Multiscale monitoring of a multispecies case study: two grass species at Sevilleta

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Abstract

Monitoring multiple species and their interactions at multiple scales is critical for any useful habitat conservation plans and for adaptive ecosystem management programs. Viability of single species can be understood only in the context of ecological interactions with other species at multiple spatial and temporal scales. Here, we present a case study of the spatial and temporal dynamics for two perennial grasses, *Bouteloua eriopoda* and *B. gracilis*, by using long-term, high resolution transect data from 1989 to 1998 at two sites in the Sevilleta National Wildlife Refuge (Deep Well and Five Points) in central New Mexico, USA. Information entropy was used to describe the spatial distribution of each species and the fractal dimension of information entropy was used to characterize the complexity of species dynamics across scales. When considered individually, the spatial distribution of each species was scale-invariant. However, species joint occurrences changed as scale of resolution increased at both sites. Interactions changed at scales less than 3.2 m at Deep Well and less than 1.6 m at Five Points. Across years, the interactions of these species at Deep Well were significantly different in 1989 from all other years. Our results argue that monitoring multiple species at multiple spatial and temporal scales is necessary to better understand multispecies interactions and community dynamics both of which have important conservation implications under changing environmental conditions.

Introduction

The current single species approach to monitoring is inefficient and ineffective when conservation plans often cover more than one species. There are several problems confronting the single species approach to conservation (Root et al. 2003). First, entire communities rather than single species need to be the focus of conservation efforts. Second, information about vulnerable communities and their constituent species may be limited. Third, species are always interacting in complicated ways. The effects of several competitors may exist on one species, and complex environmental fluctuations through ecosystems have implications for different species interactions. Such emergent properties can not be predicted by the single species approach.

Multiple species habitat conservation plans (MSHCPs) have emerged for implementing species

protection mandates. They are designed to minimize conflicts from the single species approach, and aim at conserving the biodiversity of a region by ensuring that a representative set of species is protected (Akcakaya 2000; Scott and Sullivan 2000). The paradigm of conservation has been shifting from the management of individual species within habitats to the preservation of entire communities within ecoregions (The Nature Conservancy 1999; Gaston et al. 2001). Currently there are several ongoing MSHCPs, including those in southern California (Loew 2000). Yet observations at different scales may yield different ecological patterns (Wiens 1989; Levin 1992). How to monitor these multispecies communities at proper spatial and temporal scales is a critical requirement of habitat conservation plans. Finding simple and easy ways to monitor the interactions and dynamical relationships of multiple species assemblages under changing environmental conditions are needed for local and regional MSHCPs.

Here we use the information entropy method on long-term and high resolution field survey data of two dominant perennial grasses, *Bouteloua eriopoda* and *B. gracilis*, in short-grass steppe and desert grassland at the Sevilleta National Wildlife Refuge to compare single species and joint species dynamics at different spatial and temporal scales. The aims of this research are to (1) illustrate why monitor only single species dynamics is insufficient for understanding community dynamics; and (2) explain why we should monitor the interactions of multiple species at multiple spatial and temporal scales in order to get greater monitoring and conservation information.

Methods

Study area

Bouteloua erpioda and *B. gracilis* are two dominant perennial C4 grasses monitored by the Sevilleta Long-Term Ecological Research (LTER) Program in the central New Mexico, USA. This region is an ecotone for the biomes of the cold desert of the Great Basin, the warm Chihuahuan desert, and the semi-arid short-grass steppe (Gosz 1993). The Sevilleta LTER contains an environmental and compositional gradient that ranges from Chihuahuan desert grassland and shrubland to Great plains short-grass steppe. *Bouteloua gracilis* is characteristic of the short-grass steppe to the north whereas *B. erpioda* is characteristic of the Chihuahuan desert vegetation to the south. The mean monthly air temperatures in this region are from 2.5 °C to 27 °C, and the annual mean precipitation is about 280 mm, with considerable inter-annual variability (Gosz 1993).

Sampling protocol

Information on these two species was obtained at 1 cm resolution during spring and late summer of each year from 1989–1998 along two 400 m line intercept transects (named Deep Well and Five Points). Although these transects were sampled twice each year, here we use only the data from spring samples for our comparative analyses in order to be in consistent form. Records of plant frequency for these two species within 10 cm intervals along each 400 m transect at both sites were used. 10 cm is 1 unit of scale, and these data are combined into data set of scales in 1, 2, 4, 8, 16, 32, 40, 50 and 80 units by pooling of contiguous intervals along these transects. All raw data and metadata for these transect samples are available as dataset SEV004 at http://sev.lternet.edu/.

Data analyses

The Shannon entropy $H_\varepsilon(x)$ of species x at different scales of ε was calculated as follows (Jumarie 2000; Li 2000):

$$H_\varepsilon(x) = -\sum p_\varepsilon(x)\log_{10}p_\varepsilon(x)$$

where $p_\varepsilon(x)$ is the probability of observing species x at the ith patch element measured using samples of ε units in size. Here H_ε describes the spatial distribution of species occurrences along the transect at length scale ε. Higher values of $H_\varepsilon(x)$ represent higher spatial evenness of the abundance for species (x). The Shannon entropy of the joint two species occurrences is estimated by the joint probability $p_\varepsilon(x,y)$ of species x and y at length scale ε. $p_\varepsilon(x,y)$ was estimated by choosing the

minimum abundance of species x and y at ith patch element (Jumarie 2000).

The fractal dimension (D_I) at each scale ε in every year is used to measure the complexity or the change of H_ε at different scales along the time series, and it was estimated by (Jumarie 2000; Li 2000)

$$D_I = \lim \frac{H(\varepsilon)}{\log_{10}(1/\varepsilon)}$$

for both single and joint species measures.

Results

At Deep Well and Five Points the fractal dimensions of information entropy for *B. eriopoda* were 0.6817 and 0.7460 (Figure 1), respectively. At both sites, the information entropy for *B. eriopoda* was scale-invariant. Moreover, the fractal dimensions of information entropy between the two sites were not significantly different. Although inter-annual fluctuations in scaling exponents occurred, these fluctuations were not statistically significant.

Scale invariance also existed for *B. gracilis* at Deep Well and Five Points (Figure 2). The fractal dimensions of information entropy for *B. gracilis* at these sites were 0.6359 and 0.5943 and these values were not significantly different. Thus, the spatial scale at which single species monitoring occurs is spatially flexible.

Unlike the individual species analyses the fractal dimensions of the information entropy of the joint occurrences of *B. eriopoda* and *B. gracilis* changed with scale at both Deep Well and Five Points (Figure 3). At Deep Well, the fractal dimension of information entropy was 0.5715 when the scale was above 3.2 m, and the scale domain changed below the scale of 0.8 m. A scale transition zone occurred between the scales 0.8 and 3.2 m at Deep Well. Inter-annual fluctuations in fractal dimension of information entropy existed and the entropy trajectory in 1989 was significantly different from that in other years. At Five Point the fractal dimension of information entropy was 0.5045 when the scale was above 1.6 m, and the scale domain also changed below 0.8 m. Unlike at Deep Well, a scale transition zone was not obvious at Five Points.
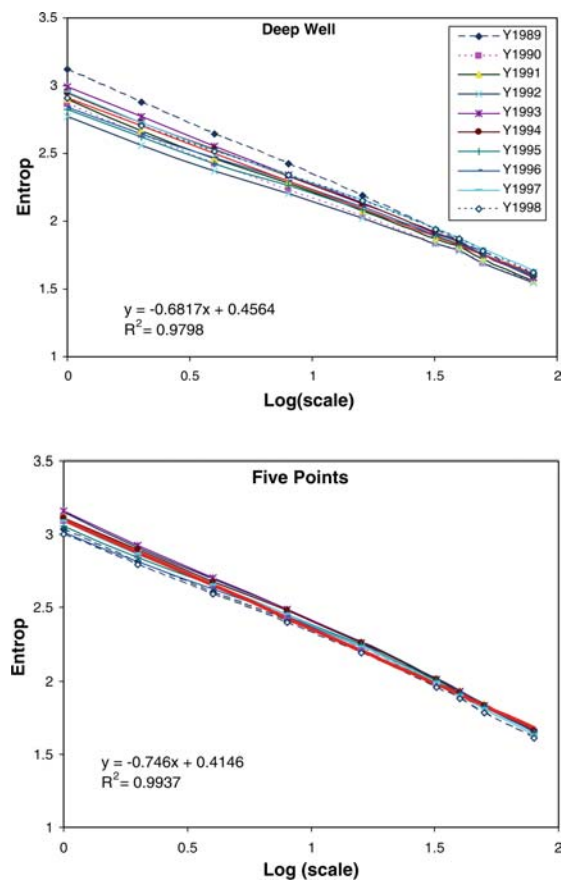

Figure 1. The dynamics of information entropy for *B. eriopoda* at Deep Well and Five Points at different scales from 1989 to 1998 (The equation and R^2 value shown on each graph represented the average.).

Discussion

It is obvious that scale invariance existed for individual occurrences of *B. eriopoda* and *B. gracilis* at both sites. Although there were inter-annual fluctuations, differences between years were not significant. Our results estimated by multiscale information entropy are consistent with earlier single-species analyses (Anand and Li 2001; Wang 2001).

However, the scaling relationship for the joint occurrences of *B. eriopoda* and *B. gracilis* changed at larger scales. In addition, at one of our sites (Deep Well) the entropy trajectory of the joint species occurrences in 1989 behaved differently from those in all other years. By monitoring two species jointly we gain information on the emergent properties of two species, which presumably reflect
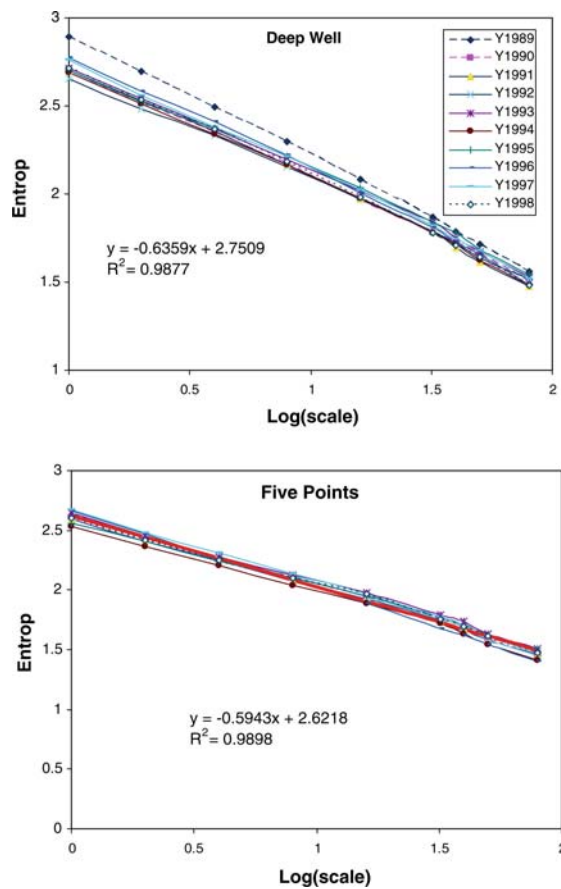
Figure 2. The dynamics of information entropy for *B. gracilis* at Deep Well and Five Points at different scales from 1989 to 1998 (The equation and R^2 value shown on each graph represented the average.).

Figure 3. The dynamics of information entropy for joint *B. eriopoda* and *B. gracilis* at Deep Well and Five Points at different scales from 1989 to 1998.

to some extent interactions between these species, even though the dynamics of each species individually did not change significantly. Furthermore, if our analyses were not limited to each single year we might not detect this phenomenon. The main causes of the change in the scaling relationship may be the non-linear interaction between these two species under fluctuating environmental conditions. *B. gracilis* is the characteristic dominant species of the short-grass steppe to the north (Peters 2002) and *B. eriopoda* is dominant in Chihuahuan desert grasslands to the south (Hochstrasser and Peters 2004). Both are common constituents in our study area at the Sevilleta. Although species responses to environmental variability may differ or be similar in the scales of their ecological neighborhoods, studies of interactions among species should be particularly sensitive
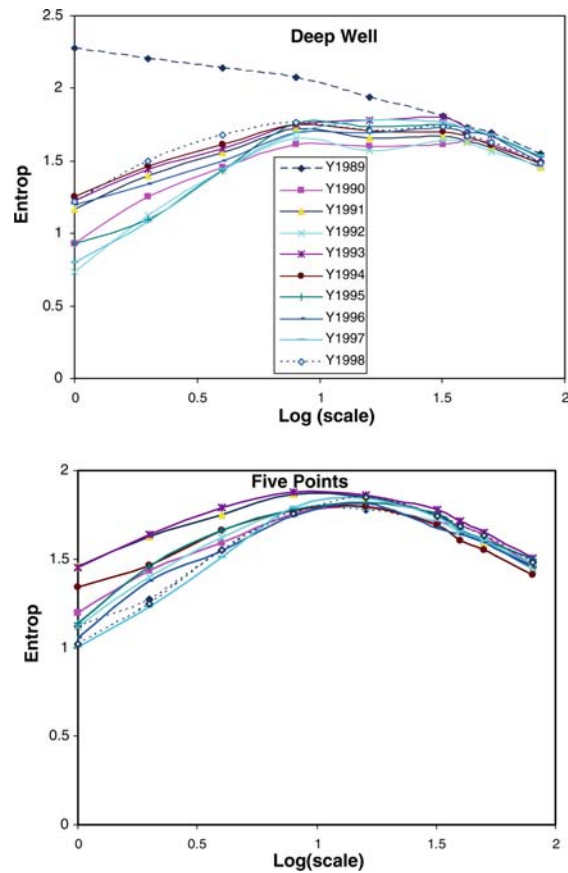
to scaling (Wiens 1989). Threshold scales differed somewhat between our study sites. *B. gracilis* accounts for about 25% of the vegetation cover at Deep well but only about 12% on average at Five Points. Therefore, choosing the proper spatial and temporal scale is important for monitoring the interaction of these. Previous multiscale studies considered patterns at three to five scales (Wiens et al. 1986; Wiens 1989). Our results indicate that it would be better to consider ecological pattern across multiple scales or at dynamic scales in order to determine patterns of species distribution and interaction. Wellnitz et al. (2001) suggested that organisms respond to environmental gradients at different spatial scales and that the processes driving these responses may change with scale. Arbitrarily selected scales on a scale spectrum may not properly reflect natural processes (Li 2000).

In this study, we also observed the change in scale domain. Scale domain refers to the regions of the scale spectrum, if the scale spectrum is not continuous, over which a particular phenomenon in a particular ecological system is scale invariant or changes monotonically with a change in scale (Wiens 1989). Domains are separated by transitions from one domain to another domain. The scale transition zone at Deep Well seemed broader than that of Five Points. Findings or results at a particular scale may be extrapolated to other scales within the same domain, but it will be difficult to extend them across the transition between domains because of the instability and chaotic dynamics of the transition zone (Wien 1989). Moreover, boundaries of even well-defined domains may not be fixed but may vary in time (Peters et al. submitted). Englund et al. (2001) proposed that the scale domain concept is useful when designing and interpreting field experiments. In this study scaling relationships in 1989 differed from those of other years. Precipitation in 1989 was 40% below the long-term average of 250 mm per year for this site (http://sevilleta.unm.edu/research/local/climate/meteorology/summaries/longterm/images/dwppt02.gif).

In conclusion, although for *B. eriopoda* and *B. gracilis* individually scale invariance of information entropy existed at both sites, the fractal dimensions for their joint information entropy changed below the scale domain of 3.2 m at Deep Well and 1.6 m at Five Points. The main cause of this change in scale domain may be due to the non-linear interaction between these two species under different soil textures and fluctuations in seasonal and annual precipitation. Therefore, monitoring at multiple spatial and temporal scales is a useful first step for detecting multispecies interaction potential. Such changes in scale domain are important for understanding ecological phenomenon. Non-arbitrary, operational ways of defining and choosing proper scales are necessary for long-term ecological research into factors controlling the distribution and abundance of species and the dynamics of plant communities.

Acknowledgements

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