

SPECIAL INVITED PAPER—GLOBAL BIOLOGICAL CHANGE

**COMMUNITY SHIFTS UNDER CLIMATE CHANGE:
MECHANISMS AT MULTIPLE SCALES¹**

ELISE S. GORNISH^{2,4} AND JASON M. TYLIANAKIS³

²Department of Biological Science, Florida State University, Tallahassee, Florida 32306-4295 USA; and ³School of Biological Sciences, University of Canterbury, Private Bag 4800, Christchurch, New Zealand

- *Premise of the study:* Processes that drive ecological dynamics differ across spatial scales. Therefore, the pathways through which plant communities and plant–insect relationships respond to changing environmental conditions are also expected to be scale-dependent. Furthermore, the processes that affect individual species or interactions at single sites may differ from those affecting communities across multiple sites.
- *Methods:* We reviewed and synthesized peer-reviewed literature to identify patterns in biotic or abiotic pathways underpinning changes in the composition and diversity of plant communities under three components of climate change (increasing temperature, CO₂, and changes in precipitation) and how these differ across spatial scales. We also explored how these changes to plants affect plant–insect interactions.
- *Key results:* The relative frequency of biotic vs. abiotic pathways of climate effects at larger spatial scales often differ from those at smaller scales. Local-scale studies show variable responses to climate drivers, often driven by biotic factors. However, larger scale studies identify changes to species composition and/or reduced diversity as a result of abiotic factors. Differing pathways of climate effects can result from different responses of multiple species, habitat effects, and differing effects of invasions at local vs. regional to global scales. Plant community changes can affect higher trophic levels as a result of spatial or phenological mismatch, foliar quality changes, and plant abundance changes, though studies on plant–insect interactions at larger scales are rare.
- *Conclusions:* Climate-induced changes to plant communities will have considerable effects on community-scale trophic exchanges, which may differ from the responses of individual species or pairwise interactions.

Key words: composition; diversity; global warming; herbivore; landscape; pollinator; scale effects; species interaction.

As a result of rising atmospheric CO₂ levels, average temperatures are increasing worldwide, and the variability associated with precipitation is increasing (IPCC, 2007). Consequently, ecosystem processes are being modified in a variety of ways (Norby and Luo, 2004; Norby and Zak, 2011). In addition to the direct effects of climate on species, changes to plant communities have bottom-up, indirect effects on other taxa (Parmesan and Matthews, 2006; Tylianakis et al., 2008a; Robinson et al., 2012). For example, a large number of studies have examined interactions between specific plants and herbivores under climate change (see reviews by Hodkinson, 2005; Tylianakis et al., 2008a), often motivated by concerns about insect-pest outbreaks (e.g., Cannon, 1998).

Responses of species to climate change depend on a variety of intrinsic (Rehfeldt et al., 2002; Lloret et al., 2009), and extrinsic (Tylianakis et al., 2008a; Dijkstra et al., 2010) variables. As a result, the biotic or abiotic pathways through which climate change

effects are expressed could be context-dependent, and context-dependency of ecological relationships, especially across spatial scales, has been relatively well documented in studies of population dynamics (e.g., Melbourne and Chesson, 2006; Latimer and Jacobs, 2012) and community ecology (e.g., Kneitel and Chase, 2004; Powell et al., 2013). Although the effects of climate change can occur across ecological scales, the magnitude and direction of these effects, and the mechanisms that drive them, can also depend on scales of time, space, and levels of biotic organization (Leuzinger et al., 2011) (Fig. 1). Specifically, responses of organisms to environmental changes can differ across scales because, as spatial scale increases, experimental site size and number increase, thereby introducing more environmental variation and species interactions (Melbourne and Chesson, 2006). Larger experiments (as a function of plot size within an area or plot number across an area) capture more environmental variation than smaller experiments because a larger portion of a habitat is physically included in the area of investigation. As abiotic and biotic heterogeneity increase with spatial extent of an experiment, the factors that modify a species' response to environmental change increase in number as well. For example, the number and frequency in which species encounter one another increases with spatial scale, and each of these interactions will contribute to how an individual responds to a changing environment.

Despite the implications of changing dynamics with scale, studies that investigate scale-dependency of the factors that drive plant community responses to climate change are relatively uncommon (but see Leuzinger et al., 2011; Chave, 2013),

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⁴Author for correspondence (e-mail: egornish@ucdavis.edu), present address: Department of Plant Sciences, University of California, Davis, California 95616 USA

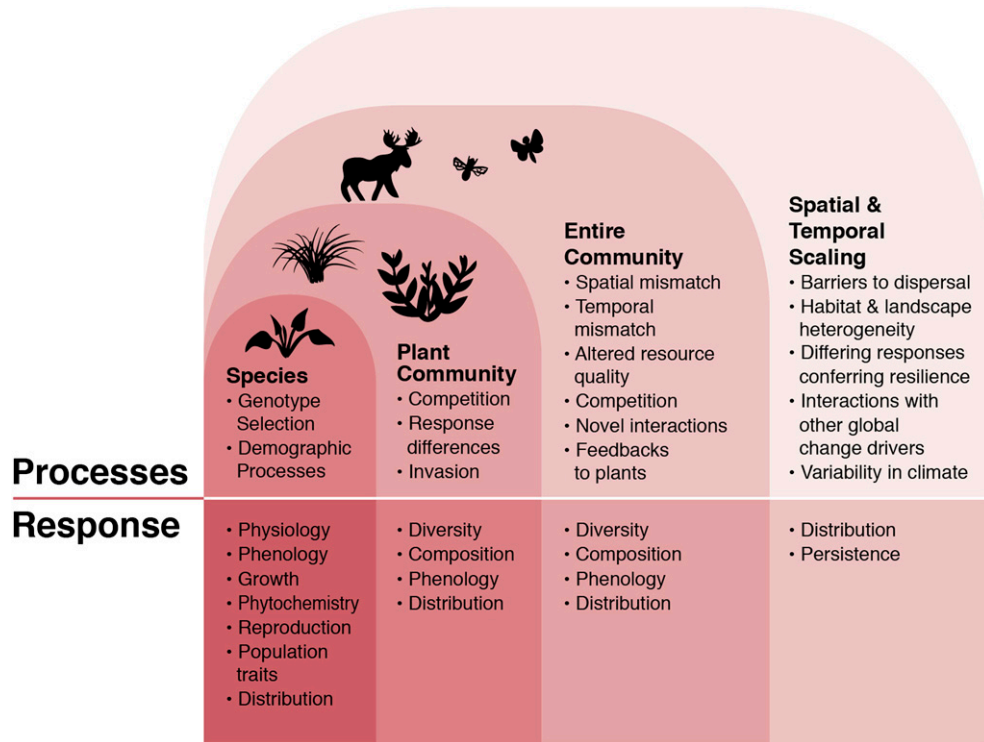


Fig. 1. Scaling of climate change effects. Responses to climate can be observed from individual plant species to plant communities and entire communities (including species that interact with plants, e.g., herbivores and pollinators). At each of these scales of organization, different processes can drive a response. For example, climate may select for certain traits of individuals of a species, which causes a shift in mean trait values of the population (the response), and trait differences across species may alter competitive interactions (process) within the plant community. Additional processes operating on species and communities can determine how their responses scale in space and time.

as are studies on the scale-dependent mechanisms through which plants interact with animals. Understanding how biotic and abiotic factors drive plant community response to climate change across scales may be useful for deriving general rules governing context dependency of ecological relationships and could facilitate more accurate model predictions.

Plant community responses to climate change are not localized to their own trophic level. Apart from the direct effects of climate change on insect groups (e.g., Sternberg, 2000; Staley et al., 2006), insect herbivores and pollinators can experience particularly strong indirect effects of climate change mediated through the plant communities with which they strongly interact. This can occur, for example, through phenological mismatch between plants and herbivorous insects, different responses across insect guilds to phytochemical or plant community changes, or changes to plant quality and chemical defenses (Hodkinson, 2005; Parmesan, 2006; Tylianakis et al., 2008a; Robinson et al., 2012). Community-wide trophic interactions may govern the responses of species to climate change (Suttle et al., 2007), yet they can be difficult to extrapolate from the responses of single species (Tylianakis et al., 2008a). Moreover, spatial scale effects, which can be important drivers of insect dynamics (e.g., Diaz-Forero et al., 2013), can also play a role in modifying insect groups in response to plant community change. Despite this wealth of information on pairwise species responses, surprisingly little work has examined the responses of communities of consumers or pollinators to climate-induced changes in plant communities. The pathways through which climate effects propagate across scales of organization, from

plant communities to communities involving plant–animal interactions, cannot be extrapolated from plant responses alone, yet understanding these effects is crucial for managing both agricultural and natural ecosystems.

Here we provide a synthesis of the literature on climate change effects on plant communities. We briefly summarize changes to plant diversity within the context of altered community composition and address different changes at local, regional, continental, and global scales. Specifically, we attempt to identify patterns in the factors responsible (biotic or abiotic) for changes in plant community composition and diversity in response to warming, increased CO₂ and changes in precipitation. We explicitly address the scale-dependence of many climate effects by emphasizing why community responses may not be predictable from the responses of single species or pairwise interactions and by discussing why local community changes (at a single site) may differ from those generated by regional-scale (multisite) processes. We also explore how these changes can affect communities of organisms that interact with plants (using herbivores and pollinators as case studies) across scales. Finally, we use examples of scale-dependent pathways of response to present a conceptual framework for scaling the effects of climate from species to communities, and we end by highlighting areas in need of future research.

DETECTING PATTERNS OF COMMUNITY CHANGE

Two of the most significant effects of climate change on vegetation have been concomitant changes in community composition

and species diversity (McCarty, 2001; Wing and Harrington, 2001; Willis and MacDonald, 2011). A change in community composition can occur as a result of a change in either the presence or the abundance (or cover) of particular species or functional groups and can include partial or complete replacement of plant types. In general, reorganization in the functional and morphological groups that dominate plant communities is expected because individual species respond in different ways to environmental changes (see, e.g., Weltzin et al., 2000; Tylianakis et al., 2008a; Kardol et al., 2010b). Despite the species-specific nature of such responses, groups of related species in a given study appear to respond similarly to climate change (Willis et al., 2008), and the relationship between species traits and climate can even allow the prediction of future trait states (Sandel and Dangremond, 2012). For example, groups of fast-growing or short-lived species may be expected to decline disproportionately in abundance or become extinct from a community, as these plants are less likely to have traits associated with stress tolerance (MacGillivray et al., 1995). Subsequently, community composition changes as these groups are replaced by those that are better adapted for the new environmental conditions (Moles et al., 2008; Lenoir et al., 2010).

Trait-based changes in the plant community as a response to climate change can affect the insects that rely on particular characteristics of the original community. For example, altered flowering phenology could accompany climate-induced plant community reorganization, subsequently driving community-level changes in pollinators and their interactions with plants. The extent to which it does so was examined by Memmott et al. (2007), who used a highly resolved data set on plant–pollinator interactions to simulate shifts in phenology under predicted climate-change scenarios. They found that, depending on the average extent of phenological shifts, up to 50% of pollinator species could face disruption of their food supply, mostly as a result of periods without food at the beginning or end of their activity period (Memmott et al., 2007). The network approach used in that study holds great potential for elucidating changes to entire plant–pollinator communities, as the robustness of pollination networks and loss of individual interactions are known to be affected by the arrangement and strength of all the interactions within the network (Bascompte et al., 2006; Thébault and Fontaine, 2010; Aizen et al., 2012). To determine how phenology contributes to the structure and stability of such networks, Encinas-Viso et al. (2012) used a general dynamic model wherein the strengths of interactions were determined by the degree of temporal overlap (i.e., the inverse of mismatch) in the phenology of interacting mutualists. This approach was in keeping with previous suggestions from theoretical and empirical work that phenological synchrony is a major determinant of observed links in mutualistic interaction networks (Vázquez et al., 2009; Olesen et al., 2010). Encinas-Viso et al. (2012) found that network structure was drastically affected by changes in the starting date and length of flowering or pollinator phenology and that the change could reduce plant and pollinator diversity through extinctions during the dynamical process. Spatial or temporal mismatches may also arise for plant–herbivore interactions under climate change (Parmesan, 2006; Tylianakis et al., 2008a), though this remains to be explored within a multispecies network context.

One of the most significant community-level effects of climate change is thought to be the widespread shift in local abundances and geographic ranges observed for many plant and pollinator species (Crimmins et al., 2009; Hegland et al., 2009; Lavergne et al., 2010). Species often track climate to maintain their distribution within a thermal optimum (see, e.g., Lemoine et al., 2007; Holzinger et al., 2008), resulting in novel interactions

between species that move into an area and the natives already residing there (Parmesan, 2006). The ability of mutualistic interactions such as pollination to persist at the community level depends on the extent of range shifts exhibited by different species (in particular the differences among species; Cleland et al., 2006; Crimmins et al., 2010) and by the pollinator or plant communities as a whole.

Changes in plant community composition can also have bottom-up effects on herbivore communities through alterations in resource availability and microclimate. For example, drought conditions have been shown to reduce the water, soluble protein, nitrogen, and phenol content and to increase the carbohydrate content of a grass species (Walter et al., 2012). These changes altered the development of a generalist butterfly larva feeding on the grass, but the composition of the surrounding plant community affected the grass's production of defensive compounds and, to a lesser extent, its protein and carbohydrate content (Walter et al., 2012). In this case, the plant community altered the response of a specific plant–herbivore interaction to drought (indicating that the drought response depended on the level of biotic organization from species to community), but drought can also affect plant-mediated interactions between herbivores. Using an experiment with above- and belowground herbivores on wild basil (*Clinopodium vulgare*), Staley et al. (2007) showed that the normal negative plant-mediated indirect effects of the root chewer on the leafminer did not occur on drought-treated plants, possibly because of reduced root size or slower root-chewer growth rates. However, a previous study found an increase in the strength of positive indirect interactions between above- and belowground herbivores under drought conditions (Gange and Brown, 1989), indicating that conclusions about plant-mediated indirect effects cannot yet be generalized across taxa.

Changes in diversity are also expected in climate change scenarios. In systems where climatic changes provide a release from resource limitation, plant diversity is expected to decrease (Pimm et al., 1995; Reich, 2009), and extinction risk is expected to increase (Thomas et al., 2004), in response to climate change. A scenario of reduced diversity is typified by arid environments, where an increase in the occurrence or intensity of precipitation events results in a resource pulse, which can be exploited by existing vegetation (Zavaleta et al., 2003b). This pulse occurs because the increased resource availability increases aboveground net primary productivity (Shaw et al., 2002; Belote et al., 2003), resulting in the competitive exclusion of rarer species (Stevens et al., 2006) as dominant species benefit disproportionately (Bakelaar and Odum, 1978). In the tundra, for example, studies have found that warming extends the growing season (the resource being degree days conducive for growth), resulting in larger plants (Sullivan and Welker, 2005). Rare species can be competitively excluded either by a reduction in available soil resources, resulting from increased biomass of dominants, or through a reduction in light availability due to shading by dominants (Reich, 2009). Climate change can also assist the movement and establishment of invasive species, subsequently facilitating the decline of native species through local competitive exclusion or global extinction (Parmesan and Yohe, 2003; Lockwood et al., 2007).

Studies have begun to examine community-wide responses of insects to plant diversity responses to climate change. For example, Suttle et al. (2007) manipulated the seasonality and intensity of rainfall in Californian grassland and found that extended spring rainfall initially promoted plant diversity, which combined with greater primary production and water availability to support a more abundant and diverse invertebrate community including herbivores, predators, and parasitoids. Later, however, they found

that forbs were outcompeted by grasses and that herbivore and natural-enemy abundances declined by around 50% and diversity by about 20%. In contrast, winter watering tended to produce the highest density and diversity of consumers.

Yet, effects of climate on diversity of consumers can depend largely on the spatial and temporal scale of study. For example, de Sassi et al. (2012) assessed the biotic homogenization of caterpillars across a temperature gradient. They found that species richness was higher in warmer plots, so temperature positively affected diversity at this smallest scale. Higher temporal turnover in species in warmer sites (de Sassi et al., 2012) means that increasing the temporal scale of study would increase the apparent positive effect of temperature on diversity. In contrast, essentially the same species were found in all the warmed plots, so there was very low spatial turnover, meaning that diversity at the regional scale was negatively affected by warmer temperatures.

To further explore how responses of plant communities to climate may depend on the scale of study, we reviewed data on changes in plant community composition and diversity in response to increased temperature, CO₂, and changes in precipitation across spatial scales. We paired these studies with research illustrating the bottom-up effects of plant community change on insect groups. Suitable studies for our review were identified using Web of Science (ISI) searches and the key words “climate change”, “community”, “composition”, “diversity”, “warming”, “CO₂”, “precipitation”, and “drought”. To ensure adequate assessment of community response, we chose studies that included multiple functional groups (groups of plants that share morphological, physiological or phenological traits that indirectly affect fitness; Violle et al., 2007). We defined the spatial scale of each study as local, regional, continental, or global. We

classified our spatial scales based on the amount of environmental heterogeneity they encompass, assuming that noncontiguous areas are likely to be more dissimilar than contiguous areas. The local scale is characterized by individual assessments in small-sized areas (<10 ha; does not capture spatial variability) within a single system. The regional scale is characterized by either (1) individual assessments of large-sized areas (>10 ha; captures spatial variability) within a single system; (2) single assessments across several systems (i.e., plots extend across an elevation range on a mountain); or (3) multiple assessments across a contiguous region (i.e., a province). The continental scale is characterized by multiple assessments across a contiguous country. Finally, the global scale is characterized by multiple assessments across noncontiguous countries. We organized our findings according to the main response variable of the study for plants, and although there are very few studies to date of plant-community effects on animals at larger scales, when possible we highlight the plant variable that mediates the response for herbivores and pollinators.

STUDIES ON PLANT COMPOSITION

Warming—At local scales, two biotic factors were primarily responsible for changes in plant community composition in response to warming (Table 1). First, significant changes in dominant species largely accounted for rearrangements in plant community composition. Since a reduction in soil moisture often occurs simultaneously with warming, drought-tolerant species might be expected to become more common members of a plant community following temperature increases (Schroter et al., 2005). At local scales, stress tolerant species that can

TABLE 1. Responses of plant communities to experimental or natural warming across spatial scales. Data reflects significant changes at $P \leq 0.05$ in the final year of the study. Citations preceded by an asterisk (*) indicate model results (non-experimental). For composition response, Δ indicates a change in composition; 0 indicates no change in composition. For diversity, 0 indicates no change in diversity; a + indicates an increase in diversity; a minus sign (–) indicates a decrease in diversity.

| Scale | System | Country | Response | Abiotic or biotic pathway of effect | References |
|-------------|-----------|---------------|--|--|-----------------------------|
| Local | Alpine | Norway | Δ composition | Overshading via biomass increases | Klanderud and Totland, 2005 |
| | Arctic | Norway | 0 composition | Higher survival of all species | Robinson et al., 1998 |
| | Bog | Sweden | 0 diversity | Dominants unaffected | Keuper et al., 2011 |
| | Grassland | United States | 0 composition | Dominants unaffected | Zavaleta et al., 2003b |
| | | England | 0 composition | Slow growth strategies of plants | Grime et al., 2008 |
| | | United States | 0 diversity | Dominants unaffected | Zavaleta et al., 2003b |
| | Montane | England | – diversity | Increased mortality due to limited soil moisture | Sternberg et al., 1999 |
| | | England | – diversity | Loss of early season species | Grime et al., 2008 |
| | | United States | Δ composition | Shift to low productivity species | Saleska et al., 2002 |
| | Old-field | United States | Δ composition | Abundance changes across most species | Harrison et al., 2010 |
| | | United States | – diversity | Dominance of stress-tolerant species | Harrison et al., 2010 |
| | | United States | 0 composition | Community not temperature limited | Kardol et al., 2010a |
| | Peatland | United States | Δ composition | Decrease in dominant species | Weltzin et al., 2003 |
| | Shrubland | Spain | 0 composition | Community not temperature limited | Lloret et al., 2009 |
| | Steppe | United States | Δ composition | Increase of exotics | Alward et al., 1999 |
| Germany | | | Decrease in dominant species | Matesanz et al., 2009 | |
| Canada | | 0 diversity | Dominants unaffected | Hill & Henry, 2011 | |
| Regional | Desert | France | – diversity | Temperatures limiting persistence | Gaudnik et al., 2011 |
| | Grassland | United States | 0 composition | Resorting of species within functional groups | *Currie, 2001 |
| | | New Zealand | – diversity | Increase of exotics | de Sassi et al., 2012 |
| | Montane | Austria | + diversity | Colonization from lower elevations | Grabherr et al., 1994 |
| | | Switzerland | + diversity | Niche openings | *Kienast et al., 1998 |
| | Tundra | Canada | Δ composition | Differences in biomass response of functional groups | Walker et al., 2006 |
| | | Canada | – diversity | Change in dominant species | |
| Continental | Europe | – diversity | Range loss and limited dispersal | *Thuiller et al., 2005 | |
| Global | Tundra | Δ composition | Differences in response of functional groups | Elmendorf et al., 2012 | |

quickly take advantage of the negative effects of warming on extant vegetation, a characteristic of exotics, often play a large role in modifying a community (e.g., de Sassi et al., 2012). Changes in floral features of each species such as flowering date, flower number, flower size, and the ratio of male to female flowers could accompany this warming-induced turnover in dominant plant species (Hoover et al., 2012). These floral traits are known to influence visitation rates by different pollinator species (see, e.g., Schemske and Bradshaw, 1999), and if these effects differ in different plant species, then community-wide patterns of who pollinates whom might be affected by changes to floral characteristics.

In particular, subtle differences between the climate cues used by plants and those used by pollinators could promote systematic uncoupling of interactions. For example, Forrest and Thomson (2011) looked for correlations between air temperature, flowering dates, and insect emergence times from standardized nesting sites, and used reciprocal transplant experiments to determine the genetic and local environmental determinants of plant and pollinator phenology. They found that warming (increasing degree days) tended to advance the phenology of both plants and insect pollinators but that the details of when warming occurred could affect plants and insects differently; plants were more likely than insects to advance their phenology in response to early morning or springtime warming. These subtle differences in responses to climate could alter temporal co-occurrence patterns of plants and pollinators in their study region, although the changes would probably pertain to the extent of overlap in peak abundance rather than complete decoupling of plant–pollinator interactions (Forrest and Thomson, 2011).

Across single experimental sites, plant invasions following warming can generate bottom-up effects on herbivore communities. For example, de Sassi et al. (2012) found that higher temperatures were associated with overall higher caterpillar abundances and the advancement of peak larval abundance by 1 mo. The effects of climate on herbivore community composition were most strongly mediated by changes in the abundance of exotic grasses, but the authors were unable to test the extent

to which effects on herbivore phenology were mediated by changes to the plant community.

Alternatively, at larger spatial scales, the role of abiotic pathways in driving responses to warming became more apparent. Broad changes in resource availability likely interacted with microsite differences across sites (Harrison et al., 2006), resulting in the predominantly idiosyncratic responses of functional groups to warming (Körner et al., 2005).

Interspecific differences in community response to temperature change have also been documented for insects, and these between-species differences can ultimately alter the dominance of different taxa within a community (Richardson et al., 2002, Tylianakis et al., 2008a), emphasizing the need for community-wide studies of warming response.

CO₂—At local scales, there was an absence of a clear biotic or abiotic pathway of community change in response to elevated CO₂ (Table 2). Elevated CO₂ is expected to result in a concomitant increase in carbon uptake by plants, facilitating plant growth and increasing biomass, which may alter the performance or even composition of the herbivore community (Tylianakis et al., 2008a). Moreover, bigger plants often produce more numerous flowers, which can influence visitation rates by different pollinator species (see, e.g., Schemske and Bradshaw, 1999). Unexpectedly, experiments conducted at a single site actually found the opposite: a lack of biomass change or idiosyncratic responses of biomass to elevated CO₂ (Ainsworth and Long, 2005). The duration of these smaller-scale experiments (average of 4 yr across our studies) could explain this lack of response, as community reorganization induced by elevated CO₂ can sometimes require several seasons (Lichter et al., 2005), particularly for slow-growing species like forest dominants. Communities composed mostly of species that respond very slowly to CO₂ could then obfuscate responses of more rapidly responding species.

Precipitation—Community composition can be affected by changes in precipitation that alter the production and abundance

TABLE 2. Responses of plant communities to experimental or natural increase in CO₂ across spatial scales. Data organized as in Table 1.

| Scale | System | Country | Response | Abiotic or biotic pathway of effect | References |
|---------------|-----------------------|---------------|--|--|---------------------------|
| Local | Forest | United States | 0 composition | Idiosyncratic species response | Bandeff et al., 2006 |
| | | United States | 0 composition | No effect on total aboveground biomass | Souza et al., 2010 |
| | Grassland | United States | 0 composition | No effect on total aboveground biomass | Zavaleta et al., 2003b |
| | | Switzerland | 0 diversity | No effect on total aboveground biomass | Leadley et al., 1999 |
| | | United States | 0 diversity | No effect on total aboveground biomass | Henry et al., 2006 |
| | | Switzerland | 0 diversity | Idiosyncratic effects on biomass | Niklaus et al., 2001 |
| | | France | 0 diversity | Idiosyncratic species response | Teyssonneyre et al., 2002 |
| | | Switzerland | Δ composition | Overshading via biomass increases | Warwick et al., 1998 |
| | | United States | Δ composition | Change in dominant species | Owensby et al., 1999 |
| | | Switzerland | Δ composition | Replacement by species better adapted to low productivity environments | Niklaus et al., 2001 |
| | | United States | Δ composition | Idiosyncratic species response + positive species interactions | Reich et al., 2004 |
| | | France | – diversity | Change in dominant species | Teyssonneyre et al., 2002 |
| | United States | – diversity | Dominant species diversity change | Fay et al., 2012 | |
| | Old-field | United States | 0 composition | Idiosyncratic species response | Kardol et al., 2010a |
| Canada | | + diversity | Decreased extinction and slower turnover | Potvin & Vasseur, 1997 | |
| United States | | 0 composition | Increased biomass across all groups | Morgan et al., 2001 | |
| Regional | NE forests | United States | Δ composition | Increased survival of early successional species | *Bolker et al., 1995 |
| | CA Floristic Province | United States | – diversity | Local extirpations and limited dispersal for recolonization | *Loarie et al., 2008 |
| Continental | None | | None | None | None |
| Global | None | | None | None | None |

of specific functional groups. Such changes are expected when water availability changes, because species in these groups have different resource-acquisition strategies that might allow them to persist under water stress (Wellstein et al., 2011). Although community composition did not respond in a consistent way to changes in precipitation (Table 3), biotic pathways appeared to be responsible for determining community responses to water amendments across scales. At the local scale, compositional changes in response to water amendments were primarily driven by changes in seedling survival and certain groups (exotics, drought tolerant species) disproportionately benefiting from a change in water availability. This increase in nonnative and stress tolerant species could reduce foliar quality, affecting the timing of herbivore life-history events, herbivore performance, and host-plant choice (Awmack and Leather, 2002; Morrison and Hay, 2011).

At the regional scale, however, different responses of functional groups changed the composition of plant communities following increased precipitation. But these changes in plant community composition across larger spatial scales might not result in significant effects on insect groups. For example, the timing of reproduction and feeding by herbivores can sometimes track the phenology of their host plants at large scales (when a gradient in plant phenology occurs with, e.g., elevation or latitude), and concentrated reproduction at high elevation can even allow some herbivore species to recalibrate their life cycles when they become uncoupled from that of the host plant at low latitudes (Peterson, 1997). Nevertheless, the degree of concordance between herbivore phenology and that of their host plants can have important effects on local-scale survival and population densities of herbivores, and their impacts on host plant populations (Russell and Louda, 2004), potentially leading to outbreaks of herbivorous insects during years with high plant-herbivore synchrony (van Asch and Visser, 2007).

STUDIES ON PLANT DIVERSITY AND BIOMASS

Warming—At local scales, dominant species showed little or no response to elevated temperature (Table 1), resulting in a general maintenance of diversity. This lack of response was unexpected because warming is predicted to induce changes in productivity of dominant species (Rustad et al., 2001), and stress-tolerant species should reduce diversity by competitively excluding species that cannot persist on drier soils. Yet, dominance by a tolerant species only drove a reduction in diversity in one study from Table 1 (Harrison et al., 2010). The large number of studies showing no change in diversity could be the result of a complex interaction between changes in the biomass of dominant species and of more rare stress tolerant species in response to warming (reviewed in Tylianakis et al., 2008a). Similar responses have been documented for insects when, for example, the absence of a pollinator species at a point in space or time may be compensated for by the presence of other species (Ricketts, 2004).

Warming-related changes in productivity have both direct and indirect effects on insect communities. A recent study of tussock grassland communities in New Zealand (de Sassi and Tylianakis, 2012) used both a warming experiment and a natural temperature gradient to show that herbivore biomass responded positively to plant biomass but increased more than plant biomass with elevated temperature. Moreover, the biomass of natural enemies of the herbivores (parasitoid wasps) responded more weakly to herbivore biomass under warmer temperatures, producing lower attack rates on herbivores at higher temperatures (de Sassi and Tylianakis, 2012). If warming (and nitrogen availability, which was also manipulated in this study) are viewed as energy inputs into this system, then loss of energy with increasing trophic level may be the mechanism underpinning this result, though the general prevalence of such an effect needs to be tested in other systems. Furthermore,

TABLE 3. Responses of plant communities to experimental or natural changes in precipitation across spatial scales. A + indicates an increase in precipitation and a - indicates a decrease in precipitation (drought conditions). Data organized as in Table 1.

| Scale | System | Country | Response | Abiotic or biotic pathway of effect | References |
|-------------|------------------|----------------|-----------------------------------|--|----------------------------|
| Local + | Arctic Grassland | Norway | 0 composition | Plants not limited by moisture | Robinson et al., 1998 |
| | | United States | Δ composition | Increased seedling survival | Zavaleta et al., 2003b |
| | | United States | 0 diversity | No effect on total aboveground biomass | Harpole et al., 2007 |
| | | England | + diversity | Reduction in seedling mortality and increased lifespan of adults | Sternberg et al., 1999 |
| | Old-field | United States | + diversity | Increased resource availability | Zavaleta et al., 2003b |
| | | United States | Δ composition | Change in dominant species | Kardol et al., 2010a |
| | | United States | + diversity | Increase in germination or survival | Stevens et al., 2006 |
| | | Spain | Δ composition | Differences in response of functional groups | Pérez-Camacho et al., 2012 |
| | Steppe | China | Δ composition | Differences in response of functional groups | Yang et al., 2011 |
| | | Germany | Δ composition | Increased resource availability | Jentsch et al., 2011 |
| | | England | + diversity | No effect on total aboveground biomass | Morecroft et al., 2004 |
| | | United States | + diversity | No effect on total aboveground biomass | Harte et al., 2006 |
| Local - | Grassland | Estonia | 0 composition | Shift to drought tolerant species | Ingerpuu and Kupper, 2007 |
| | | United States | Δ composition | Differences in response of functional groups | Suttle et al., 2007 |
| | | England | Δ composition | Increase of exotics | Grime et al., 2008 |
| | | United States | Δ composition | Shift to more unproductive species | Potts et al., 2012 |
| | United States | - diversity | Increase of exotics | Suttle et al., 2007 | |
| | England | - diversity | Shift to drought tolerant species | Grime et al., 2008 | |
| | Meadow Shrubland | Switzerland | Δ composition | Differences in response of functional groups | Stampfli, 1995 |
| | | Spain | Δ composition | Shift to drought tolerant species | Lloret et al., 2009 |
| Regional + | Desert | United States | Δ composition | Differences in response of functional groups | Brown et al., 1997 |
| | Grassland | Czech Republic | Δ composition | Differences in response of functional groups | Dostalek and Frantik, 2011 |
| Continental | None | | None | None | None |
| Global | None | | None | None | None |

this combination of reduced top-down control of herbivores and increasing herbivore-to-plant biomass ratios could have important implications for community-wide plant biomass under warmer climates. Using data from the natural temperature gradient, the authors showed that changes in herbivore abundance were associated largely with plant compositional changes at warmer temperatures, specifically the increase in nonnative grass cover (de Sassi et al., 2012). This example highlights that, in addition to altered nutritional quality of plant individuals or species, the community-wide availability of preferred food plants may be altered by climate and may in turn affect the herbivore community.

At larger spatial scales, warming effects across multiple sites can extend over entire species ranges, and abiotic factors that serve to decrease diversity include modifications to colonization opportunities (Table 1). Reductions in diversity can occur through reductions of water availability (Owensby et al., 1999; Sternberg et al., 1999) and soil nutrients (Pastor and Post, 1988), which can be patchy. These interactions subsequently affect dispersal characteristics, modifying persistence and colonization abilities of a species in different ways across its range (e.g., He et al., 2005).

CO₂—Elevated CO₂ typically increases aboveground (Dieleman et al., 2012) and belowground (Henry et al., 2006) plant biomass production, so species diversity is expected to decrease with increasing CO₂ as plants become over shaded. Table 2 illustrates idiosyncratic diversity responses to elevated CO₂ at local scales, which can be expected from plants differentially benefiting from a change in carbon availability. For example, C₃ plants in particular are expected to benefit from increased CO₂ because their photosynthesis is currently unsaturated (Wang et al., 2012). Change in dominant species and subsequent overshading (Newman, 1973) was also a dominant biotic driver of decreasing diversity with elevated CO₂ at local scales.

Changes in the dominant species within a plant community might lead to mismatching between individual plants and insects through, for example, phenological shifts. Insect communities can be affected by the timing of a variety of plant phenological events, such as budburst, leaf flushing and maturity, leaf senescence, flowering, and seed development (see review by Hodkinson, 2005). These phenological shifts may carry fitness costs for plants, even though insect communities may compensate for lost visits through the phenological uncoupling of specific plant–insect interactions. For example, Rafferty and Ives (2012) manipulated the flowering times of two wildflower species and examined the effects on the identity and effectiveness of visiting pollinator species. Importantly, they found that earlier flowering resulted in lower pollinator effectiveness (i.e., fewer seeds produced from each flower visit) and that this effect was driven by a combination of changes in the pollinator community composition and changes to the effectiveness of certain pollinator taxa through time. This study highlights the importance of temporal scale for understanding how pollination responds to climate change.

Drivers of decreasing diversity in response to CO₂ at regional scales were similar to those documented for warming (Table 2). Colonization was restricted at larger scales through effects on dispersal, possibly through direct effects on seed characteristics important for dispersal efficiency (e.g., McPeck and Wang, 2007). We did not find any studies of CO₂ effects on plant communities at continental or global scales, presumably because of

a lack of strong natural gradients and the extreme difficulty of manipulating CO₂ at large scales. This presents an opportunity for global-scale modeling or time-series analyses to address community responses to CO₂.

Precipitation—Because average precipitation is expected to have a positive relationship with plant biomass (Huxman et al., 2004), diversity is expected to decrease in response to increased rainfall. However, this might not be the case with changes in the variability of precipitation (e.g., Derner et al., 2011), which can be more detrimental to plant fitness through effects on pollinator species (Olesen et al., 2010; Wall et al., 2003). Indeed, at local scales, diversity responses to increased precipitation occurred as a result of increased survival and reproduction across all species (Table 3). Decreased diversity occurred at these smaller spatial scales due to changes in biotic factors such as an increase in exotics and drought tolerant species in the presence of higher-stress, drought conditions.

These higher stress conditions can have considerable indirect effects on insects. For example, herbivore communities on drought-stressed pines have been found to have different composition, 10% of the abundance and around 50% of the diversity of communities on trees grown under better conditions (Trotter et al., 2008), possibly because of reduced resin defenses, lower tree growth rates and less living biomass. Stressed plants can also demonstrate changes in amino-acid and sugar concentrations in nectar, and climate-induced changes in nectar chemistry have even been shown to reduce bee longevity (Hoover et al., 2012).

In addition to plant-mediated effects of climate on pollinator communities, the direct response of pollinators to climate may feed back to plant community structure. For example, precipitation in the current and previous year has been shown to drive variation in bee and hummingbird abundance, and declining pollinator availability at climate range edges can limit the ability of plants to expand their own ranges (Chalcoff et al., 2012; Moeller et al., 2012).

OVERALL PATHWAYS OF RESPONSE ACROSS SCALES

At the local scale, climate changes can reduce diversity as species invade an area to track ideal environmental conditions (Loarie et al., 2008), often resulting in competitive exclusion of native species. But, many species can simultaneously be lost at the regional scale as both abiotic (e.g., physical isolation or habitat patchiness) and biotic (competitive exclusion) factors limit dispersal and persistence of existing species on the periphery of their climatic tolerance. Broadly, this result arises because drivers of plant community response to climate change can be different at different scales, such that changes in composition at single sites that always select for the same species could generate decreases in diversity across multiple sites. Recent work has highlighted the variable ways in which climate change encourages invasion (Thomsen et al., 2006; Bradley et al., 2010). For example, changes in species composition and abundance of herbaceous and woody understory plants under ambient and elevated CO₂ were mediated by the cover of two dominant, invasive plants (Belote et al., 2003). Globally, the number of species becoming invasive in new habitats could increase as a result of hybridization (Ellstrand and Schierenbeck, 2000), but at the local to regional scale, invasion is not necessarily coincident with native extinction or emigration and has

been shown to sometimes even increase diversity (Sax and Gaines, 2003), at least in the short term.

Environmental variation, which increases with spatial scale, can also play a role in modifying plant community response to climate change in several ways. For example, heterogeneity in resource availability and quality can modify plant development and demography (see, e.g., Hook et al., 1991), adaptation and tolerance to environmental stress (see, e.g., Jackson and Caldwell, 1996), complementarity effects on productivity (Tylianakis et al., 2008b), and species coexistence (Connell, 1979), all factors that can be responsible for the type and magnitude of climate change response.

Flowering phenology at a community level can be strongly affected by climate warming (Cleland et al., 2007; Diez et al., 2012), particularly through changes to early spring temperatures (Fitter and Fitter, 2002) and their effect on snowmelt times (Price and Waser, 1998; Inouye, 2008). Yet, the large phenological shifts expected to accompany plant community changes and changes in resource availability might not be detrimental to all plant–insect interactions. Some of the scarce empirical studies of climate induced phenological shifts for entire communities suggest that pollinator phenology (at least of generalist species) is keeping pace with changing plant phenology. For example, Hegland et al. reported in their 2009 review, that both plant flowering and pollinator activity appeared to respond linearly to observed temperature increases and that the similarity of their responses might prevent the uncoupling of plant–pollinator interactions. Similarly, Bartomeus et al. (2011) used literature records and 130 yr of museum data to demonstrate that the phenology of 10 wild bee species had advanced by an average of 10 d, in parallel with changes in the plants they visit. This absence of broad trends of plant and insect phenological responses contrasts with the pollination network research discussed already and highlights the importance of monitoring the strength of each interaction within the community, rather than just the average phenological response across species. Reduced temporal overlap (partial uncoupling) was found by Forrest and Thomson (2011) to be more likely than total phenological mismatch, and such partial uncoupling affected the structure of pollination networks in the study of Memmott et al. (2007) and their dynamics in the Encinas-Viso et al. (2012) study (all discussed earlier). Thus, full-season records of flower–pollinator temporal overlap, rather than short-term snapshots or the presence of any overlap, will be needed to fully understand the impacts of community phenology on plant–pollinator interactions, necessitating sampling regimes over longer temporal scales.

For community composition, we did not find clear overall patterns of response across systems, although we did detect scale-dependent differences in response across systems for some climate change factors (Table 1; Körner, 2009), perhaps due, in part, to microsite differences within systems. Soil types, for example, can differ both within and across grasslands, and these environmental differences have been shown to modify climate change effects (Fay et al., 2012). Generally, at local scales, community composition was affected by biotic factors, including climate-driven changes in biomass across all functional groups, possibly due to reduced competitive pressure from dominant species, which have been shown to be particularly vulnerable to the effects of climate change (Lauber and Körner, 1997).

For diversity, we found no consistent overall pattern of climate change-induced decline across climate drivers, scales, or ecosystem types (Beier et al., 2008). When a significant effect

of climate (particularly warming) was observed, it tended to be a reduction in diversity, often caused by range contractions driving long-term extinctions (Dullinger et al., 2012). An exception to this pattern is expected at high elevations, where temperature limits many species (Grabherr et al., 1994), so diversity should respond favorably to warming (Theurillat and Guisan, 2001).

A reduction in diversity through range contractions can potentially further exacerbate any negative climate effects on communities because less diverse communities are expected to be less resilient to the effects of global change (Frank and McNaughton, 1991) as there is a smaller likelihood that extant species will be well adapted to new conditions (Naeem et al., 1994). Likewise, diverse pollinator assemblages are better able to compensate for the absence of key species, particularly if pollinators are relatively opportunistic in the plants they visit (Petanidou et al., 2008). Therefore, when it does occur, loss of diversity will likely reduce the opportunity for temporal niche complementarity (e.g., Yachi and Loreau, 1999), and this reduction may distinguish the ecosystem-wide impacts of diversity loss at short vs. long temporal scales.

In addition to these changes across spatial scales, plant communities can be differently affected by climate as a function of different levels of biological organization (Diez et al., 2012; Fig. 1). Including interactions with animals, which can alter observed plant responses to climate, for example, if interactions with herbivores alter plant community responses to precipitation (Perez-Camacho et al., 2012) or temperature (Post and Pedersen, 2008). Some changes (e.g., phenological responses) occur within individuals (according to their genotype, location, neighborhood interactions, and microclimate), but overall species responses depend on the different responses of individuals and populations. These responses may in turn differ from those of community structure and interactions, which will depend on species traits, interspecific interactions, ecosystem type (e.g., alpine, semiarid), functional groupings, phylogenetic relationships, differences across species, and large-scale environmental drivers (Suttle et al., 2007; Diez et al., 2012; Stevnbak et al., 2012). In fact, Diez et al. (2012) modeled three North American plant communities and found that responses of different species to climate can be highly variable, but that overall plant communities may show similar responses to temperature (after the exclusion of variation due to regional variables). This conclusion is consistent with findings that, although individual species may be lost from interaction networks, the overall structure and functional capacity of the community network can be robust to these losses (Bascompte et al., 2006). Nevertheless, species-level differences in responses to climate can alter the community-wide phenological response (de Sassi et al., 2012; Diez et al., 2012), highlighting that the combined effects of climate at multiple levels of organization underpin the overall community response.

The studies included in our synthesis employed different methods to detect responses of plant communities across scales. Due to the subtle ways in which treatment effects can differ (e.g., Kennedy, 1995), the magnitude and even the type of plant community response can differ depending on experimental method. Therefore, we interpret comparisons across studies with caution. Broadly, these studies indicate that attempts to predict plant community changes based on climate-driven alterations on small assemblages of species at single experimental sites is largely complicated by differences in responses across

TABLE 4. Responses of plant communities to interactions between experimental or natural changes in climate change factors across spatial scales. Data organized as in Table 1.

| Scale | System | Country | Response | Abiotic or biotic pathway of effect | References | |
|---------------|---------------------------|---------------|--|---------------------------------------|-----------------------------------|----------------------|
| Local | Arctic | Norway | 0 composition | Higher survival of all species | Robinson et al., 1998 | |
| | Warming × precipitation | Grassland | England | 0 compositional | Slow growth strategies of plants | Grime et al., 2008 |
| | | Old-field | England | – diversity | Loss of drought sensitive species | |
| | Warming × CO ₂ | Grassland | United States | Δ composition | Change in dominant species | Kardol et al., 2010a |
| United States | | | – diversity | Decrease in total aboveground biomass | Hoeppner and Dukes, 2012 | |
| United States | | Δ composition | Functional-group specific increases in seedling survival | Zavaleta et al., 2003b | | |
| Regional | None | | None | None | None | |
| Continental | United States | | – diversity | Temperatures limiting persistence | *Currie, 2001 | |
| Global | None | | None | None | None | |

species. Similarly, insect guilds often demonstrate idiosyncratic responses to both the direct and indirect effects of climate change (e.g., Ritchie, 2000).

WHERE DO WE GO FROM HERE?

Research on how components of climate change affect plant communities and the higher-level trophic consequences of these changes has been ongoing. However, developing a comprehensive understanding of community responses to climate change, for predictive efforts and conservation strategies (Ackerly et al., 2010), will require that future investigators increase the biological realism of their experimental designs. We suggest several ways in which research questions and approaches can be modified to facilitate the identification of more comprehensive community-level effects of a changing climate.

(1) Where doing so is feasible, experimenters should attempt to identify scale effects. This goal can be implemented either at the experimental-design stage, where single plots or transects encompass small-scale experiments nested within a larger spatial area, or in a more theoretical framework, where responses at smaller scales are used for global-scale model development. Models of global-scale vegetation-community response that incorporate climate interactions, as well as interactions among species, are more realistic and therefore have more power to provide information on how vegetation response responds to scale. The growth of research on ecological networks (e.g., Ings et al., 2009), such as food webs and mutualist networks, is resulting in the collection and analysis of large sets of data on multispecies assemblages and the application of these to conservation problems (Tylianakis et al., 2010). The scaling of species interactions to entire networks has been a subject of much research, but a growing number of data sets will allow meta-analytical tests of geographic scaling of food-web and mutualistic network responses. Currently, our understanding of scaling effects in the responses of species to climate change is hindered by the paucity of studies at larger scales (Tables 1–3).

(2) Separate global-change drivers have been shown to have non-additive (i.e., interactive) effects on plant physiology (Robinson et al., 2012), diversity (Zavaleta et al., 2003a; Dukes et al., 2005; Reich, 2009), species interactions (Tylianakis et al., 2008a; Schweiger et al., 2010; Hoover et al., 2012), and community structure (de Sassi et al., 2012). Moreover, effects of multiple co-occurring drivers of environmental change on insect groups can also be complex (Hoover et al., 2012; de Sassi et al., 2012) and widespread (Tylianakis et al., 2008a; Schweiger et al., 2010) and

may greatly alter the net effect of global changes such as climate on biodiversity (Sala et al., 2000). Multifactor global-change experiments are slowly becoming more common, and these more realistic experiments that cross multiple drivers of global change must become a more regular part of the field if we are to understand fully the interactive effects and community changes in real-world environments (see, e.g., Andresen et al., 2010; Hoeppner and Dukes, 2012). Specifically, we noted a dearth of studies that incorporated CO₂ interactions at higher spatial scales, and in fact, there were few studies in general of any interactions at larger scales (Table 4). Although multidriver experiments involve clear methodological challenges, a viable alternative, where practical, would be to record the environmental context (e.g., background nitrogen-deposition rates, extent of invasion or habitat modification) so that these can be tested in future meta-analyses (e.g., Robinson et al., 2012).

(3) Finally, an important avenue will be to refocus on elucidating the mechanisms that drive patterns in diversity and composition, rather than simply attempting to document patterns themselves. This avenue is particularly relevant for patterns that are driven by both abiotic and biotic changes (e.g., direct vs. indirect, plant-mediated effects of climate on other trophic levels), such as spatial or temporal range shifts in pollinators or herbivores that require the presence of specific plants. Path-analytical approaches will be an important tool for teasing apart the direct effects of climate and the indirect effects of climate-induced changes to interacting species. Recent studies have made valuable progress in elucidating the community-level effects of climate change, and developments such as those outlined here will continue to advance the field in the future.

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