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Proceedings Editor: D. A. McGilloway

Publisher: Wageningen Academic Publishers, The Netherlands

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Soil biology and the emergence of adventive grassland ecosystems

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Key points

1. Understanding the role of biodiversity in ecosystem function has dominated the research efforts of grassland ecologists in recent years. Research indicates that the trophic complexity of the soil biota precludes simple predictive responses to manipulations of intact soil systems.
2. The composition and activity of the soil biota are sensitive to environmental drivers and changes in plant species composition. The emergence of adventive ecosystems, generated by introduced species and new environmental conditions of grasslands, demands a research emphasis to assess the ecosystem services provided by the soil biota while concurrently addressing species conservation concerns.

Keywords: biodiversity, environmental change, invasive species, nitrogen deposition

Introduction

The last few years have seen an explosion of information on the responses and feedbacks of soil biota to species and environmental changes. Soil biologists, plant ecologists, and biogeochemists have been searching for patterns, generality and predictability in these relationships. A few brave souls have had the courage to assemble comprehensive assessments of soil biology in our rapidly changing world. Several years ago, I reviewed Wardle's (2002) book emphasising the links between above- and belowground components of ecosystems. That activity – as well as the present one – provided me with the opportunity to survey recent findings in soil biology. I have attempted to synthesise that information with respect to conservation and management issues. This analysis suggests that our scientific endeavours continue to advance the goal of providing sustainable, productive grasslands. At the same time, nevertheless, I sense growing urgency to identify the consequences of inevitable abiotic and biotic change on the structure and function of grassland soil ecosystems.

The current research foci of grassland ecologists

To assess recent research emphasis among grassland ecologists, I conducted a subject-directed literature search for 2001- 2004. The Science Citation Index (Web of Science) was used to assess grassland research topics published in two journals each in North America (*Ecology* and *Ecological Applications*), the United Kingdom (*Journal of Ecology* and *Journal of Applied Ecology*) and mainland Europe (*Oecologia* and *Oikos*). Topics included 1) climate change, 2) carbon dioxide, 3) nitrogen deposition, 4) invasions, 5) land use, 6) historical range of variability (disturbance, fire, and floods) and 7) biodiversity. The effort was iterated several times using various word combinations to provide some confidence that the analysis reflects activity on the research topics. Of the total 4333 papers accessed, 2039 were from the mainland European publishers, 1600 from North America, and 694 from the UK. From this analysis, grassland publications on the above topics totalled 77, 79, and 58, in these sources, respectively. In terms of percentage of total publications, the UK journals have the greatest

emphasis on grassland topics. Grassland citations represented 4%, 5%, and 8% of total publications in mainland Europe, USA, and UK, respectively.

Clearly, the amount of science directed at grasslands is disproportionately low for the relative global coverage of grasslands. Grassland publications represented only about 5% of the subject area of the 4333 papers searched in this effort. For comparison, I repeated this exercise a few months later using the terms ‘forest’ and ‘desert’ in the same journals and found 1231 of 4705 citations (*ca* 26%), on these topics, mostly on forests. This discrepancy may be made up in speciality journals emphasising soils, soil ecology, and agroecosystems, but it does show a lack of emphasis on grassland studies *per se*. A search for topics on ‘desertification’, ‘forestation or deforestation’, ‘grassification’ and ‘grasslandification’ provides additional proof of this bias. Humans have been in the business of creating grasslands and grazing lawns for centuries (or ‘grassified’, see Baker, 1978), but the process of growing grass (as opposed to growing trees) is defined by what is lost, not what is gained. The term ‘grasslandification’ is not recognised except in those regions where invasive grasses are now replacing shrubland and desert flora.

Collectively, authors of grassland studies see biodiversity as the dominant research agenda, with 42% of grassland papers addressing this issue (Figure 1). The topic was particularly dominant in European publications, where the subject occupied almost 60% of grassland publications. This emphasis was reinforced when these same topics were searched using a broader array of ecology journals. Disturbance ecology and invasions were of secondary importance. The global change drivers of climate, carbon dioxide (CO₂), and nitrogen (N) deposition, somewhat surprisingly accounted for <10% of publications. The ecological community’s interest in effects of external ecosystem drivers is overwhelmed by interest in internal dynamics. For example, when the phrase “nitrogen deposition” or “nitrogen input” is shortened to “nitrogen” in the search, citations increased from 13 to 599 citations from a search of 4705 papers. Causes and consequences of nitrogen availability in grassland soils remain a key interest to ecologists.

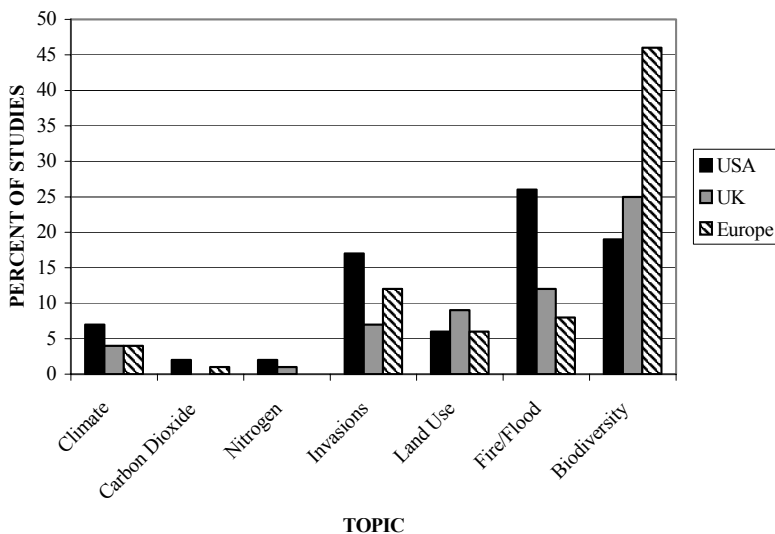


Figure 1 Research topics of grassland ecologists published in six ecological journals, 2001-2004

Differences might be expected between the research foci of scientists occupying a continent that has been under extensive human dominance for many centuries, and one that has been transformed relatively recently. North American publications emphasise change in historical ranges of variability, biodiversity and invasive species, with about equal emphasis on all three topics (Figure 1). The reduced emphasis on biodiversity *per se* makes sense in that, relative to the UK and Europe, many grasslands of North America have only recently emerged from relatively pristine conditions and are now outside their historical range of variability in terms of grazing, atmospheric chemistry, fire and flood return intervals. These transitions, with an emphasis on non-native species introductions, are perceived as both stand-alone subjects and variables affecting grassland biodiversity. Not surprisingly, this provincial bias is reflected in my analysis. My goal is to characterise the current status of most North American grasslands, and make what predictions are tenable about issues of sustainability and ecosystem services.

Advances in understanding the role of soil biodiversity

Since the publication of Wardle's (2002) analysis of controls and significance of soil biological systems, over 600 papers using the keywords of 'soil' and 'biodiversity' have appeared in the literature. Nevertheless, besides some stellar exceptions, our assessment of biodiversity remains, at most, fragmentary. Any attempt to sketch an authentic food web emphasises the complexity that biologists confront in the soil (Mikola *et al.*, 2002, Moore *et al.*, 2003). While manipulations of food chains above ground may produce trophic cascade effects, similar manipulations below ground produce less-predictable responses due to the true web-like complexity of the food web (e.g. Wardle & van der Putten, 2002; Moore *et al.*, 2004). Even if we understood this structure completely and further understood how different management scenarios altered this structure for a particular grassland, generalising how this structure would vary across resource gradients and how that variation translates into changes in the functional attributes of grassland ecosystems would be tenuous at best. While we may be able to identify our favourite species, and discuss how the abundance and activity of these organisms influence function, our ability to provide managers with an adequate assessment of the status and trends of soil biotic diversity and its consequences on function is not forthcoming.

Soil microbiologists and nematologists now conduct molecular phylogenetic inventories to obtain censuses of bacterial, archaeal and selected eukaryal organisms. Regrettably, these tools have yet to proliferate to most soil biologists. The result is that we cannot tell the public and policy makers what is in the soil (Andre *et al.*, 2002), and, even if we could, explaining how this diversity translates to precise patterns and controls on ecosystem function would remain problematic. While there is now strong evidence that manipulations of soil biodiversity produce idiosyncratic relationships with ecosystem processes, studies of individual trophic groups or individual species almost always demonstrate positive or negative relationships (e.g. De Deyn *et al.*, 2003). What seems appropriate, therefore, is that we make every effort to conserve this diversity while we continue our attempts to identify what is there, what controls its presence and abundance, and what functions these species perform.

The key issue – the need to promote conservation while continuing the effort to provide baseline information – is itself an ongoing research issue. Studies and reviews provided by De Deyn *et al.* (2004), Wardle (2002, 2005), Wardle & van der Putten (2002) and Wardle *et al.* (2004) support the contention that resource abundance and heterogeneity are drivers of soil biodiversity. Soil biotic diversity can be facilitated by mechanisms that minimise plant

competitive exclusion via herbivory (Bardgett & Wardle, 2003) and mechanisms that reduce dominance or competitive exclusion within the soil food web itself (Moore *et al.*, 2003, 2004). Managing for high plant species diversity at local to landscape scales may therefore be the best *ad hoc* way to maximise soil biotic diversity.

Our research group (Porazinska *et al.*, 2003; Reed, 2005; Wall *et al.*, unpublished results) found strong evidence for this positive relationship between plant richness and soil species richness at the Konza Prairie Biological Station in Kansas, USA. Grass species attract unique assemblages of microbes attached to roots (Reed, 2004), as seen in similar studies of other herbaceous species (e.g., Callaway *et al.* 2004). Individual plant species therefore generate somewhat unique rhizosphere communities. These microbial and invertebrate communities impose feedbacks on the plants that can further enhance resource heterogeneity (e.g. Klironomos, 2003; Rudgers *et al.*, 2004; Coleman *et al.*, 2004). Nematode diversity in our study not only increased with plant species richness, but the patterning of plant species enhanced this diversity. A modest but statistically significant synergistic effect of species co-location was found on diversity (i.e. the nematode species richness beneath two co-located plant species was greater than the sum of the richness found when the same two plant species were sampled in isolation). We hypothesise that the combination of resource heterogeneity generated by different plant species, accompanied by temporal and spatial heterogeneity generated by root activities of different species (along with their different symbionts and pathogens), generate the highest diversity of organisms found in grasslands. This increase in species richness is generally consistent with numerical responses of herbivorous and microbivorous nematode functional groups (Todd, 1996, Blair *et al.*, 2000). Finally, our group found that richness of nematodes appeared to be related to nutrient content or physiological status of the grass species. Richness was, on average, higher under cool season grasses (C_3 species) than warm season grasses (C_4 species). Collectively, the data are consistent with findings suggesting a large role of plant diversity in maintenance of soil biotic diversity. Given a general (but not universal) trend of C_3 species replacing C_4 species in North American grasslands, an increase in local richness of the invertebrate fauna might be expected.

Historical range of variability and the emergence of adventive ecosystems

The structure and function of grasslands have been changing since the first monocots began to dominate herbaceous communities many millions of years ago. Nonetheless, factors affecting resistance and resilience properties of these systems have been a focus of study for community ecologists for the last century. Ecologists have understood that discrete and sometimes rare events such as fire or floods affect ecosystems' structure and functioning. This concept matured to one where disturbances were observed as integral components of the system and referred to in the context of 'historical range of variability' or 'natural variability' (c.f. Landres *et al.*, 1999). In North America, upland grasslands had historical fire and grazing return intervals that were strong determinants of species composition and structure, including the activities in soil biota. (e.g., Rice *et al.*, 1998; Blair *et al.*, 2000). This concept has valuable conservation management implications. For example, management to limit ungulate grazing in semiarid and arid natural areas in California and in the Great Basin of North America is based on the fact that most of these areas had few such grazers during the 12000-year interval prior to the early 19th century (c.f. Baker, 1978; Seastedt, 2002). Cattle grazing became the common scenario in this region, driving these ecosystems outside their historical range of variability. Such systems do not maintain their previous structural or functional traits. The now-altered system develops characteristics that may or may not be desirable in terms of ecosystem services, but is one clearly transformed from its previous state.

While fire and grazing intervals can be manipulated, atmospheric chemistry and climate change are not under land managers' control. Once historical ranges of important environmental drivers are exceeded, how will directional changes affect structure and function? We have been conducting this uncontrolled experiment on a global scale with atmospheric CO₂ and N concentrations. At the same time, human activities have been altering other environmental drivers at local and regional scales. New species, either in concert with environmental changes or independent of such changes, have also been added or subtracted from the system. What emerges is an altered or adventive ecosystem.

An adventive ecosystem is defined as an ecosystem containing native and non-native biological components, and exhibiting ecosystem properties resulting from a transition outside the historical range of variability (Figure 2). Causal mechanisms for the transition are attributed to both internal reorganisation and external drivers. While the devil is in the detail of this definition (and there exist a continuum of states), the term is meant to define systems that exist between those totally dominated by human forcings (i.e. synthetic ecosystems such as agroecosystems, urban, suburban areas, transport corridors, etc.) and 'pristine areas' dominated by native biota and still experiencing nominal external forcings (c.f. Williams, 1997). Adventive systems have their own ecosystem properties. While minor changes in biotic composition and biogeochemical functioning might be viewed as trivial, the argument that pristine ecosystems still exist is largely untenable. Quantifying the distance that an ecosystem has travelled from its historical range provides a 'reality check' of sorts to those interested in restoration. Further, the difference in ecosystem services provided by the adventive ecosystem provides a metric to assess sustainability concerns.

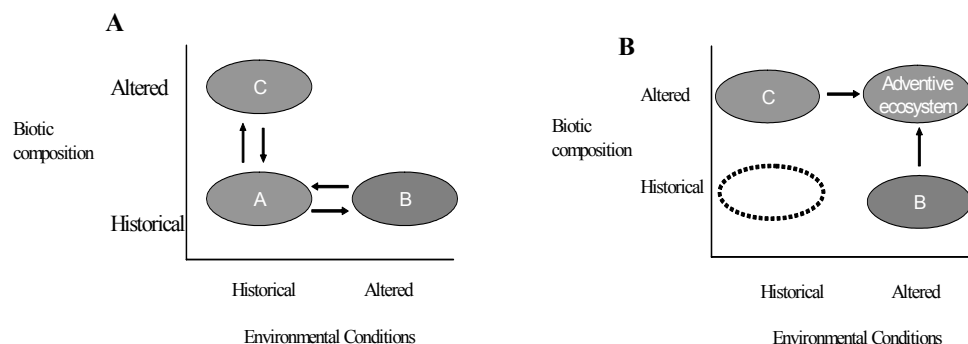


Figure 2 Creation of adventive ecosystems via biotic or abiotic change (modified from Suding *et al.*, 2004). A. an ecosystem is altered by environmental drivers (A→B) or the addition of an abundant, invasive species (A→C). Once in the new state, internal restructuring due to new competitive relationships further alters community composition (via species losses) and through changes in biogeochemical interactions. Restoration of such systems is problematic, if not impossible.

Adventive ecosystems can be constructed *via* two mechanisms. Ecosystems can be removed from their historical trajectories via physical drivers, or ecosystems can be altered by biological additions or deletions (Figure 2). With changes in biotic composition, measurable change in at least a subset of ecosystem processes is likely (Ehrenfeld, 2003). Once a system

has been removed from its historical range of variation in terms of climate, atmospheric chemistry, or disturbance return cycles, species changes and subsequent changes in biogeochemical cycling are almost certain. The causal mechanisms for change can be of biotic or abiotic origin, but the outcome may be very similar. Because both biota and environmental drivers have been altered, returning the system to its nominal state is hypothesised to be a low probability event without the application of extraordinary management procedures.

Enhanced Nitrogen Deposition + Invasive Species = Adventive Grasslands

The above 'formula' is suggested to be the current nominal status of grasslands in the USA and perhaps many other regions of the world as well. Nitrogen availability has increased above historical levels in many and perhaps most grassland ecosystems. The global source is atmospheric N deposition (Vitousek *et al.* 1997; Townsend *et al.* 2003), but this is often accompanied in grasslands by enrichment resulting from fire suppression (Blair, 1998) and by chronic grazing (McNaughton *et al.*, 2001; Johnson & Matchett, 2001). Increased N availability has a high probability of:

1. Reducing plant species richness and diversity (Stevens *et al.*, 2004).
2. Favouring a change in the functional composition of selected grasslands from C₄ dominance to C₃ dominance (especially in conjunction with fire suppression; Knapp *et al.*, 1998; Collins *et al.*, 1998).
3. Directly or indirectly reducing mycorrhizal activity (Egerton-Warburton *et al.*, 2001).
4. Favouring a subset of soil decomposers, potentially those that may stimulate decomposition and mineralisation (Callaham *et al.*, 2003; Madritch & Hunter, 2003, De Deyn *et al.*, 2004; Wall *et al.*, unpublished results), but may also be reducing the decay rates of more recalcitrant organic fractions (Neff *et al.*, 2003).
5. Slowing or inhibiting restoration efforts aimed at maintaining the historical composition of grasslands (Baer *et al.*, 2003).

The above list, not intended to be inclusive, provides recent examples of phenomena that have been under investigation for some time, and all results tend to expand upon or be supported by an abundant literature that has accumulated in the last decade. The cumulative findings of these studies suggest that deposition rates are increasing or having cumulative effects, and no grassland system is totally immune from these changes. The propensity for large-scale 'eutrophication' of plant communities by various N sources was also noted by Grime (2001). Enhanced atmospheric CO₂ may negate some of the effects of N enrichment (Hu *et al.*, 2001), but global warming has the potential to again favour the enrichment effect via enhanced decomposition and mineralisation. The lack of woody storage substrates and relatively low C:N ratio of grassland soils argue that, in contrast to forests, significant transient increases of C and N storage in grassland soils in response to enhanced N deposition are, in general, unlikely.

Increased N facilitates plant invasions in many cases (Hobbs & Huenneke, 1992). The exceptions in grasslands appear limited to those areas where invaders also facilitate more frequent fire return intervals (c.f. Ehrenfeld, 2003). Nitrogen deposition also appears to be facilitating the spread of invasive earthworm species (Callaham *et al.*, 2003). This earthworm invasion in North American grasslands may have very large effects on carbon storage and N flux since pre-existing soil faunas were often depauperate or even lacking such 'keystone' species.

Will invasions, alone, cause reductions in soil biodiversity? At present, available data exist only for plants, and these indicate that species introductions are exceeding species extirpations at regional scales (Hobbs & Mooney, 1998). A reasonable (and testable) hypothesis is that plant species changes will be responsible for much of the variation in soil communities of grasslands, and this trend could enhance soil biological diversity. In reality, the question is moot. Our research focus needs to be upon the interaction of current drivers affecting soil biodiversity, not the individual effects of the drivers, themselves. Enhanced N deposition, in conjunction with habitat destruction, fragmentation, and other drivers that amplify N enrichment effects, will ‘eutrophy’ these systems, reduce resource heterogeneity and in all likelihood over-ride any potential increases in soil biotic diversity associated with species invasions.

The recognition of our changing grasslands as adventive ecosystems offers a modest paradigm shift for soil biologists. Historically, the decomposer food web was viewed as a bottleneck for nutrients, especially N, and soil fauna were viewed as essential for providing nutrients for plant productivity (e.g. Crossley, 1977; Seastedt, 2000). Now, both basic and applied ecologists are concerned that these organisms or their newer counterparts in adventive ecosystems will contribute to excess nutrient export from managed and natural ecosystems (e.g. Bohlen *et al.*, 2004). Nitrogen retention and transformation to biologically inert forms historically has been an extremely important service provided by many if not most grasslands. Proactive management techniques to reverse the trend of N pollution in the form of nitrous oxide to the atmosphere and nitrate to aquatic systems should be a logical component of conservation management programmes for these ecosystems. In semiarid grasslands, for example, frequent fire can at least slow if not prevent changes associated with N enrichment (Seastedt *et al.*, 1991; Knapp *et al.*, 1998; Collins *et al.*, 1998), and such management maximises a key ecosystem service, plant productivity.

Examination and manipulation of individual biotic and abiotic variables within the soil independent of other concurrent changes may be a productive academic exercise, but such experiments should be conducted within a broader framework to have value to management. Adventive ecosystems are created by synergistic interactions among drivers and biota, not forcing functions acting independently. The advice to managers therefore remains unchanged by that provided by Leopold (1949) and recently by Hooper *et al.* (2005): do not throw away the parts while we continue to diagnose the system. Reducing the uncertainties associated with global environmental change and the emergence of adventive ecosystems requires realistic, complex experiments, in conjunction with expanded inventory and monitoring activities. While this conclusion is not new, the acknowledgement that adventive ecosystems will require proactive management activities to maximise conservation and ecosystem service values cannot be understated.

Acknowledgements

I thank Dr. Carl Bock for suggesting the term ‘adventive ecosystems’ as one that best describes these altered ecosystems. Drs. John Blair and Heather Reed helped improve earlier versions of this manuscript. Dr. Diana Wall’s group at CSU did the brunt of the Konza work. Our soil biodiversity research was supported by a National Science Foundation grant, DEB 9806438, to the University of Colorado.

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