



Recovery of plant species diversity during long-term experimental warming of a species-rich alpine meadow community on the Qinghai-Tibet plateau



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ABSTRACT

Climate change is predicted to dramatically alter the composition of plant communities. The impact of climate change on these communities is often based on short-term warming experiments, which have revealed marked declines in species diversity in response to relatively minor increases in average annual temperatures. The long-term effects of such warming on community diversity and composition, however, are less well understood. Here, we formalize a hypothesis of rebounding diversity, where species richness initially declines in response to warming, but subsequently recovers through a combination of colonization (via dispersal and seed banks) and competitive release (via shifts in the dominant species). We compared long-term changes in species diversity and abundance between control and experimentally warmed (1–2 °C) plots, sampled over an 18-year period, in alpine meadow communities of the Qinghai-Tibet plateau. While there was an initial decline in species diversity by c. 40% (11–19 species) over the first four years, 18 years later, diversity had rebounded to initial levels, on a par with control plots. The composition of the experimentally warmed communities, however, was significantly altered. Our study suggests that short-term experiments may be insufficient to capture the temporal variability in community diversity and composition in response to climate change. Rather, the long-term impacts of continued global warming are predicted to result in highly dynamic processes of community reassembly and turnover that do not necessarily lead to a net decline in local diversity, but do lead to the formation of novel communities.

1. Introduction

Plant diversity plays an essential role in the maintenance of ecosystem functions and services at the community level (Klein et al., 2004; Hooper et al., 2012). Human-induced climate change has been linked to short-term declines in plant diversity (Arft et al., 1999; Klein et al., 2004; Gedan and Bertness, 2009; IPCC, 2014), and thus poses a serious threat to ecosystem stability (Hillebrand et al., 2010; Isbell et al., 2015). The long-term impacts of climate change on species diversity, however, are not well understood. In particular, it is not clear how the short-term loss of species due to warming corresponds to long-term changes in community diversity and composition. As species are

lost in a community, newly available niche space may be occupied either i) by the expansion of existing species, resulting in a net decline of diversity, or ii) by the colonization of new species or re-establishment of species that were initially lost, resulting in a rebound in diversity, but with unknown consequences for community stability and species interactions (Chapin III et al., 2000; Tilman and Lehman, 2001; Grime, 2002).

Over the past two decades, numerous studies have utilized warming experiments to test the effects of climate change on a wide-variety of plant communities, such as Arctic and Antarctic tundra (Walker et al., 2006; Post and Pedersen, 2008), alpine meadows (Klein et al., 2004), salt marshes (Gedan and Bertness, 2009), Mediterranean shrubland

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(Prieto et al., 2009) and prairies (Shi et al., 2015). In general, these studies have found that increased warming results in declines in species abundance and overall community diversity (Klein et al., 2004; Walker et al., 2006; Post and Pedersen, 2008; Gedan and Bertness, 2009; Prieto et al., 2009). These studies, however, are often limited to characterizing short-term dynamics in species loss, on the scale of 3–5 years at best (though see Shi et al., 2015). This time-scale is often too short to detect the role colonization and re-establishment may play in community re-assembly. For instance, colonization via dispersal is known to play out on the scale of decades, not years (Pierik et al., 2011).

Dispersal is a major factor in driving community assembly and local diversity (Hubbell, 2001). Dispersal may facilitate colonization and recovery of communities that have experienced a major environmental change, such as climate change (Alsos et al., 2007; Gallagher et al., 2013). In addition to dispersal across space, seed banks can also act as a mechanism of temporal dispersal and contribute to post-disturbance colonization and re-establishment in plant communities (Facelli et al., 2005). Given the stochastic nature of dispersal, as well as, the length of the disturbance, the species colonizing a community are not always the same species that previously occupied it (Pierik et al., 2011).

Subsequent to the arrival of species into a given community, local biotic interactions, such as competition, pathogens, herbivores, and insect pollination, are often a decisive factor in determining local plant diversity (Chase and Leibold, 2003; Jabot and Bascompte, 2012). Long-term shifts in climate are predicted to alter the nature of these biotic interactions as the suitability of local habitat changes to favor different species (Gedan and Bertness, 2009; Doak and Morris, 2010; IPCC, 2014). For instance, the loss of one or more dominant species in a community may result in a shift in the dominance hierarchy (Klanderud and Totland, 2005; Gilbert et al., 2009), permitting the competitive release of previously weaker competitors. Mitchell et al. (2003) found that one factor of global change, elevated CO₂, has shifted competitive hierarchies in tall-grass prairie communities by increased pathogen load of dominant C₃ grasses. Similarly, Niu and Wan (2008) found that experimental warming changes plant competitive hierarchies in temperate steppe communities by suppressing the competitive ability of a dominant C₄ grass (*Pennisetum centrasiticum*) and enhancing the competitive ability of two C₃ plants, an herb (*Artemisia capillaris*) and a grass (*Stipa krylovii*).

While short-term warming experiments frequently find declines in diversity, it is unclear if these declines are permanent. Indeed, unless warming dramatically alters the diversity equilibrium for a given community, we hypothesize some degree of rebound in diversity, based on the basic principles of island biogeography (MacArthur and Wilson, 1967). In the most general terms, our hypothesis of rebounding diversity can be characterized as such: community diversity declines in response to a major environmental change (such as increased warming), but subsequently recovers through a combination of colonization/re-establishment (via dispersal and seed banks) and/or competitive release (via shifts in the dominant species) (Fig. 1). In addition, the rate of rebounding diversity could either be gradual or fast (Fig. 1), depending on the mechanisms driving community reassembly. For instance, reassembly via spatial dispersal into the community may take decades to reach equilibrium (e.g., Pierik et al., 2011), while reassembly via an existing seed bank may take only years (Facelli et al., 2005).

Alpine meadows are among the ecosystems most sensitive to the continued effects of climate change and land use development (Klein et al., 2004). Here, we take advantage of long-term (18 year) experimental warming study of Qinghai-Tibet plateau alpine meadow communities to test our hypothesis of rebounding diversity. Our initial study of the same experiment, after only four years, found that warm plots lost, on average, 11–19 species (about 39.0–40.2%) relative to control plots (Klein, 2003; Klein et al., 2004). We also examine the long-term impact of warming on community composition and the relative influences of new species colonization and pre-existing species re-

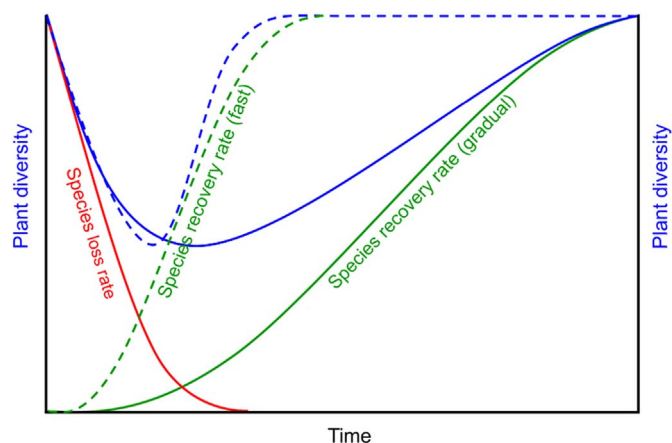


Fig. 1. Illustrated hypothesis of rebounding diversity after a major environmental change (such as warming). The figure illustrates two hypothesized pathways: long-term, gradual community reassembly and short-term, fast community reassembly. Species loss rate (red line) and species recovery rate (gradual pathway: dark green line; fast pathway: dark green dotted line) result in an initial and rapid decline in species diversity, followed by a significant recovery in diversity (gradual pathway: blue line; fast pathway: blue dotted line). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

establishment. In addition, grazing is the main land use on Qinghai-Tibet plateau. The experimental plots were maintained at two sites with distinct grazing histories (low vs. high intensity). Grazing history may mediate the response of meadow communities to long-term experimental warming. We use this historical distinction to test the impact of land-use intensity on the long-term community response to warming.

2. Material and methods

2.1. Study region

The study was carried out at the Haibei Research Station (37°37' N, 101°12' E), which is situated at Haibei, Qinghai, China, in the north-eastern Qinghai-Tibet plateau. Mean elevation of the valley bottom is 3200 m. Mean annual temperature is -1.7°C , ranging from -15.2°C in January to 9.9°C in July. Mean annual precipitation is 561 mm, mainly distributed during the short, cool summer. The growing season generally ranges from May to September. Soil type is Mollic-Cryic Cambisols (Zhao and Zhou, 1999). Vegetative communities are mainly alpine meadow and alpine shrub communities. These communities have very high plant species diversity ($30\text{--}50\text{ species m}^{-2}$). The Qinghai-Tibet plateau, in general, can be characterized as an alpine habitat, and is considered to be the center of origin for many regional alpine species (Klein, 2003). The Qinghai-Tibet plateau also has a history of seasonal grazing dating back thousands of years. In recent decades, heavy grazing has caused large-scale rangeland degradation (Klein, 2003; Ma, 2014). See Klein (2003) for more information on the study site.

2.2. Experiment design

In 1997, two field sites (about 1.5 km apart from each other; 37°37' N, 101°12' E, 3200 m above sea level) measuring $30\text{ m} \times 30\text{ m}$ and located on a flat slope ($< 1^{\circ}$) were fenced off from grazers. The two sites differed in grazing history, with one having experienced “low” grazing intensity (LG site) and one having experienced “high” grazing intensity (HG site) prior to the start of the experiment (see details in Klein, 2003). We assigned these qualitative history labels after interviewing local herders and senior researchers about land use patterns and research history at these sites beginning in 1982 (Klein, 2003). The HG site had both more animals per unit area and animals grazing for a longer duration of time (Klein, 2003). Therefore, both the grazing intensity and grazing duration differed between the grazing history sites.

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