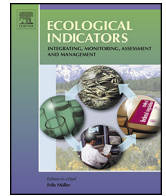




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# Interannual variability, stability and resilience in UK plant communities

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### ABSTRACT

Plant communities are often assumed to be stable on a year-to-year basis. We present evidence that species composition in permanent quadrats changes considerably between years at a range of Environmental Change Network sites across the UK. The extent of this variability varies with habitat type. Communities associated with low disturbance levels and low agricultural inputs, particularly moorland (upland grass and heath) and bog communities, are most stable.

Inter-annual variability should, therefore, be considered in designing monitoring schemes to ensure that frequency of recording is sufficient to avoid short-term fluctuations obscuring long-term trends.

More diverse communities were more stable, with less species turnover between years. However, diverse communities also tended to be dominated by slow-growing, slow-reproducing plants, adapted to low nutrient conditions, identified as 'stress tolerators' in the Grime CSR scheme and low Ellenberg N values. Species compositional stability was more strongly correlated with these indices of plant functional types than species richness. Nevertheless, a significant effect of species richness could be identified, even after other causes of variation were accounted for.

More stable communities in our study are likely to be resilient to low levels of environmental change, although they may still change, and possibly change dramatically if critical 'tipping points' are reached.

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## 1. Introduction

Increasing resilience of ecological communities is an aim of much conservation management and an important response to the risk posed by climate change and other pressures. Resilience is a broad concept, defined in a variety of ways, both within ecology and more widely. Two broad types of definition of resilience can be identified (Morecroft et al., 2012):

1. The amount of disturbance that an ecosystem can withstand without changing self-organised processes and structures (Holling, 1973; Gunderson, 2000);

2. The return time to a stable state following a perturbation. This is sometimes contrasted with resistance – the capacity to remain unchanged in the face of a disturbance (see for example Leps et al., 1982; Mitchell et al., 2000).

Both of these are useful concepts. They are however difficult to compare across different types of communities and locations given that disturbances and environmental change are not uniform and the effect of the same disturbance, for example an extreme drought, will be different on different communities. A related concept is the stability of communities which, whilst the subject of various definitions, can be regarded as the extent to which a community's composition or properties remain the same over time. Identifying more stable communities, with lower variability, is a necessary first step to identifying those factors which control this, including the capacity to withstand or recover from disturbance. An indicator of low variability is potentially easier to derive and less ambiguous than a resilience indicator.

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Vegetation can fluctuate between years, as well as in cyclical and directional ways (Miles, 1979; Watt, 1947; Wolkowitch et al., 2014). Year-to-year changes in weather conditions can exert an influence across different sites and communities and are a major cause of short-term change in vegetation, in addition to changes in local factors, including changes in management and outbreaks of pests and diseases. Interannual variability has been documented particularly for a variety of grasslands (for example Adler et al., 2006; Cleland et al., 2013; Dostalek and Frantik, 2011; Pacurar et al., 2014) and in many cases an impact of weather conditions can be identified. However, as far as we are aware, interannual variability has not been systematically quantified across a range of different sites and vegetation types.

Understanding the impact of these fluctuations on different communities is important for a number of reasons. From a methodological standpoint, it can help to establish how frequently vegetation should be monitored. Vegetation is often monitored at intervals of a few years or more on the explicit or implicit assumption that relatively little change will occur at shorter time intervals. This is an assumption which should be tested in order to develop reliable metrics and indicators.

In situations where vegetation is highly responsive to weather and other variables, long intervals between recording could lead to short-term fluctuations being identified wrongly as a long term change. Understanding the stability and resilience of different vegetation types is also essential to developing adaptation to climate change (Morecroft et al., 2012). Communities with greater inherent resilience to climate change, reflected in a more stable species composition, may be less vulnerable to climate change and may have the best chance of persisting in their current locations, at least in the short term. Interannual variability may also be a mechanism which maintains diversity (Chesson, 2000) and any changes in climate variability with climate change may cause shifts in vegetation composition in addition to the effects of any changes in the mean value of climate variables.

Various factors have been identified as potential determinants of resilience, including the diversity of the community and the traits of the species within it. The relationship between the stability of ecological communities and diversity has been subject of much study. However, this has largely focused on whether aggregate community properties, particularly productivity, are more stable in species-rich communities (Hector et al., 2010; Ives and Carpenter, 2007; Tilman et al., 2014). The stability of the community itself – its species composition – has received less attention and there are few empirical studies of it for plant communities. It is therefore not clear what role, if any, diversity might play in controlling compositional stability in natural and semi-natural communities. Theory developed from the early 1970s onwards suggests that whilst ecosystem properties, such as productivity, may be stabilised by high diversity, species populations and hence community composition should be more variable in more diverse communities (Lehman and Tilman, 2000; May, 1973; Tilman, 1999). In contrast, earlier, more anecdotal observations (Elton, 1958; MacArthur, 1955), mostly on animal populations, suggested that more diverse communities are more stable and some more recent studies support this (Valone and Hoffman, 2003; van Ruijven and Berendse, 2007). However, even if diversity has an effect on species composition there remains the question of whether it is a major determinant of stability in natural communities or whether its effects are obscured by other factors. Many studies of community variability have been based on experimental studies at single sites, in which confounding factors are minimised. However, if diversity is a major determinant of stability we would also expect to see its signal in a large scale comparison of stability in different vegetation types.

One factor which may over-ride any effects of diversity is the composition of communities in terms of functional types (Tilman, 1999) – the constituent species' ecological or physiological attributes. For example, the presence of more long-lived species may be expected to stabilise community composition. Two commonly adopted systems for describing plant functional types are those of Ellenberg (Ellenberg, 1988; Hill et al., 1999) and Grime (Grime, 1974; Grime et al., 1988). The Ellenberg system classifies species on a series of measures based on characteristics, such as fertility, of the habitats in which species typically occur. The Grime system is based on screening species for a range of attributes and classification with reference to three primary strategies – Competitor (C), Stress tolerator (S) and Ruderal (R).

We used data from a long-term monitoring scheme – the UK Environmental Change Network (ECN) – to assess interannual variability in species composition of a wide range of vegetation types at sites across the UK. The 12 terrestrial sites in the ECN are operated by different organisations, but all use a common set of protocols; vegetation data recorded annually are available for 10 of these sites.

Our aims were to:

1. Test whether vegetation composition changed by measurable amounts on a year-to-year basis and whether this might confound interpretation of change when vegetation is recorded at longer time intervals.
2. Compare the size of changes in vegetation within plots to the degree of variation between plots.
3. Identify patterns in inter-annual vegetation change between contrasting communities.
4. Test whether compositional stability is associated with species richness or indices of functional types.

## 2. Methods

### 2.1. Monitoring

Vegetation composition was recorded in 156 permanently marked sampling plots across 10 Environmental Change Network (ECN) sites throughout Great Britain and Northern Ireland in the period 1994–2006 (Table 1, Fig. 1). ECN is the UK's long-term ecosystem research site network; sites are managed by a range of organisations, but all monitor a core set of biological, physical and chemical variables using common protocols.

These sites represent a wide range of vegetation types, soils and climates (Fig. 1, Table 2). Vegetation recording followed the ECN 'fine-grain' vegetation monitoring method (Sykes and Lane, 1996) in which the presence of species is recorded in 10 randomly distributed, permanently marked 400 mm × 400 mm quadrats within a larger 10 m × 10 m square plot. Plots were selected from a baseline survey of vegetation at intersections of a grid for each site, to represent the range of vegetation present at each site.

Standard ECN protocols prescribe monitoring at intervals of 3 years and 9 years; however an additional series of surveys was carried out in support of the UK Countryside Survey, a large-scale, stratified-random field survey, to test the effect of survey year on results. Plots were recorded annually at the 10 sites between 1996 and 2000; at some sites, longer time series were available, covering all or most years from 1994 to 2006. Results from all pairwise comparisons between the same plot in two consecutive years were included (preliminary analysis showed similar patterns when analysis was restricted to plots which had been recorded for the longest continuous periods). Recording was carried out between mid-June and early-September. Where possible, the same surveyors were

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