Environmental responses consistently, but not completely, synchronize population dynamics of co-occuring grassland species

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Introduction

Asynchrony in population dynamics among co-occuring plant species stabilizes ecosystem-level properties like annual biomass production (Hector et al. 2010, Loreau and de Mazancourt 2013, de Mazancourt et al. 2013, Hautier et al. 2014). Species-specific responses to environmental conditions, in particular, can stabilize ecosystem properties even as environmental forcings fluctuate through time. Such asynchrony of species dynamics in response to the environment has the potential to buffer ecosystems subjected to an increasingly variable climate. Thus, the extent to which natural communities exhibit asynchronous dynamics determines, in part, their ability to cope with interannual climate extremes that are projected to become more common.

Theory suggests that community synchrony is driven by a combination of internal and external forces. Internal to the community, demographic stochasticity can induce asynchronous dynamics when species tend to fluctuate independently in a constant environment (Loreau and de Mazancourt 2008). However, species live in non-constant environments that act as strong external drivers of community dynamics. Environmental variability can induce asynchronous dynamics when species' responses to environmental conditions are temporally uncorrelated. When species respond similarly to environmental conditions, community dynamics become more synchronized (Gonzalez and Loreau 2009, Loreau and de Mazancourt 2008).

Given that environmental drivers can either increase or decrease species synchrony, what should be our null expectation of community synchrony? Past studies have assumed the appropriate null is independent species fluctuations (Houlahan PNAS), but this only occurs in the absence of environmental forcing. Species that co-occur but occupy the same trophic level tend to compete for similar abiotic resources, the availability of which varies annually. For example, water is the limiting resource in semi-arid grasslands so annual net primary productivity tends to track annual precipitation (Knapp citation?), regardless of species (CITATION). Taken to the limit, complete similarity among species in terms of resource use and environmentally-mediated growth rates, communities would exhibit neutral dynamics (Hubbell book). Thus, as suggested by theory (Loreau and de Mazancourt 2008) we our neutral expectation is that plant species that co-occur in water-limited grasslands will exhibit perfectly synchronous species dynamics since their growth is strongly driven by precipitation (Knapp again?).

It is impossible to draw inference on the relative contribution of demographic and environmental stochasticity on synchrony based on empirical estimates alone. Here we use exceptional longterm datasets from five North American grasslands (Chu and Adler 2015) to calculate community synchrony. We then fit multispecies population models to the data for dominant species to evaluate the relative contribution of species' environmental responses and demographic stochasticity to community synchrony. Sparse data on sub-dominant species constrained model fitting to dominant species, that account for ##% - ##% of plant abundance across the five sites. Our focus is on temporal trends of per capita growth rates becuase these best reflect the short-term responses of populations to environmental conditions that fluctuate on annual time scales.

Methods

We built environmentally and demographically stochastic multi-species integral projection models (IPMs) to simulate species' dynamics through time. The IPMs are based on vital rate regressions for survival, growth, and recruitment fit to long-term data (Fig. 1; Chu and Adler 2015). Environmental stochasticity is incorporated by fitting random year effects for the intercept of all regressions and on the plant size effect in the survival and growth regressions. Thus, for a fluctuating environment we can randomly draw year-specific regressions for each time-step of the IPM. Alternatively, to simulate the community in a constant environment we can use the mean regressions for each species. We incorporate demographic stochasticity in the IPM by making survival a binomial process (see Vindenes et al. 2011). We can remove demographic stochaticity by treating survival as a continuous rather than binomial process, as is traditionally done with IPMs (e.g., Rees and Ellner 2014).

To determine the (de)synchronizing effects of demographic stochasticity and species' responses to the environment we simulated communities using the IPM under three scenarios: (1) demographic and environmental stochasticity included, (2) demographic stochasticity removed, and (3) environmental stochasticity removed. We ran simulations for 2,500 time steps and calculated ϕ_r using the final 1,000 time steps. For each of our study sites we then calculated $\Delta(\phi)$, the difference between either scenarios 2 or 3 and the unperturbed scenario 1. The sign and magnitude of $\Delta(\phi)$ indicates the (de)synchronizing effect of removing either demographic or environmental stochasticity.

Results and Discussion

Synchrony of per capita growth rates among species in each community were in the range ## - ## with an average synchrony of ## (Table #). If our null expectation had been independent fluctuations, then we would conclude that these communities are far from exhibiting asynchronous dynamics that can stabilize annual productivity. However, based on neutral theory we expected species to fluctuate in perfect synchrony. Under that light our results show that these communities exhibit weak asynchrony since any asynchrony in temporal dynamics drives ϕ_r away from zero.

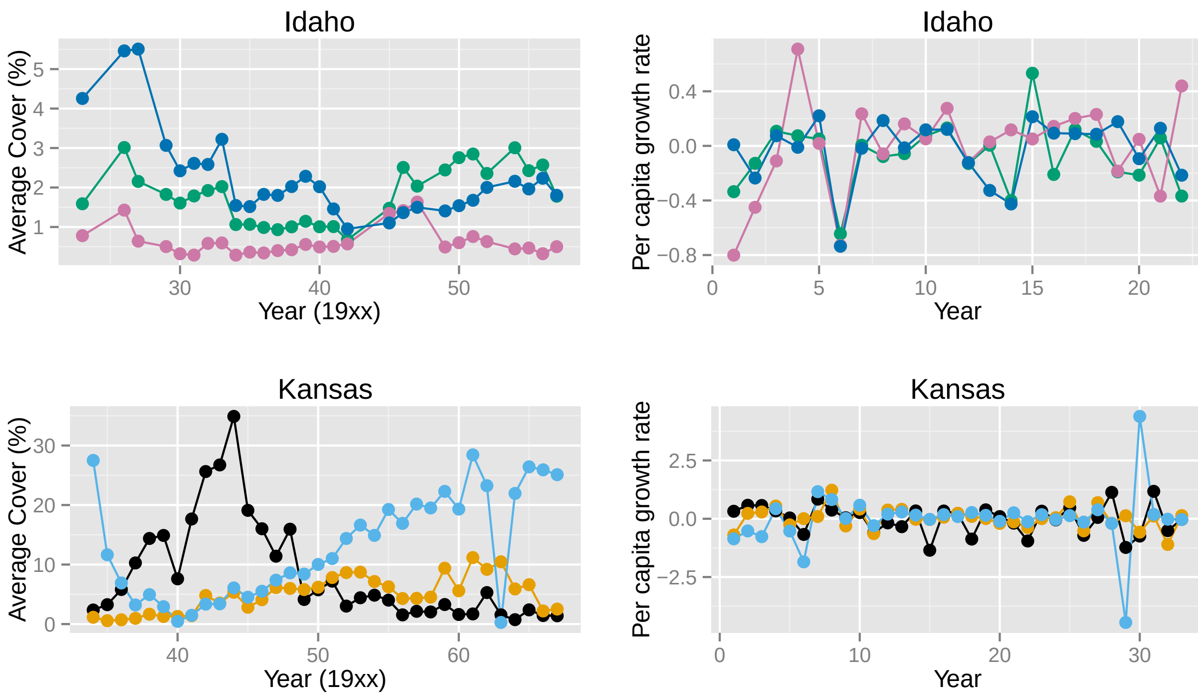

Figure 1: Longterm datasets and the observed per capita growth rates for each year for which contiguous transitions occured.

Site	Synchrony	MeanPairwiseCorrelation
Idaho	0.63	0.46
Kansas	0.48	0.17

Table 1: Community synchrony and mean pairwise correlation between species within a community.

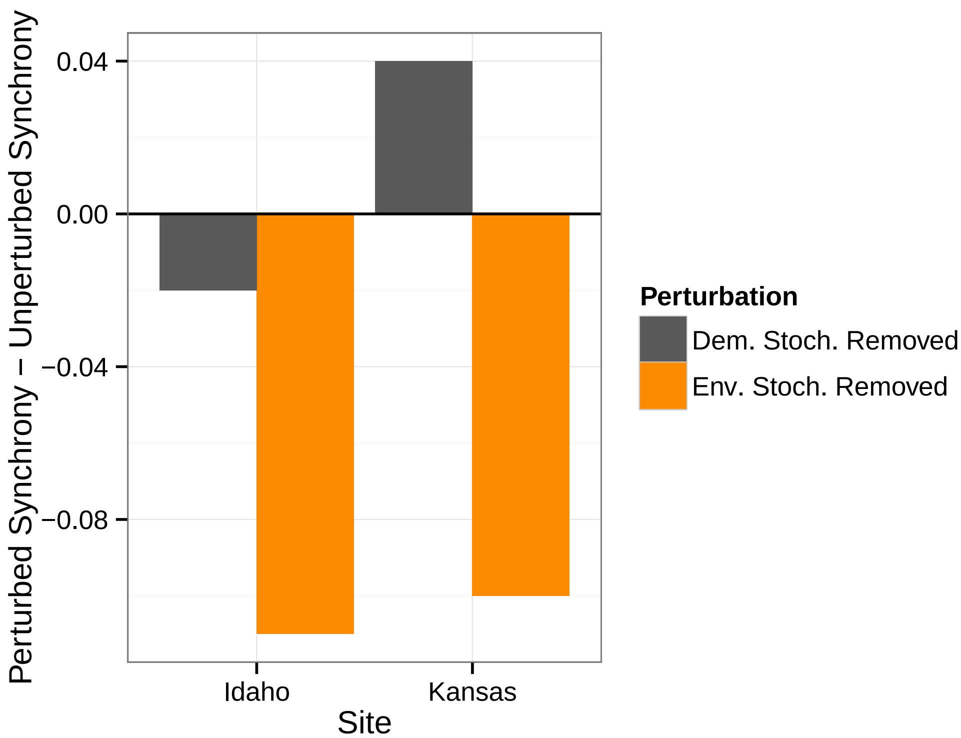

Figure 2: Effect of removing demographic and environmental stochasticity on the synchrony of population dynamics.