as well as magnitude of its change in response to even a single environmental change needs to take account of the context dependency created by different land-use legacies. More broadly, this context dependency needs considering for other ecosystem processes, the species composition of the ecosystem, and also interactions among global environmental changes.

Assumption that projecting the future only requires knowledge of the present state of a system

The lack of papers examining an interaction between land-use legacies and global change could be due to an assumption that knowing the present state of a system will allow accurate predictions. This also suggests that if accurate typologies of the myriad abiotic and biotic legacies created by different land-use histories could be synthesized (likely an impossible task: Flinn & Vellend, 2005), we could arrive at accurate projections of future ecosystem properties. However, as the thought experiment shows, ecosystems are on trajectories of change and knowledge of more than the contemporary state is required for accurate projection. Such an argument is reinforced by considering that past conditions are projected to influence future dynamics of individuals (Provenza, 1995), ecosystem processes (Ogle *et al.*, 2015) and complex systems, for example coupled socio-ecological systems (Liu *et al.*, 2007), biome states (Moncrieff *et al.*, 2014) and weather (Lynch, 2008).

Focusing on the ecological literature, there is clear evidence for the importance of lag effects on current ecosystem process rates (e.g. Anderegg *et al.*, 2015). This was recently synthesized by Ogle *et al.* (2015), who provided a general analytical framework, stochastic antecedent modelling, that highlights the importance of 'ecological memory' for fully explaining ecosystem properties, considering the lag, distribution (temporal pattern) and strength of memory. An additional 18–28% of variation in four different ecosystem properties

(stomatal conductance, soil respiration, ecosystem productivity and tree growth) was explained by applying this approach, although detailed time series were required for method utilization.

Most recently, Ryan *et al.* (2015) have shown how future ecosystem properties in the face of environmental change likely depend on antecedent conditions. Using a semimechanistic temperature-response model that synthesized 6 years of data from a prairie warming and elevated [CO₂] experiment, they revealed the incorporation of antecedent conditions and above-ground vegetation activity are critical to predicting ecosystem respiration from subdaily to annual timescales. For instance, treatment-level differences in ecosystem respiration were attributed to the effects of antecedent soil temperature and vegetation greenness on the apparent temperature sensitivity of ecosystem respiration (Ryan *et al.*, 2015).

In addition to lag effects on process rates, and the interaction with environmental change, there is also a need to consider lag effects on community composition. Different landscape dynamics and past land-use history can lead to very different compositional properties in patches that appear in a similar current context (Ramalho & Hobbs, 2012). In an increasingly fragmented landscape, it has been suggested that long-term persistence (i.e. individual plant longevity) is expected to play a more dominant role in community dynamics than long-distance dispersal (Puschke *et al.*, 2012). A history of fragmentation can lead to extinction debts and immigration credits for plants (Vellend *et al.*, 2006; Jackson & Sax, 2010), potentially influencing higher trophic levels (Bommarco *et al.*, 2014). Ficetola *et al.* (2010) showed that knowing the past history of land-use change aided prediction of the future distribution of invasive bullfrogs. These time lags in community dynamics mean that apparently similar communities can be on different developmental trajectories, and thus, their future trajectory, even in the absence of environmental change, will be different.

Difficulty to show that an interaction exists now because we are looking into the future

Despite the clear rationale for considering land-use legacies in projections of environmental change, another reason for its lack of prominence in the environmental change literature may be due to difficulties in testing the idea 'in the field'. This is perhaps why the few examples that explicitly consider an interaction have generally relied on modelling (but see Gill, 2014). However, other methods provide the opportunity to investigate the importance of interactions, in particular using resurveys across environmental and land-use

gradients, and the careful application of experimental approaches.

Observational studies are oft-criticized for confounding interpretation due to the alteration of multiple factors, making it difficult to accurately partition variation in response to specific factors, let alone attribute causation (De Frenne *et al.*, 2013a). Indeed, many land-use legacy papers contain notes to be mindful that underlying properties, for example soil type or drainage, may have varied in the 'original' landscape, and different land uses were therefore implemented in the most appropriate locations; an issue that should be borne in mind with chronosequences where the only variable is supposedly time (Johnson & Miyaniishi, 2008). Such concerns suggest that contemporary differences among sites may not be solely due to land-use legacy and thus make it difficult to unambiguously separate the effects of land-use legacy from other driving factors. However, these concerns may be alleviated with careful choice of groups of resurveyed plots (i.e. plots surveyed at least twice over time for the ecosystem property under study) (Malhi *et al.*, 2010; Verheyen *et al.*, 2012). These resurvey plots, when accurately located on orthogonal gradients of environmental factors such as climate and N deposition coupled with reliable historical data on their previous use, can also avoid issues associated with pseudoturnover (i.e. changes due to incorrect relocation rather than actual compositional change) (Vellend *et al.*, 2013), and allow reasonable attribution of driving factors behind recorded ecosystem properties. A recent application of this resurvey approach revealed that the legacy of atmospheric N deposition had an important influence on diversity changes between resurveys (Bernhardt-Römermann *et al.*, 2015).

A resurvey approach, with a long time period between surveys, is particularly useful in systems that exhibit slower dynamics, as is typical of plant communities in temperate forests or alpine meadows with many perennials (Dornelas *et al.*, 2013). Resurveys have an added benefit of taking account of gradients of change which may reveal nonlinearities in response which is typically lacking from two-level, factorial experimental approaches which characterize much of the environmental change literature (Bradford *et al.*, 2012). If enough spatially replicated resurvey plots across environmental gradients can be found, it may be possible to reveal interactive effects among environmental changes as seen elsewhere (Didham *et al.*, 2007; Dieleman *et al.*, 2012), as well as between land-use legacies and changing environments. The ability to analyse multiple resurveys at any given location would be especially beneficial in the latter case, as similar ecosystem properties at some middle time point but different

distributions before and afterwards would confirm that the accurate projection of future properties requires knowledge of the past, and not just characterization of the present state of a system.

Experimental approaches offer a means to unambiguously separate out ecosystem response drivers, and tease apart the direct and indirect effects of environmental change and land-use legacy on ecosystem function. Common-garden experiments using soils from across large-scale spatial gradients with alternative land-use legacies, with additional environmental change treatments, could be usefully employed to disentangle the effects of legacies and environmental change on ecosystem response, and complement paired approaches such as adopted by Gill (2014). The common-garden experiments could manipulate composition and environmental change, to separate direct and indirect effects, in a similar manner to Manning *et al.* (2006b) and Fry *et al.* (2013), across land-use legacies. In addition, these experiments, if performed over a sufficiently long period, may also be able to take advantage of developing analytical approaches that account for nonadditivity among environmental drivers and separate out direct and indirect environmental change effects on community dynamics (Farrer *et al.*, 2014). Experimental approaches offer the ability to test for responses in likely future novel conditions (Williams & Jackson, 2007), which, by definition, plants in resurvey plots have not yet experienced.

Synthesis: a trait-based framework for elucidating land-use legacies and environmental change

The interaction among land-use legacies and environmental change on ecosystem properties may be conceptually synthesized using a trait-based approach (Fig. 2) (e.g. Diaz *et al.*, 1999). This approach allows the integration of the traditionally divergent fields of community and ecosystem-level research (Lavorel & Garnier, 2002; Norberg, 2004; McGill *et al.*, 2006). In the context of land-use legacies and contemporary environmental change, the framework needs to consider how the fundamental processes of community dynamics, that is drift, speciation, ecological selection and dispersal (Vellend, 2010) relate to traits, in addition to trait relationships with the direct and indirect effects of forcing factors on resources and conditions and consequent ecosystem function (Suding *et al.*, 2008; Smith *et al.*, 2009).

The trajectories of species composition and diversity depend on community assembly as well as related population processes (Peet & Christensen, 1987). Assembly can be related to four, logically distinct, fundamental processes. Species are added to communities via speciation and dispersal, with relative abundances then being determined by drift and selection as well as ongoing dispersal (Vellend, 2010). The outcome of two of these processes, dispersal and selection, clearly depend on species traits; the others (drift and speciation) influence

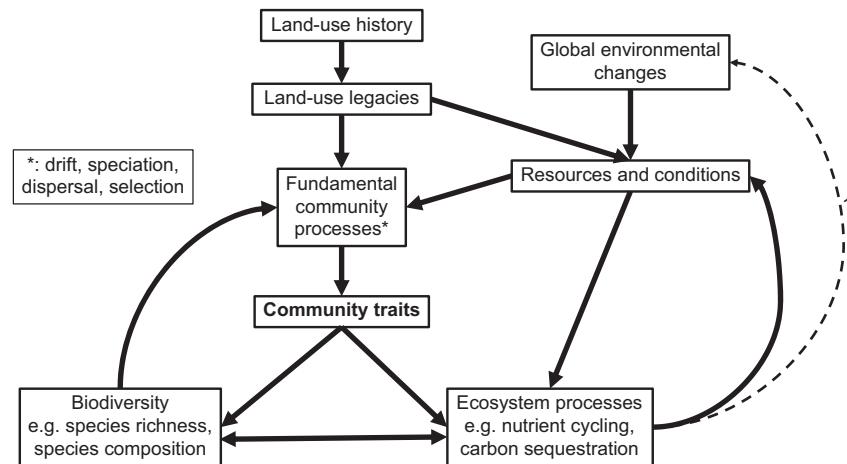


Fig. 2 A trait-based framework to understanding the interactive effects of land-use legacies and global environmental changes on ecosystem properties. Compositional and functional effects on ecosystems can be synthesized through the bridge provided by functional community traits. The distribution of these traits in an ecosystem depends on fundamental community processes set in train by land-use legacies as outlined in the main text. Legacies, and contemporary global environmental changes, affect resources and conditions which, mainly through selection, further influence community trait distributions while directly affecting ecosystem processes. Trait distributions can be related to species composition (Laughlin, 2014) and ecosystem function (Eviner & Chapin, 2003). The biotic milieu can also influence community processes while ecosystem processes feedback on resources and conditions. Ultimately, the fundamental process of speciation can depend on the rarity of the specific resources and conditions at a given site. Ecosystem processes, aggregated across many sites, feedback to influence global environmental change (dashed arrow 1).

trait distributions, fundamentally in the case of speciation by potentially adding new trait values. Below, we concentrate on the deterministic processes of selection and dispersal, but the potential for trait values to be modified by drift and speciation should be borne in mind (e.g. Baeten *et al.*, 2010; Thomas, 2015). In particular, the rate at which species, and therefore new trait values are produced, could depend on the frequency of abiotic conditions which will be altered by environmental change (Vellend, 2010).

There is clear evidence that fast colonizing species are favoured by certain plant traits (e.g. seed size, seed release height, dispersal syndrome) (Verheyen *et al.*, 2003) at least partly due to phylogenetic relatedness (Thomson *et al.*, 2011; Baeten *et al.*, 2015). Organisms possessing advantageous dispersal rates will preferentially arrive into the patch. This though does not mean they will establish and persist, as a species' demography will depend upon a suite of traits and the selective environment. The selective environment can be considered to have three interdependent axes – abiotic resources, conditions and the biotic milieu. Land-use legacy leads to altered resources and variation in growth conditions as explained previously. These different resources and conditions select for different trait values (and thus plant species) from the pool of available traits, an availability that is determined by biotic contingency, via dispersal and the species left from the previous land use. This can lead to a potential convergence of associated traits through environmental filtering, although priority effects may mean that certain trait values persist by virtue of species arrival order. Biotic interactions between the remaining species refine the trait distribution further, potentially leading to trait divergence to allow partitioning of resources and conditions among the surviving species (Laughlin *et al.*, 2012).

Importantly, alterations in resources and conditions engendered by contemporary environmental change can lead to predictable, although not always consistent, variation in trait distributions due to species responses to the environment (Pakeman, 2004; Pakeman *et al.*, 2009; Amatangelo *et al.*, 2014). Thus, it is important to consider how the conditions and resources induced by a given land-use legacy interact with any given set of global change drivers to influence the community. Larger community changes may be expected when the summed net effects on resources and conditions are larger. However, there could also be nonlinear responses to some drivers, for example when the soil switches from the cation to aluminium (Al) pH buffer range as a result of acidification, and toxic Al becomes bioavailable (Blaser *et al.*, 2008). Traits are also well-established drivers of ecosystem functions, both

above- and below-ground (Eviner & Chapin, 2003; Bardgett *et al.*, 2014). Taking account of dynamic environmental filters should therefore allow projection of trait responses to the environment and effects on ecosystems (Suding *et al.*, 2008; Webb *et al.*, 2010), providing co-variation among traits can be elucidated (Bardgett *et al.*, 2014). This analysis of covariation needs extending to dispersal and persistence traits, given their importance in determining community dynamics and subsequent ecosystem function.

The resurvey approach, in conjunction with species trait data that relate species and functional trait values [e.g. from databases such as LEDA (Kleyer *et al.*, 2008) and TRY (Kattge *et al.*, 2011)], can allow the analysis of interactions among environmental changes and land-use legacies (Fig. 3), as can experimental approaches. Trait distributions can also be converted into both compositional and functional outcomes by taking advantage of recent analytical developments (Laughlin, 2014), providing relationships among traits, species identity and ecosystem function are robust. By considering trait distributions, intra- as well as interspecific variation can also be accounted for, although it is likely this will

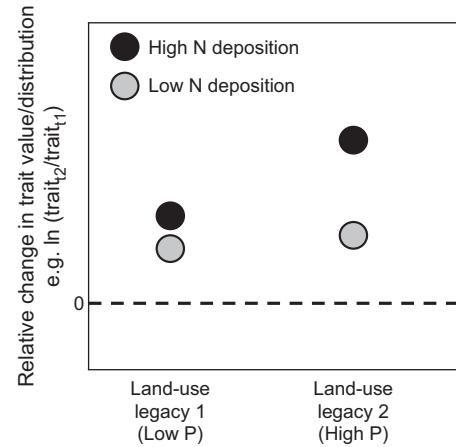


Fig. 3 Applying the trait-based framework to reveal how environmental change can modulate the trajectory of ecosystem responses to land-use legacy using resurvey data. At low nitrogen (N) deposition, a low (Land-use legacy 1) and high (Land-use legacy 2) soil phosphorus (P) content have similar responses between resurvey periods (t_1 and t_2) in their trait distributions (the response ratio shown on the y-axis). However, with high N deposition, a high soil P legacy from the former agricultural land use allows a much greater response in the trait response ratio due to hypothesized N limitation. In contrast, the attainment of P limitation at site 1 constrains the trait response to additional N deposition. In this hypothetical scenario, all other variables appear equal, for example overstorey composition, water, light, soil pH and temperature environment and, for simplicity, we do not consider additional environmental changes and their interactions, which may further modify trait distributions.

require in-field collection efforts as trait databases would tend to favour the use of single mean values. This intraspecific variation may be important for community processes (Bolnick *et al.*, 2011) and may be related to resources and conditions (Kumordzi *et al.*, 2014).

Concluding remarks

The past has already been shown to be important in predicting the future in dynamic systems, ecological or otherwise. However, we are generally ignorant of the past's absolute and relative importance in determining ecosystems' likely future properties in the face of multiple environmental changes. We suggest that abiotic and biotic legacies of former land use can modulate the impact of multiple environmental changes on future ecosystem composition and function. Effects will be dependent on the extent to which global change drivers alter the resources, conditions and community processes that are themselves legacies of historical land use. Virtually all existing investigations have used modelling approaches to explore this interaction. We highlight that opportunities exist through observational resurvey and experimental avenues to further elucidate the importance of land-use legacies to better understand the impacts of environmental changes across systems. A trait-based framework that especially considers the fundamental community processes of dispersal and selection, while being mindful of speciation and drift, offers the means to synthesize compositional and functional responses. This framework can also consider the direct and indirect functional effects of changes in resources and conditions brought about by multiple environmental changes and land-use legacies when combined with suitable experimental tests. Elucidating these pathways will have valuable implications as we try to mediate biodiversity loss and maintain ecosystem services through management actions. This imperative is gaining in importance as more and more of the globe is recognized as having legacies associated with previous land use. We suggest that only by recognizing the importance of land-use legacies will we achieve a synthetic understanding of environmental change effects on ecosystems.

Acknowledgements

We thank two anonymous referees for helpful comments and the European Research Council for funding this research through the PASTFORWARD project [ERC Consolidator Grant 614839]. PDF and LB were supported by a postdoctoral fellowship of the Research Foundation – Flanders (FWO), and LB also thanks the Special Research Fund of Ghent University (BOF).

The authors declare that they have no conflicts of interest in relation to this work.

References

- Adler PB, Byrne KM, Leiker J (2013) Can the past predict the future? Experimental tests of historically based population models. *Global Change Biology*, **19**, 1793–1803.
- Amatangelo KL, Johnson SE, Rogers DA, Waller DM (2014) Trait-environment relationships remain strong despite 50 years of trait compositional change in temperate forests. *Ecology*, **95**, 1780–1791.
- Anderegg WRL, Schwalm C, Biondi F *et al.* (2015) Pervasive drought legacies in forest ecosystems and their implications for carbon cycle models. *Science*, **349**, 528–532.
- Arce-Nazario JA (2007) Human landscapes have complex trajectories: reconstructing Peruvian Amazon landscape history from 1948 to 2005. *Landscape Ecology*, **22**, 89–101.
- Baeten L, Hermy M, Van Daele S, Verheyen K (2010) Unexpected understorey community development after 30 years in ancient and post-agricultural forests. *Journal of Ecology*, **98**, 1447–1453.
- Baeten L, Verstraeten G, De Frenne P, Vanhellemont M, Wuyts K, Hermy M, Verheyen K (2011) Former land use affects the nitrogen and phosphorus concentrations and biomass of forest herbs. *Plant Ecology*, **212**, 901–909.
- Baeten L, Warton DI, Van Calster H *et al.* (2014) A model-based approach to studying changes in compositional heterogeneity. *Methods in Ecology and Evolution*, **5**, 156–164.
- Baeten L, Davies TJ, Verheyen K, Van Calster H, Vellend M (2015) Disentangling dispersal from phylogeny in the colonization capacity of forest understorey plants. *Journal of Ecology*, **103**, 175–183.
- Bardgett RD, Mommer L, De Vries FT (2014) Going underground: root traits as drivers of ecosystem processes. *Trends in Ecology & Evolution*, **29**, 692–699.
- Bernhardt-Römermann M, Baeten L, Craven D *et al.* (2015) Drivers of temporal changes in temperate forest plant diversity vary across spatial scales. *Global Change Biology*, **21**, 3726–3737.
- Blaser P, Walther L, Pannatier EG (2008) The sensitivity of Swiss forest soils to acidification and the risk of aluminium toxicity. *Journal of Plant Nutrition and Soil Science*, **171**, 605–612.
- Bolnick DI, Amarasekare P, Araujo MS *et al.* (2011) Why intraspecific trait variation matters in community ecology. *Trends in Ecology & Evolution*, **26**, 183–192.
- Bommarco R, Lindborg R, Marini L, Öckinger E (2014) Extinction debt for plants and flower-visiting insects in landscapes with contrasting land use history. *Diversity and Distributions*, **20**, 591–599.
- Bossuyt B, Hermy M (2001) Influence of land use history on seed banks in European temperate forest ecosystems: a review. *Ecography*, **24**, 225–238.
- Bradford MA, Wood SA, Maestre FT, Reynolds JF, Warren II RJ (2012) Contingency in ecosystem but not plant community response to multiple global change factors. *New Phytologist*, **196**, 462–471.
- Cleveland CC, Reed SC, Townsend AR (2006) Nutrient regulation of organic matter decomposition in a tropical rain forest. *Ecology*, **87**, 492–503.
- Comita LS, Thompson J, Uriarte M, Jonckheere I, Canham CD, Zimmerman JK (2010) Interactive effects of land use history and natural disturbance on seedling dynamics in a subtropical forest. *Ecological Applications*, **20**, 1270–1284.
- Cramer VA, Hobbs RJ, Standish RJ (2008) What's new about old fields? Land abandonment and ecosystem assembly. *Trends in Ecology & Evolution*, **23**, 104–112.
- Dambre E, Dupouey J-L, Laüt L, Humbert L, Thimon M, Beaufils T, Richard H (2007) Present forest biodiversity patterns in France related to former Roman agriculture. *Ecology*, **88**, 1430–1439.
- De Cáceres M, Brotons L, Aquilué N, Fortin M-J (2013) The combined effects of land-use legacies and novel fire regimes on bird distributions in the Mediterranean. *Journal of Biogeography*, **40**, 1535–1547.
- De Frenne P, Brunet J, Shevtsova A *et al.* (2011) Temperature effects on forest herbs assessed by warming and transplant experiments along a latitudinal gradient. *Global Change Biology*, **17**, 3240–3253.
- De Frenne P, Graae BJ, Rodriguez-Sánchez F *et al.* (2013a) Latitudinal gradients as natural laboratories to infer species' responses to temperature. *Journal of Ecology*, **101**, 784–795.
- De Frenne P, Rodríguez-Sánchez F, Coomes DA *et al.* (2013b) Microclimate moderates plant responses to macroclimate warming. *Proceedings of the National Academy of Sciences of the United States of America*, **110**, 18561–18565.
- Díaz S, Cabido M, Zak M, Martínez Carretero E, Aranibar J (1999) Plant functional traits, ecosystem structure and land-use history along a climatic gradient in central-western Argentina. *Journal of Vegetation Science*, **10**, 651–660.

- Didham RK, Tylianakis JM, Gemmell NJ, Rand TA, Ewers RM (2007) Interactive effects of habitat modification and species invasion on native species decline. *Trends in Ecology & Evolution*, **22**, 489–496.
- Dieleman WJJ, Vicca S, Dijkstra FA *et al.* (2012) Simple additive effects are rare: a quantitative review of plant biomass and soil process responses to combined manipulations of CO₂ and temperature. *Global Change Biology*, **18**, 2681–2693.
- Dornelas M, Magurran AE, Buckland ST *et al.* (2013) Quantifying temporal change in biodiversity: challenges and opportunities. *Proceedings of the Royal Society of London B: Biological Sciences*, **280**, 20121931.
- Dupouey JL, Dambrine E, Laffite JD, Moares C (2002) Irreversible impact of past land use on forest soils and biodiversity. *Ecology*, **83**, 2978–2984.
- Egler FE (1954) Vegetation science concepts I. Initial floristic composition, a factor in old-field vegetation development with 2 figs. *Vegetatio*, **4**, 412–417.
- Ehrlén J, Morris WF (2015) Predicting changes in the distribution and abundance of species under environmental change. *Ecology Letters*, **18**, 303–314.
- Evner VT, Chapin FS III (2003) Functional matrix: a conceptual framework for predicting multiple plant effects on ecosystem processes. *Annual Review of Ecology, Evolution and Systematics*, **34**, 455–485.
- Ewers RM, Didham RK, Pearse WD *et al.* (2013) Using landscape history to predict biodiversity patterns in fragmented landscapes. *Ecology Letters*, **16**, 1221–1233.
- Farrer EC, Ashton IW, Knape J, Suding KN (2014) Separating direct and indirect effects of global change: a population dynamic modeling approach using readily available field data. *Global Change Biology*, **20**, 1238–1250.
- Ficetola GF, Maiorano L, Falcucci A *et al.* (2010) Knowing the past to predict the future: land-use change and the distribution of invasive bullfrogs. *Global Change Biology*, **16**, 528–537.
- Flinn KM (2007) Microsite-limited recruitment controls fern colonization of post-agricultural forests. *Ecology*, **88**, 3103–3114.
- Flinn KM, Marks PL (2007) Agricultural legacies in forest environments: tree communities, soil properties, and light availability. *Ecological Applications*, **17**, 452–463.
- Flinn KM, Vellend M (2005) Recovery of forest plant communities in post-agricultural landscapes. *Frontiers in Ecology and the Environment*, **3**, 243–250.
- Foster D, Swanson F, Aber J, Burke I, Brokaw N, Tilman D, Knapp A (2003) The importance of land-use legacies to ecology and conservation. *BioScience*, **53**, 77–88.
- Fraterrigo JM, Turner MG, Pearson SM, Dixon P (2005) Effects of past land use on spatial heterogeneity of soil nutrients in Southern Appalachian forests. *Ecological Monographs*, **75**, 215–230.
- Fraterrigo J, Turner M, Pearson S (2006) Interactions between past land use, life-history traits and understory spatial heterogeneity. *Landscape Ecology*, **21**, 777–790.
- Freschet GT, Östlund L, Kichenin E, Wardle DA (2014) Aboveground and below-ground legacies of native Sami land-use on boreal forest in northern Sweden 100 years after abandonment. *Ecology*, **95**, 963–977.
- Fry EL, Manning P, Allen DGP, Hurst A, Everwand G, Rimmell M, Power SA (2013) Plant functional group composition modifies the effects of precipitation change on grassland ecosystem function. *PLoS One*, **8**, e57027.
- Garbarino M, Lingua E, Weisberg PJ, Bottero A, Meloni F, Motta R (2013) Land-use history and topographic gradients as driving factors of subalpine *Larix decidua* forests. *Landscape Ecology*, **28**, 805–817.
- George LO, Bazzaz FA (1999) The fern understory as an ecological filter: growth and survival of canopy-tree seedlings. *Ecology*, **80**, 846–856.
- Gill RA (2014) The influence of 3-years of warming and N-deposition on ecosystem dynamics is small compared to past land use in subalpine meadows. *Plant and Soil*, **374**, 197–210.
- Gilliam FS (2007) The ecological significance of the herbaceous layer in temperate forest ecosystems. *BioScience*, **57**, 845–858.
- Gimmi U, Poultier B, Wolf A, Portner H, Weber P, Bürgi M (2013) Soil carbon pools in Swiss forests show legacy effects from historic forest litter raking. *Landscape Ecology*, **28**, 835–846.
- Halofsky JE, Hemstrom MA, Conklin DR, Halofsky JS, Kerns BK, Bachelet D (2013) Assessing potential climate change effects on vegetation using a linked model approach. *Ecological Modelling*, **266**, 131–143.
- Hansen MC, Stehman SV, Potapov PV (2010) Quantification of global gross forest cover loss. *Proceedings of the National Academy of Sciences of the United States of America*, **107**, 8650–8655.
- Haug RD, Hall SA, Gray EM, Gonzalez P, Bakker JD (2010) Influences of climate, fire, grazing, and logging on woody species composition along an elevation gradient in the eastern Cascades, Washington. *Forest Ecology and Management*, **260**, 2204–2213.
- Henne PD, Elkin C, Colombaroli D, Samartin S, Bugmann H, Heiri O, Tinner W (2013) Impacts of changing climate and land use on vegetation dynamics in a Mediterranean ecosystem: insights from paleoecology and dynamic modelling. *Landscape Ecology*, **28**, 819–833.
- Hermy M, Verheyen K (2007) Legacies of the past in the present-day forest biodiversity: a review of past land-use effects on forest plant species composition and diversity. *Ecological Research*, **22**, 361–371.
- Holl KD, Cronk EE, Schultz CB (2003) Landscape restoration: moving from generalities to methodologies. *BioScience*, **53**, 491–502.
- Hooper TD, Compton JE (2003) Forest ecosystem carbon storage and nitrogen accumulation during the first century after agricultural abandonment. *Ecological Applications*, **13**, 299–313.
- Hovenden MJ, Newton PCD, Wills KE (2014) Seasonal not annual rainfall determines grassland biomass response to carbon dioxide. *Nature*, **511**, 583–586.
- Hurt GC, Chini LP, Frolik S *et al.* (2011) Harmonization of land-use scenarios for the period 1500–2100: 600 years of global gridded annual land-use transitions, wood harvest, and resulting secondary lands. *Climatic Change*, **109**, 117–161.
- Jackson ST, Sax DF (2010) Balancing biodiversity in a changing environment: extinction debt, immigration credit and species turnover. *Trends in Ecology & Evolution*, **25**, 153–160.
- Jarvis S, Woodward S, Alexander IJ, Taylor AFS (2013) Regional scale gradients of climate and nitrogen deposition drive variation in ectomycorrhizal fungal communities associated with native Scots pine. *Global Change Biology*, **19**, 1688–1696.
- Johnson EA, Miyaniishi K (2008) Testing the assumptions of chronosequences in succession. *Ecology Letters*, **11**, 419–431.
- Kattge J, Diaz S, Lavorel S *et al.* (2011) TRY – a global database of plant traits. *Global Change Biology*, **17**, 2905–2935.
- Kearney M, Porter W (2009) Mechanistic niche modelling: combining physiological and spatial data to predict species' ranges. *Ecology Letters*, **12**, 334–350.
- Kleyer M, Bekker RM, Knevel IC *et al.* (2008) The LEDA Traitbase: a database of life-history traits of the Northwest European flora. *Journal of Ecology*, **96**, 1266–1274.
- Koerner W, Dupouey JL, Dambrine E, Benoit M (1997) Influence of past land use on the vegetation and soils of present day forest in the Vosges mountains, France. *Journal of Ecology*, **85**, 351–358.
- Kumordzi BB, Nilsson M-C, Gundale MJ, Wardle DA (2014) Changes in local-scale intraspecific trait variability of dominant species across contrasting island ecosystems. *Ecophere*, **5**, doi: 10.1890/ES13-0033.1.
- Langley JA, Megonigal JP (2010) Ecosystem response to elevated CO₂ levels limited by nitrogen-induced plant species shift. *Nature*, **466**, 96–99.
- Laughlin DC (2014) Applying trait-based models to achieve functional targets for theory-driven ecological restoration. *Ecology Letters*, **17**, 771–784.
- Laughlin DC, Joshi C, Van Bodegom PM, Bastow ZA, Fulé PZ (2012) A predictive model of community assembly that incorporates intraspecific trait variation. *Ecology Letters*, **15**, 1291–1299.
- Lavorel S, Garnier E (2002) Predicting changes in community composition and ecosystem functioning from plant traits: revisiting the Holy Grail. *Functional Ecology*, **16**, 545–556.
- Liu J, Dietz T, Carpenter SR *et al.* (2007) Complexity of coupled human and natural systems. *Science*, **317**, 1513–1516.
- Löhmus K, Paal T, Liira J (2014) Long-term colonization ecology of forest-dwelling species in a fragmented rural landscape – dispersal versus establishment. *Ecology and Evolution*, **4**, 3113–3126.
- Lunt ID, Spooner PG (2005) Using historical ecology to understand patterns of biodiversity in fragmented agricultural landscapes. *Journal of Biogeography*, **32**, 1859–1873.
- Luo Y, Gerten D, Le Maire G *et al.* (2008) Modeled interactive effects of precipitation, temperature, and [CO₂] on ecosystem carbon and water dynamics in different climatic zones. *Global Change Biology*, **14**, 1986–1999.
- Lynch P (2008) The origins of computer weather prediction and climate modeling. *Journal of Computational Physics*, **227**, 3431–3444.
- MacDonald GK, Bennett EM, Tararu ZE (2012) The influence of time, soil characteristics, and land-use history on soil phosphorus legacies: a global meta-analysis. *Global Change Biology*, **18**, 1904–1917.
- Maes SL, De Frenne P, Brunet J *et al.* (2014) Effects of enhanced nitrogen inputs and climate warming on a forest understory plant assessed by transplant experiments along a latitudinal gradient. *Plant Ecology*, **215**, 899–910.
- Malhi Y, Silman M, Salinas N, Bush M, Meir P, Saatchi S (2010) Introduction: elevation gradients in the tropics: laboratories for ecosystem ecology and global change research. *Global Change Biology*, **16**, 3171–3175.
- Manning AD, Fischer J, Lindenmayer DB (2006a) Scattered trees as keystone structures – implications for conservation. *Biological Conservation*, **132**, 311–321.
- Manning P, Newington JE, Robson HR *et al.* (2006b) Decoupling the direct and indirect effects of nitrogen deposition on ecosystem function. *Ecology Letters*, **9**, 1015–1024.

- Mayle FE, Langstroth RP, Fisher RA, Meir P (2007) Long-term forest-savannah dynamics in the Bolivian Amazon: implications for conservation. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **362**, 291–307.
- McEwan RW, Dyer JM, Pederson N (2011) Multiple interacting ecosystem drivers: toward an encompassing hypothesis of oak forest dynamics across eastern North America. *Ecography*, **34**, 244–256.
- McGill BJ, Enquist BJ, Weiher E, Westoby M (2006) Rebuilding community ecology from functional traits. *Trends in Ecology & Evolution*, **21**, 178–185.
- McLauchlan K (2006) The nature and longevity of agricultural impacts on soil carbon and nutrients: a review. *Ecosystems*, **9**, 1364–1382.
- McLauchlan KK, Hobbie SE, Post WM (2006) Conversion from agriculture to grassland builds soil organic matter on decadal timescales. *Ecological Applications*, **16**, 143–153.
- Meunier J, Brown PM, Romme WH (2014) Tree recruitment in relation to climate and fire in northern Mexico. *Ecology*, **95**, 197–209.
- Mitchell CE, Turner MG, Pearson SM (2002) Effects of historical land use and forest patch size on myrmecochores and ant communities. *Ecological Applications*, **12**, 1364–1377.
- Moncrieff GR, Scheiter S, Bond WJ, Higgins SI (2014) Increasing atmospheric CO₂ overrides the historical legacy of multiple stable biome states in Africa. *New Phytologist*, **201**, 908–915.
- Moore PT, Van Miegroet H, Nicholas NS (2007) Relative role of understory and overstory in carbon and nitrogen cycling in a southern Appalachian spruce-fir forest. *Canadian Journal of Forest Research*, **37**, 2689–2700.
- Mouquet N, Lagadeuc Y, Devictor V et al. (2015) Predictive ecology in a changing world. *Journal of Applied Ecology*, **52**, 1293–1310.
- Navarro-González I, Pérez-Luque AJ, Bonet FJ, Zamora R (2013) The weight of the past: land-use legacies and recolonization of pine plantations by oak trees. *Ecological Applications*, **23**, 1267–1276.
- Norberg J (2004) Biodiversity and ecosystem functioning: a complex adaptive systems approach. *Limnology and Oceanography*, **49**, 1269–1277.
- Ogle K, Barber JJ, Barron-Gafford GA et al. (2015) Quantifying ecological memory in plant and ecosystem processes. *Ecology Letters*, **18**, 221–235.
- Ollinger SV, Aber JD, Reich PB, Freuder RJ (2002) Interactive effects of nitrogen deposition, tropospheric ozone, elevated CO₂ and land use history on the carbon dynamics of northern hardwood forests. *Global Change Biology*, **8**, 545–562.
- Olsson MO, Falkengren-Grerup U (2003) Partitioning of nitrate uptake between trees and understory in oak forests. *Forest Ecology and Management*, **179**, 311–320.
- Pakeman RJ (2004) Consistency of plant species and trait responses to grazing along a productivity gradient: a multi-site analysis. *Journal of Ecology*, **92**, 893–905.
- Pakeman RJ, Lepš J, Kleyer M, Lavorel S, Garnier E, The VISTA Consortium (2009) Relative climatic, edaphic and management controls of plant functional trait signatures. *Journal of Vegetation Science*, **20**, 148–159.
- Peet RK, Christensen NL (1980) Succession: a population process. *Vegetatio*, **43**, 131–140.
- Peet RK, Christensen NL (1987) Competition and tree death. *BioScience*, **37**, 586–595.
- Pereira HM, Leadley PW, Proença V et al. (2010) Scenarios for global biodiversity in the 21st century. *Science*, **330**, 1496–1501.
- Perring MP, Hedin LO, Levin SA, McGroddy M, De Mazancourt C (2008) Increased plant growth from nitrogen addition should conserve phosphorus in terrestrial ecosystems. *Proceedings of the National Academy of Sciences of the United States of America*, **105**, 1971–1976.
- Perring MP, Standish RJ, Price JN et al. (2015) Advances in restoration ecology: rising to the challenges of the coming decades. *Ecosphere*, **6**, doi: 10.1890/ES15-00121.1.
- Provenza FD (1995) Tracking variable environments: there is more than one kind of memory. *Journal of Chemical Ecology*, **21**, 911–923.
- Purschke O, Sykes M, Reitalu T, Poschlod P, Prentice H (2012) Linking landscape history and dispersal traits in grassland plant communities. *Oecologia*, **168**, 773–783.
- Ramalho CE, Hobbs RJ (2012) Time for a change: dynamic urban ecology. *Trends in Ecology & Evolution*, **27**, 179–188.
- Rhemtulla JM, Mladenoff DJ, Clayton MK (2009) Legacies of historical land use on regional forest composition and structure in Wisconsin, USA (mid-1800s–1930s–2000s). *Ecological Applications*, **19**, 1061–1078.
- Ryan EM, Ogle K, Zelikova TJ, Lecain DR, Williams DG, Morgan JA, Pendall E (2015) Antecedent moisture and temperature conditions modulate the response of ecosystem respiration to elevated CO₂ and warming. *Global Change Biology*, **21**, 2588–2602.
- Savage KE, Parton WJ, Davidson EA, Trumbore SE, Frey SD (2013) Long-term changes in forest carbon under temperature and nitrogen amendments in a temperate northern hardwood forest. *Global Change Biology*, **19**, 2389–2400.
- Smith MD, Knapp AK, Collins SL (2009) A framework for assessing ecosystem dynamics in response to chronic resource alterations induced by global change. *Ecology*, **90**, 3279–3289.
- Staland H, Salmonsson J, Hörnberg G (2011) A thousand years of human impact in the northern Scandinavian mountain range: long-lasting effects on forest lines and vegetation. *The Holocene*, **21**, 379–391.
- Suding KN, Lavorel S, Chapin FS III et al. (2008) Scaling environmental change through the community-level: a trait-based response-and-effect framework for plants. *Global Change Biology*, **14**, 1125–1140.
- Szitár K, Ónodi G, Somay L, Pándi I, Kucs P, Kröel-Dulay G (2014) Recovery of inland sand dune grasslands following the removal of alien pine plantation. *Biological Conservation*, **171**, 52–60.
- Talhelm AF, Pregitzer KS, Kubiske ME et al. (2014) Elevated carbon dioxide and ozone alter productivity and ecosystem carbon content in northern temperate forests. *Global Change Biology*, **20**, 2492–2504.
- Thomas CD (2015) Rapid acceleration of plant speciation during the Anthropocene. *Trends in Ecology & Evolution*, **30**, 448–455.
- Thomson FJ, Moles AT, Auld TD, Kingsford RT (2011) Seed dispersal distance is more strongly correlated with plant height than with seed mass. *Journal of Ecology*, **99**, 1299–1307.
- Treseder KK, Vitousek PM (2001) Effects of soil nutrient availability on investment in acquisition of N and P in Hawaiian rain forests. *Ecology*, **82**, 946–954.
- Vellend M (2004) Parallel effects of land-use history on species diversity and genetic diversity of forest herbs. *Ecology*, **85**, 3043–3055.
- Vellend M (2010) Conceptual synthesis in community ecology. *The Quarterly Review of Biology*, **85**, 183–206.
- Vellend M, Verheyen K, Jacquemyn H, Kolb A, Van Calster H, Peterken G, Hermy M (2006) Extinction debt of forest plants persists for more than a century following habitat fragmentation. *Ecology*, **87**, 542–548.
- Vellend M, Brown CD, Kharouba HM, McCune JL, Myers-Smith IH (2013) Historical ecology: using unconventional data sources to test for effects of global environmental change. *American Journal of Botany*, **100**, 1294–1305.
- Verheyen K, Honnay O, Motzkin G, Hermy M, Foster DR (2003) Response of forest plant species to land-use change: a life-history trait-based approach. *Journal of Ecology*, **91**, 563–577.
- Verheyen K, Baeten L, De Frenne P et al. (2012) Driving factors behind the eutrophication signal in understorey plant communities of deciduous temperate forests. *Journal of Ecology*, **100**, 352–365.
- Webb CT, Hoeting JA, Ames GM, Pyne MI, Poff NL (2010) A structured and dynamic framework to advance traits-based theory and prediction in ecology. *Ecology Letters*, **13**, 267–283.
- Williams JW, Jackson ST (2007) Novel climates, no-analog communities, and ecological surprises. *Frontiers in Ecology and Environment*, **5**, 475–482.