Interactive effects of anthropogenic nitrogen enrichment and climate change on terrestrial and aquatic biodiversity

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Abstract Biodiversity has been described as the diversity of life on earth within species, among species, and among ecosystems. The rate of biodiversity loss due to human activity in the last 50 years has been more rapid than at any other time in human history, and many of the drivers of biodiversity loss are increasing, including habitat loss, overexploitation, invasive species, climate change, and pollution, including pollution from reactive nitrogen (Nr). Of these stressors, climate change and Nr from anthropogenic activities are causing some of the most rapid changes. Climate change is causing warming trends that result in poleward and elevational range shifts of flora and fauna, and changes in phenology, particularly the earlier onset of spring events and migration, and lengthening of the growing season. Nitrogen (N) enrichment can enhance plant growth, but has been shown to favor, fast-growing, sometimes invasive, species over native species adapted to low N conditions. Although there have been only a few controlled studies on climate change and N interactions, inferences can be drawn from various field observations. For example, in arid ecosystems of southern California, elevated N deposition and changing precipitation patterns have promoted the conversion of native shrub communities to communities dominated by annual non-native grasses. Both empirical studies and modeling indicate that N and climate change can interact to drive losses in biodiversity greater than those caused by either stressor alone. Reducing inputs of anthropogenic Nr may be an effective mitigation strategy for protecting biodiversity in the face of climate change.

Keywords Climate change · Reactive nitrogen · Biodiversity

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Introduction

Biodiversity is the foundation of the integrity, resilience and beauty of nature. Simply defined, biodiversity is the variety of life on earth, including all species,

the diversity of genes in these species, and the communities and ecosystems they inhabit. A more complete definition from the Convention on Biological Diversity states:

> Biological diversity means the variability among living organisms from all sources including, inter alia, terrestrial, marine and other aquatic ecosystems and the ecological complexes of which they are part; this includes diversity within species, between species and of ecosystems" (CBD 1992).

Biodiversity influences—either directly or indirectly—nearly every ecological process. Changes in biodiversity alter the structure and function of ecosystems which can, in turn, affect the production of ecosystem services and human well-being in a variety of ways (Chapin et al. 2000; Millennium Ecosystems Assessment (MEA) 2005; Secretariat of the Convention on Biological Diversity 2010). Biodiversity is positively associated with a number of key ecosystem processes, in particular primary and secondary productivity, resistance to invasion and consumption, erosion control, and nutrient cycling (Balvanera et al. 2006). The benefits of biodiversity become more apparent when multiple ecosystem functions are considered because different species often perform different functions in ecosystems, or at different times (Hector and Bagchi 2007; Scherber et al. 2010; Zavaleta et al. 2010). More biodiverse systems tend to be more stable when processes are measured either through time (Hector et al. 2010; Yachi and Loreau 1999; Tilman et al. 1998) or over larger spatial regions (Loreau et al. 2003).

Biodiversity is declining globally despite international agreements to stem this loss. In 2002, over 150 nations signed the agreement under the Convention on Biodiversity "to achieve by 2010 a significant reduction of the current rate of biodiversity loss" (Secretariat of the Convention on Biological Diversity 2003). Recent analyses have found that, despite some notable successes, and the increasing expansion of protected areas globally, these goals are not being met nor are they expected to be met in the coming decades (Butchart et al. 2010; Secretariat of the Convention on Biological Diversity 2010; Kleijn et al. 2011; Pereira et al. 2010). Biodiversity within the United States (US) is similarly threatened, with the US Fish and Wildlife Service listing 587 animals and 794 plants as threatened and endangered in 2011 (US-Fish and

Wildlife Service (USFWS) 2011). Various analyses, including with the Globio3 model, project significant declines in biodiversity in the future, both in the US and globally, due to human activities (Alkemade et al. 2009; Secretariat of the Convention on Biological Diversity 2006; Pereira et al. 2010).

Land use change has been a major driver of losses in biodiversity, as natural areas have been converted to agricultural or urban uses, patterns of wildfires and other disturbances have been altered, and new species have been introduced into ecosystems (MEA 2005; Sala et al. 2000; McKee et al. 2004; Alkemade et al. 2009; van Oorschot et al. 2010). Land use change often results in increases in nitrogen (N) released to the environment by increased vehicle emissions, agricultural emissions, and runoff. Increasingly, climate change and increases in reactive nitrogen (Nr) are being recognized as significant drivers of ecosystem changes leading to biodiversity losses (MEA 2005; Rockström et al. 2009). These stressors interact in important ways that can either amplify or mitigate changes in biodiversity (Sala et al. 2000).

Historically, fluctuations in climate and nutrient availability are common in natural systems, but the magnitude of recent changes over a relatively short time period is unprecedented in the Holocene (Rockström et al. 2009). Changes in climate generally occurred over much longer time scales and over interconnected natural landscapes. Species ranges shifted accordingly, although many went extinct if migration was impeded or if extant species prevented their immigration to new habitats (Pimm et al. 1995; IPCC 2007). Under more rapid climate change, with a highly fragmented landscape, species migrations are even less likely to be successful (IPCC 2007). Changes in average precipitation and in the frequency and intensity of storms are also expected to impact biodiversity, although the effects of these factors are less well understood. The timing of biological activity, including associations with pollinators, pests, and herbivores, are also expected to change. Finally, one of the primary drivers of climate change, elevated carbon dioxide (CO_2), can have a variety of effects on biodiversity through its influence on plant growth, soil water availability, tissue stoichiometry, and trophic interactions (Reich 2009; Reich et al. 2006).

Unprecedented increases in Nr are also expected to drive losses in biodiversity. Nitrogen availability has historically been low in many ecosystems, limiting

primary production (Vitousek and Howarth 1991). Against this backdrop of low N availability and tight recycling in undisturbed natural ecosystems, globally available N has increased tenfold from 1860 to the early 1990s due to industrial and agricultural activities (Galloway et al. 2004). Indeed, it is estimated that human-derived Nr surpassed all natural processes combined sometime around the 1980s, a trend that is projected to increase Nr another 70 % by 2050 (Galloway et al. 2004; Vitousek et al. 1997). It follows that species distributions that evolved under largely N-limited natural conditions are likely to have changed and will change further.

Nitrogen enrichment impacts biodiversity in a variety of ways. For plants, these are usually categorized into four mechanisms: eutrophication, acidification, direct damage, and through secondary factors (Bobbink et al. 2010; Dise et al. 2011; Pardo et al. 2011a, b). Nitrogen is a commonly limiting resource for autotrophic plants, and excess amounts can lead to eutrophication of ecosystems, thus favoring fast-growing species in terrestrial and aquatic systems. This increased growth can reduce light penetration at the soil layer (or underwater for submerged macrophytes) and reduce belowground nutrient availability for other species, leading to overall declines in biodiversity and shifts in species composition (Hautier et al. 2009; Dise et al. 2011). Nitrogen enrichment can also acidify soil and water, lead to losses of base cations from the soil, nutrient imbalances, and increases in toxic compounds in the soil (e.g., aluminum, Al^{3+}) (Dise et al. 2001), also leading to reductions in biodiversity and selection for acid-tolerant species. Finally, N enrichment can aggravate the impact on biodiversity of secondary stressors such as fire, pests, and climate extremes (including frost and drought). Vulnerable plant communities can become more simplified in structure and less diverse in species than their undisturbed counterparts, harming animals that depend on certain plant species for food, habitat, or other resources (Dise et al. 2011; McKinney and Lockwood 1999). Biodiversity of other biota, including soil microbes, can also be directly affected by Nr enrichment, showing shifts in composition and reductions in beneficial populations (Johnson et al. 2003).

Nitrogen can interact with climate in several ways to affect biodiversity. *Additive* effects occur when N and climate affect biodiversity independently of one another. *Interactive* effects occur when the impact of

one (e.g., N enrichment) is contingent on the effect of the other (e.g., climate change). When impacts are additive, total effects can be estimated by their sum (even though some may be positive and some negative), whereas, when impacts are interactive, total effects can lead to disturbances not anticipated from considering either separately. *Compensatory* (or antagonistic) effects occur when an interaction causes the combined effect of the two factors (net impact) to be dampened or offset by each other. *Synergistic* effects occur when an interaction causes the net impact from factors to be amplified.

In this review, we focus on how interactions between climate change and N enrichment influence biodiversity within the US. Our conceptual model (Fig. 1) illustrates how changing climate, CO_2 and N can independently affect biodiversity, and also how biotic and abiotic factors can interact to influence biodiversity. Our discussion is limited by available data and information from research on these topics. As such, there is a focus on biodiversity at the scale of species, especially plants, with somewhat more information available for terrestrial systems than aquatic systems. We describe several major factors affecting biodiversity and how climate and Nr may interact to influence these factors (section "Introduction"), using examples from several ecosystems and taxa (section "Sensitivity of specific ecosystems to climate–N interactions"). We then discuss to the implications of this research, including evaluating risks to biodiversity from Nr enrichment and climate change using critical loads and other tools (section "Evaluating risks from nitrogen enrichment and climate change on biodiversity"), modeling efforts to assess climate and Nr interactions (section "Modeling"), and potential adaptation and mitigation efforts to reduce these interactions (section "Management and policy options for reducing impacts on biodiversity"). Lastly, we highlight some recommended areas of research (section "Summary and key research needs").

Factors that determine biodiversity

Biodiversity within a given region is determined by complex interacting abiotic and biotic controls (Gaston 2000; Ricklefs 2004), which can be influenced by anthropogenic N enrichment and climate change (Sala et al. 2000; Chapin III et al. 2000). A full account of the factors influencing biodiversity is beyond the
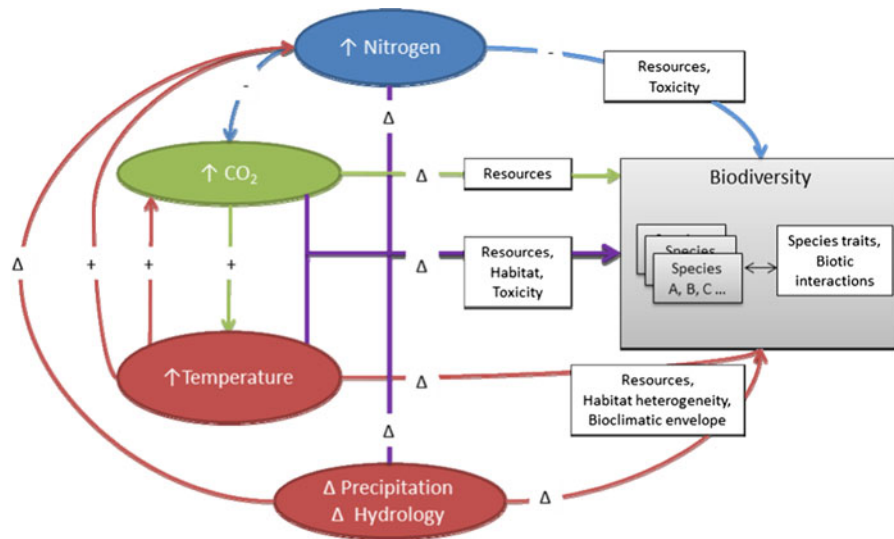
Fig. 1 Conceptual model of the direct and indirect effects of global change factors on biodiversity. Shown are effects on ecosystem biodiversity (*gray box*) from elevated nitrogen, elevated CO_2 and climate change (elevated temperature and changes in precipitation and hydrology). Predominant direction of effect is shown as positive (+), negative (−) or as a possible change in either direction (Δ). Changes in nitrogen, CO_2 and climate can influence biodiversity (shown as *red*, *blue* and *green arrows*, respectively). Nitrogen and CO_2 also can interact with climate to effect on biodiversity (*purple lines*). *White boxes* represent the additional factors mediating the effects on biodiversity, such as availability of other resources or species traits

scope of this review, but there are some general processes that operate in most systems for most taxa. Generally, for any particular species or individual to survive in an area, it must pass through "environmental filters" (Zobel 1997). Initial filters include the biogeographic distribution of species, and whether local dispersal occurs. Establishment within a site is determined by suitable abiotic conditions (e.g., climate), and biotic interactions that can limit (e.g., competition, predation) or enhance (e.g., presence of pollinators) the abundance of a species. The sections below describe the major factors involved in this filtering process, and how N enrichment and climate change can interactively influence some of these factors. In many cases, the influence of one factor accentuates the influence of the other, with the net result being greater changes (usually decreases) in biodiversity.

Bioclimatic conditions

To establish viable populations at a site, organisms must be able to physiologically withstand the range of climatic conditions present at that site, including extremes in temperature, solar radiation, and water availability. Climate change has and will continue to alter the range of these conditions, and the survival of species under changing conditions will depend on the pace of change and the biological attributes and phenology of individual species. Much of the available evidence for effects is based on small-scale, short-term experiments and should be interpreted with caution, since biodiversity at the landscape level may respond very differently as species redistribute under new climatic conditions.

The few controlled studies on the impact of changes in precipitation on biodiversity are largely from herbaceous communities, and are of relatively short duration (e.g., a few years). Research from Mediterranean systems (Zavaleta et al. 2003a, c) and tall-grass prairie (Collins et al. 2012) found that increased precipitation had a small positive or negligible effect, respectively, on species richness. Similar findings have been reported in China (Yang et al. 2011a, b).

A study from California shrub and grass ecosystems indicated that an increase of about 1 °C above ambient temperature applied over 3 years had a negligible effect on biodiversity (Zavaleta et al. 2003a, c); in contrast, evidence from grasslands in China indicated a decrease with a similar increase in temperature.

These diverging effects likely stem from differing impacts of simulated changes on other factors, such as changes in soil moisture (Zavaleta et al. 2003b; Yang et al. 2011a, b).

Extreme changes in temperature (e.g., hot periods and/or cold periods) and water availability (e.g., drought or flood) can subject populations to local extinction. If widespread population extinctions occur, the potential for species extinctions increases (Jeffries 2006; Parmesan 2006; Sinervo et al. 2010; Tilman and Haddi 1992).

Interactions with N and climate anthropogenic N input has the potential to change the capacity of species to tolerate altered climatic conditions. For example, earlier snowmelt in high elevation sites has caused earlier starts to the growing season, thus increasing the exposure of some plants to killing frosts (Inouye 2008; Fig. 2). Deposition of N has been associated with greater frost sensitivity in conifer species (Sheppard and Pfanz 2001), and the combination of more frequent frosts and greater plant sensitivity to those frosts can increase mortality rates. Nitrogen can also increase the capacity of species to tolerate a changing climate, for example, promoting growth and expansion of deciduous shrubs in tundra, while decreasing overall species richness (Chapin et al. 1995).Thus, in general, climate change and N may act synergistically or antagonistically on biodiversity, depending on system-specific and taxa-specific dynamics.

Movement of species

A species must be able to colonize new areas to expand its range, and diversity in a given habitat is strongly influenced by the number of species that can successfully disperse there (Zobel 1997). For example, remote islands generally have fewer species than mainland areas of similar size and conditions, often because of the difficulty of reaching these isolated habitats (Ricklefs 2004; Rosenzweig and Abramsky 1993; Rosenzweig 1995). Dispersal may limit diversity even in non-isolated areas: for example, the addition of seeds to some plant communities often leads to increases in diversity (Foster and Tilman 2003; Hubbell 2001; Hurtt and Pacala 1995).

Interactions with N and climate the successful movement of species across landscapes is a complex process, including reproduction (for sessile organisms like plants), dispersal, and establishment in a new habitat. Climate change and N enrichment can alter each of these steps and thus expand or contract the potential range of a species. Overall declines in plant diversity associated with anthropogenic N deposition, described primarily in grasslands (Stevens et al. 2004, 2010; Clark and Tilman 2008; Dupré et al. 2010; Maskell et al. 2010), will affect dispersal and establishment by decreasing the pool of plant species available to migrate and form new communities as climate change occurs. And although N enrichment tends to increase seed production and nutritional quality in plants (Throop and Lerdau 2004), species may respond differently. For example, in Minnesota, elevated N increased seed production for C_4 herbaceous species, and decreased seed production for C_3 species (HilleRisLambers et al. 2009). In addition, elevated CO_2 has also been found to increase seed production for many crop and annual species (Ackerly and Bazzaz 1995; Jablonski et al. 2002; Huxman et al. 1999), although other studies suggest that perennial species and undomesticated species may respond differently (Jablonski et al. 2002; Thurig et al. 2003; HilleRisLambers et al. 2009).

Because of these complexities, and because few experiments have examined the effects of global change on reproduction and dispersal, there is little detailed information on how ecosystems will shift with climate in the US or globally. Most modeling efforts assume that species ranges will shift with climate, though researchers acknowledge this is only a first approximation (Guisan and Thuiller 2005; Pereira et al. 2010).

Disturbance

Disturbance, or physical alteration of the habitat, plays an important role for biodiversity at the local and landscape scales. Both the frequency and intensity of disturbance are important. Areas that are either frequently or infrequently disturbed often have lower levels of biodiversity than areas with a moderate amount of disturbance. For example, rivers that experience high levels of flow variability have, in general, reduced food chain length and fewer numbers of species (Sabo et al. 2010). Disturbances influenced by climate, including fires, severe storms, and floods, are expected to change over the next century, although all are anticipated to occur more frequently and be more intense (Karl et al. 2009).
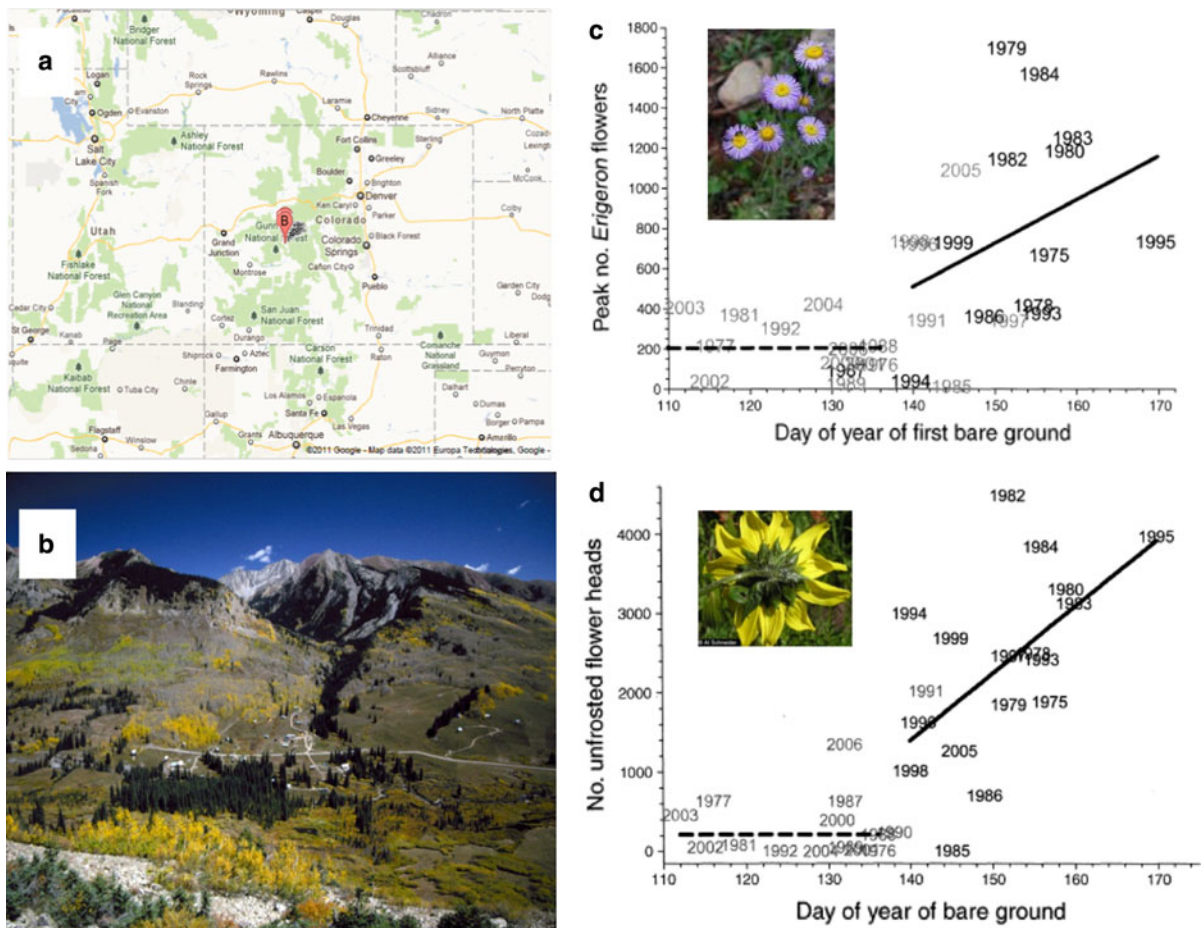
Fig. 2 Results from a study in Colorado on the effects of changes in climate on wildflower reproduction. The study location and photo (a, b; photo courtesy of David Inouye), the Rocky Mountain Biological Laboratory. The peak number of wildflowers (*Erigeron speciosus*) was lower when the season started earlier (c), and more flower heads were killed (*Helianthella quinquenervis*,) by frost (d) (modified from Inouye 2008)

Interactions with N and climate nitrogen enrichment has the potential to alter the response of ecological communities to climate change-driven disturbance. As an example, N enrichment and changes in precipitation patterns in the Mojave Desert have been implicated in the success of invasive annual grasses, which increase fuel loadings and carry fires in a native shrub community not well adapted to fire (Rao et al. 2010; Fig. 3). Similarly, increased fire frequencies in chaparral vegetation, in combination with greater N availability, enhances the replacement of native shrubs with weedy non-native annual grasses (Haidinger and Keeley 1993). Elevated N inputs can shift allocation of plant biomass from belowground to

aboveground, which tends to reduce the stabilizing influence of belowground biomass on the soil (Adair et al. 2009). Conversely, more aboveground biomass coverage can reduce the impact of rain droplets on destabilizing soil, and provide a physical barrier to storm flows in and along riverbanks, thereby reducing the potential for landslides and flooding (Korner 2004).

Hydrology

Climate change is anticipated to increase the duration of low flow periods in streams and rivers and the frequency of extreme events (e.g., drought and flood)
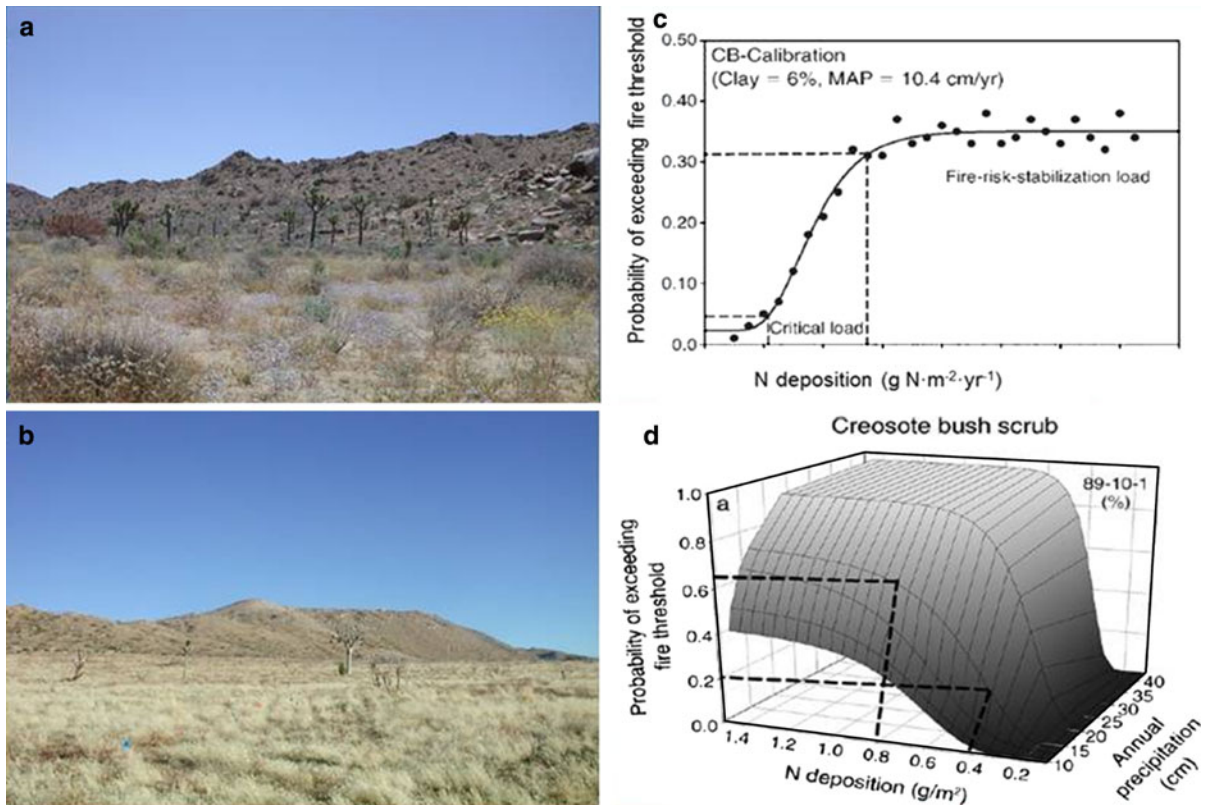
Fig. 3 The interactive effects of nitrogen (N) and climate on the probability of fire in the Mojave Desert, CA. N deposition facilitates the growth of invasive grasses in the spaces historically bare between shrubs (low invasion and high invasion/post-fire in (**a**) and (**b**) respectively; photos courtesy of Dr. Edith Allen). **c** Fire risk increasing in the creosote bush scrub community (CB) as N deposition increases; MAP is mean annual precipitation. **d** The probability of fire is enhanced with N deposition and increased precipitation (**c**, **d** adapted from Rao et al. 2010)

across much of the planet (IPCC 2007). During the twentieth century approximately half of the world's wetlands have disappeared (Zedler et al. 2001), and freshwater extraction in some regions is so extreme that some major rivers, including the Nile, Yellow, and Colorado Rivers, no longer flow to the sea either seasonally or entirely (MEA 2005). Climate change will alter the delivery of water to many areas by affecting how much rain falls versus snow, changes in snowmelt timing and also changes in water flows to estuaries and coastal zones.

Interactions with N and climate in alpine lakes, altered snowmelt timing and increases in glacial melting can increase nutrient loading and alter lake diatom communities (Saros et al. 2010). Storms and increases in precipitation increase nutrient loads to coastal zones, and droughts increase residence times,

promoting algal growth, including growth of harmful cyanophytes and bloom-forming flagellates (Paerl and Scott 2010). Altered hydrology can cause wholesale shifts in habitat, and if areas dry up, can cut off connectivity in streams or reduce habitat in wetlands.

Resource supply

The supply of resources (e.g., water, light, nutrients) is an important control on biodiversity. The supply of N in many ecosystems is restricted by climatic factors that constrain the turnover of organic matter, including low soil temperature and both high and low soil moisture (Hobbie 1996). Studies across major biomes have found that, in general, increased biodiversity is associated with increased fertility and productivity which is positively correlated with soil N content

(Chase and Leibold 2002; Waide et al. 1999). However, in more focused investigations of terrestrial and marine ecosystems and some fresh water ecosystems, diversity has been found to be inversely correlated with N inputs (Stevens et al. 2004, 2010, Clark and Tilman 2008; National Research Council 2000; Dudgeon et al. 2006). Thus, it appears to be the interplay of resource supply with other factors such as dispersal, scale, species interactions, and others that determine the net effect of resource supply on biodiversity.

Interactions with N and climate climate change may increase N availability in many ecosystems, potentially enhancing the effect of additional N enrichment on changes in diversity. For example, melting alpine glaciers are releasing Nr into receiving streams and lakes, where increasing N has been linked to shifts in diatom species assemblages from oligotrophic to mesotrophic species (Saros et al. 2010; Baron et al. 2009; Wolfe et al. 2001). Warming increases N mineralization in soils, increasing N availability in peat bogs (Keller et al. 2004; Weedon et al. 2012), subarctic heath-lands (Hartley et al. 1999), and a New England forest (Butler et al. 2011). In tundra, greater shrub cover promoted by N enrichment can enhance the development of an earlier insulating snow cover, increasing decomposition during the winter and thus the supply of plant-available N (Sturm et al. 2005). Elevated CO_2, on the other hand, may decrease N supply to plants due to shifts in the balance of C and N causing a slowdown in decomposition (Hu et al. 2001).

## Species interactions: consumptive and non-consumptive

Species interactions, including non-consumptive functions such as competition and facilitation, and consumptive processes such as herbivory, parasitism, and predation, can influence the success or failure of species within a community, and subsequently influence its biodiversity (Ricklefs 1987). The spatial and temporal extent, intensity, and outcome of these interactions often depend on the climatic conditions and variations in the supply of resources such as N.

Interactions with N and climate competition for N by autotrophs could decrease under climate warming and N enrichment scenarios by shifting the limiting resource(s) from N to phosphorus (P) in aquatic systems (Elser et al. 2009), and P, light, or water in

terrestrial systems (Hautier et al. 2009). However, the overall intensity of competition could increase as well. In California, simulated elements of a global change scenario (elevated N deposition, temperature, CO_2, and precipitation) influenced diversity, as measured by total grasslands species richness, in different ways. For example diversity increased with elevated precipitation alone, was unaffected by elevated temperature alone, and decreased with increasing N and temperature (Zavaleta et al. 2003a, c). All factors in combination caused changes in the relative dominance of forbs and grasses, with decreases in forb abundance. Forbs make up most of the plant biodiversity in these systems (Fig. 4a, b). Elevated N and CO_2 reduced the difference in flowering date between the two groups, increasing temporal overlap and leading to greater overall competition between these two functional groups, with the grasses subsequently dominating (Fig. 4c). The highly invasive yellow starthistle, *Centaurea solstitialis* L., also benefited disproportionately under altered climate and N regimes (Fig. 4d). However, the only other experiment examining the impact of both elevated N and CO_2 on biodiversity in the US (Reich 2009), found that, although N addition reduced diversity in a Minnesota grassland over 10 years (−16 %), elevated CO_2 mitigated about half of this loss. Thus, although elevated N reduces biodiversity in general, other global change factors may interact to affect this response.

Climate change and N enrichment may have an additive effect on increasing the amount of consumption and population growth of consumers (e.g., herbivores, carnivores, etc.). Greater consumption rates can increase diversity when a dominant competitor is the preferred target species, or decrease diversity when rare species are preferentially consumed (Olff and Ritchie 1998). Many consumers, particularly herbivores, are growth-limited by the supply of N (Mattson 1980). Growth may increase substantially in response to N enrichment as forage quality increases with higher N concentrations in plants, lower concentrations of defensive compounds, and shifts to higher dominance of more palatable species (Throop and Lerdau 2004). Climate change in temperate and arctic climates will benefit many invertebrate consumers due to a longer growing season (Bale et al. 2002) that allows some insect herbivore species to complete more than one life cycle in a year (Roy et al. 2009; Mitton and Ferrenberg
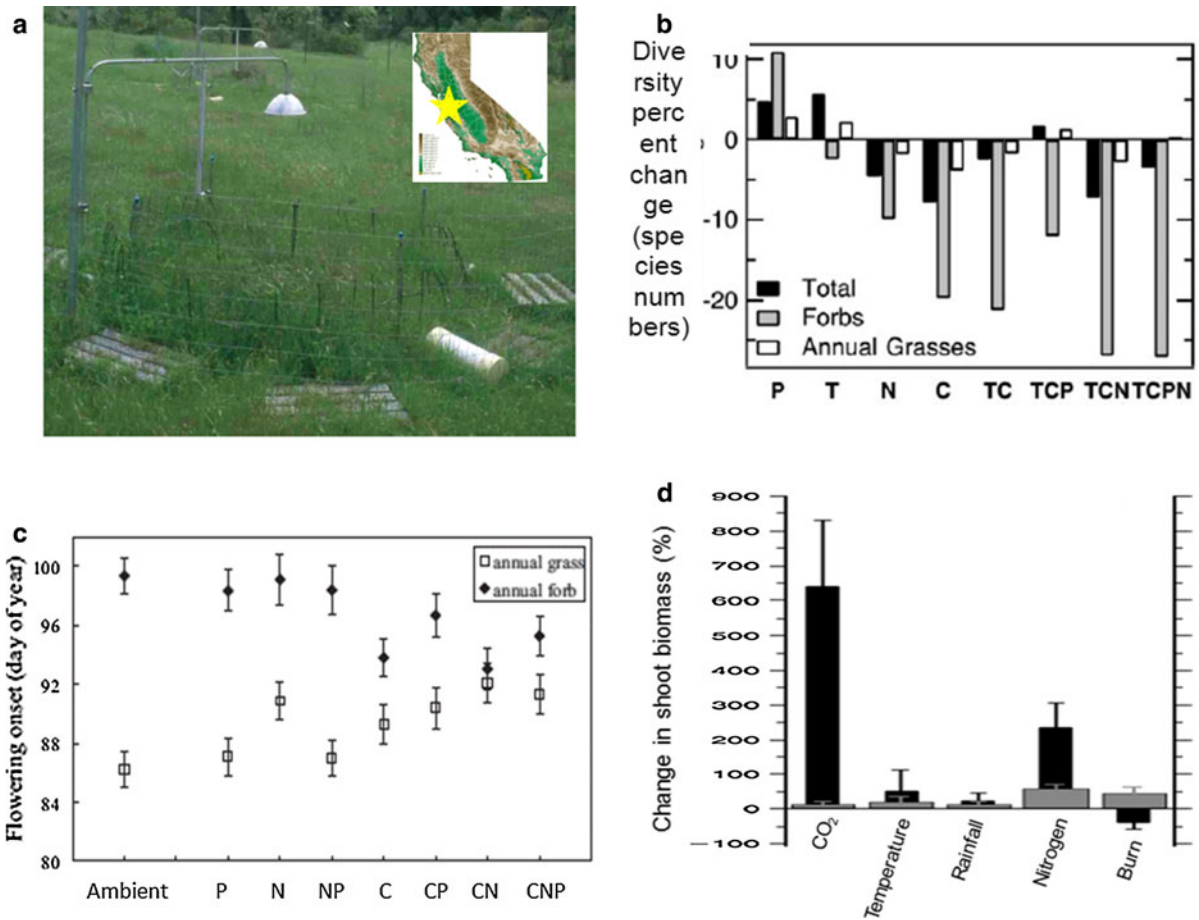
Fig. 4 Results from a global change experiment in California on the individual and interactive effects on plant diversity from four global change factors (elevated temperature (T), precipitation (P), nitrogen (N), and CO_2 concentrations (C); Shaw et al. 2002; Zavaleta et al. 2003a; Cleland et al. 2007, Dukes et al. 2011). **a** A typical plot and the geographic location of the experiment (modified from Shaw et al. 2002). Results of the overall diversity changes are shown in (**b**) (Zavaleta et al. 2003a) related to individual and combined treatments. Shifts in phenology for annual grasses and forbs are shown in (**c**) (Cleland et al. 2006, Copyright 2006 National Academy of Sciences, USA). Responses of the invasive star thistle (*thin black bars*) and the extant community (*thick grey bars*) are shown in (**d**) (Dukes et al. 2011)

2012). The longer growing season is implicated as one factor contributing the outbreak of mountain pine beetles in western North America (Raffa et al. 2008; Bentz et al. 2010).

Habitat heterogeneity

Generally speaking, more heterogeneous habitats, or areas with many different kinds of habitats, can support more species (Ricklefs 2004). For example, mixed forest stands usually support more species than single-species stands, and old growth forests more species than mixed stands.

Interaction of N and climate some species preferentially benefit from increases in N, leading to an overall simplification of the habitat. This is often termed "biotic homogenization" and can be driven by a number of factors such as the spread of few numbers of invasive species (McKinney and Lockwood 1999). In terrestrial ecosystems N deposition can reduce local variation in soil N availability, which is an important contributor to diversity (Gilliam 2006). In grasslands N-addition experiments, reductions in plant diversity led to a reduction in the diversity of insects (Haddad et al. 2000). Climate change may exacerbate this simplification, both through its effects on species diversity and habitat diversity.

Sensitivity of specific ecosystems to climate–N interactions

Reviewing the interactions between N and climate change is challenging since many studies address these impacts individually rather than together. Few manipulation experiments alter temperature or precipitation and nutrient availability; fewer still examine the impacts on biodiversity. Reich et al. (2006) reviewed all known studies combining N enrichment and elevated CO_2 treatments, and found only eight that they considered representative of natural responses (e.g., field-based, replicated, long term), with none in mature mixed forests. Globally, the Jasper Ridge FACE experiment in Stanford, California (Shaw et al. 2002) is the only field experiment examining the impact on biodiversity of increasing N deposition, temperature, CO_2, and precipitation, both singly and in combination. Clearly there is growing recognition of the importance of these interactions, and a need for more information. Complementary approaches exist, however, such as modeling, regional gradient surveys, and re-surveys or retrospective analyses of existing long-term data sets. Evidence for single factor and interactive effects by ecosystem is shown in Table 1; detailed information and case studies by region are summarized in the Supplementary table. In this section we use this combined evidence to examine the sensitivity of different ecosystems and regions to changes in N and climate. Section "Evaluating risks from nitrogen enrichment and climate change on biodiversity" will integrate this knowledge with future projections of N deposition and climate to explore risk and vulnerability.

Forests

Some forest ecosystems are sensitive to the interactions between N and climate change, and many of the interactions are synergistic. Anthropogenic increases in N loading to forests are mainly via atmospheric deposition, and thus regions with higher N deposition are more at risk (see section "Evaluating risks from nitrogen enrichment and climate change on biodiversity" for more specific discussions of risk and vulnerability). Across the Northeastern US, higher N deposition is associated with enhanced tree growth for most species (Thomas et al. 2010). Nitrogen loading preferentially affects certain species as a consequence of species traits, and in some cases alters the

bioclimatic envelope of these species, causing them to be more sensitive to climate change. For example, increased N stimulates leaf area growth, which has been speculated to reduce drought resistance (McNulty and Boggs 2010). Increased N deposition also contributes to soil acidification and subsequent loss of base cations, including calcium. Decreased calcium availability can compromise plant cell membrane integrity, thereby decreasing cold tolerance and increasing the potential for freezing injury (DeHayes et al. 1999; Schaberg et al. 2002). Thus N and climate change interact to alter species composition through drought or frost damage, driven by the plants' response to increased N.

Moreover, much of the biodiversity of forests is in the understory herb and shrub layer rather than in the overstory tree layer (Gilliam 2006). These taxa are poorly studied in the literature, but sensitivity to N deposition and interactions with climate change are likely (Gilliam 2006; Wu and Driscoll 2010).

Tundra

In the Arctic, warming has contributed to dramatic increases in shrub cover, as documented by aerial photographs at thousands of locations between the Brooks Range and the Arctic Coast in 1948–1950 and later in 1999–2000 (Sturm et al. 2001). This has led to a shift in community type from more open graminoid ecosystems to areas dominated by shrubs. Experiments at the Toolik Lake Arctic LTER site confirmed that elevated temperature enhanced shrub production and reduced production of non-vascular plants. Elevated N increased growth and production of deciduous shrubs but reduced growth of evergreen shrubs and non-vascular plants, while combined N and temperature treatments reduced species richness 30–50 % due to loss of less abundant species (Chapin et al. 1995).

Grasslands

Grasslands are likely to be especially sensitive to changes in N and climate for many reasons. Compared with forests, grasslands are dominated by plants that have a strong capacity for rapid changes in growth (Knapp and Smith 2001). Grasslands are often limited by N availability, or co-limited by N and other resources such as water or P (Elser et al. 2007; Hooper and Johnson 1999; LeBauer and Treseder 2008).

Table 1 Impacts of nitrogen, climate and nitrogen-climate (NxCC) interactions for major ecosystems in the US

Ecosystem	Major Impacts of Climate Change (NCA 2009)	Major impacts of N	Nitrogen references	Impacts of NxCC	NxCC References
Tundra	More rapid climate change that rest of US, longer growing season, permafrost warming, changes in soil temperature and moisture, increased fire	Increased productivity, shifts towards graminoids and shrubs from bryophytes and lichens, increased decomposition	Shaver et al. (1998), Nowinski et al. (2008), Arens et al. (2008), van Wijk et al. (2004), Cornelissen et al. (2001)	Additive—both increase N availability, warming increases nitrogen mineralization, increasing shrubs trap more snow, wetness decreases sensitivity to N	
Taiga	More rapid climate change that rest of US, Increase in pest outbreaks and fire, Longer growing season, permafrost warming and forest declines, changes in soil temperature and moisture, increased fire frequency increases, drier soils	Increased decomposition, shift in species composition (from shrubs to grasses; lichen community composition)	Aerts and Chapin, (2000), Gough et al. (2000), Nordin et al. (2005), Geiser and Nadelhoffer (2011)	Increasing temperature and N → increase in green algae	
Alpine	Shorter duration of snowpack, longer growing season, increased exposure to freezing events, movement of invasive species into alpine area	Alteration of species, decreased diversity and whole community composition	Bowman et al. (2006), Bowman and Steltzer (1998)	Additive - warming will increase nutrient supply, greater species pool combined with higher N makes it a more inevasible system	
Conifer forests	Southeast—longer growing seasons, hotter summers and drought; reduced forest production under drought, reduced snowpack, increased fire, pest outbreaks, hurricanes and flooding; range shifts	Shifts in understory herbaceous species composition, shifts in microbial assemblages	Thomas et al. (2010), Lilleskov et al. (2008)	Synergistic—N deposition and productivity (C sequestration)—species specific; drought, elevated tissue N and pest susceptibility, N increases susceptibility to disease, to abiotic stresses → shifts in species composition	McNulty and Boggs (2010)
Hardwood forests	Northeast—longer growing seasons, hotter summers and drought; increased fire, ice storm, heavy precipitation, extreme events, flooding, reduced extent and duration of snowpack, increased exposure to soil freezing events, range shifts	Shifts in understory herbaceous species composition, shifts in microbial assemblages	Thomas et al. (2010), Gilliam (2006), Hurd et al. (1998)	N dep and productivity (C sequestration)—species specific; drought, elevated tissue N and pest susceptibility, N increases susceptibility to disease, to abiotic stresses → shifts in species composition	Halman et al. (2011)
Grasslands	Longer growing season, warmer, wetter → greater biomass production, potential for increased fire intensity, impacts on dispersal because of prior fragmentation, range shifts, spread of pests and weeds	Compositional shifts towards fast-growing (often C3) grasses, structurally simplified, increased competition for light, alter microbial assemblages, reduced insect diversity and shift towards generalists	Tilman (1993), Wedin and Tilman (1996), Clark and Tilman (2008)	Warmer, wetter → intensify N limitation (which could lead to a greater impact if soil N availability is low or a smaller impact if soil N availability increases with CC, reduce water limitation), interaction of elevated CO_2 + N may reduce species loss from elevated N input alone	Knapp et al. (1993, 1996, 1998)
Deserts	Reductions in water supply. increased temperature, drought, fire and invasive species will affect the landscape	Alterations in species composition, increases in exotic species biomass, decrease in native species	Allen et al. (2009), Rao and Allen (2010), Rao et al. (2010)	Increased N deposition leading to increased biomass accumulation, increasing fire frequency	Brooks et al. (2004), Brooks and Minnich (2006)

Table 1 continued

Ecosystem	Major Impacts of Climate Change (NCA 2009)	Major impacts of N	Nitrogen references	Impacts of NxCC	NxCC References
Shrubland	Decreased precipitation, increased temperature, more storms, increased fire. Increased die-off of pinyon pine and alteration of pine-rich biodiversity hot spots. Range shifts, spread of invasive species	N addition decreasing soil moisture in sagebrush steppe. Air quality in the southwest expected to decline. Ozone and other pollutants can impact these ecosystems. Increase in invasive species, decrease in shrub cover and native species.	Inouye (2006), Fenn et al. (2010)	NxCC may interact to lead to even drier soils and increased fire	
Wetlands	Intense droughts in the northeast and especially southeast, leading to local or global extinctions, flooding and sea level rise, decline in dissolved oxygen leading to loss of aquatic species	Nitrogen generally increases production and decreases diversity, particularly in high N load setting like coastal zone (sea grass decline); invasion of non-native species, altered competition, loss of N-sensitive species like eelgrass	Aldous (2002), Bedford et al. (1999), Darby and Turner (2008a, b), Mendelssohn (1979), Tyler et al. (2007), Wigand et al. (2003), Tyler et al. (2007), Crain (2007), Mendelssohn (1979), Wigand et al. (2003), Latimer and Rego (2010)	Drying and increases in anthropogenic nitrogen will together strongly alter and likely reduce biodiversity. In freshwater wetlands, N inputs increase CH_4 and N_2O production	Liu and Greaver (2009)
Lakes	Lakes are projected to shrink and become less connected with warming and decreasing flow; so less habitat aquatic habitat overall (happening quickly in Alaska where migrating birds are at risk). Decreases in extent and duration of lake ice; snowmelt changes and extreme events increase. Residence times and turnover may change as well leading to more intense stratification and fish kills.	In N-limited systems, productivity increases, diatom communities are altered; hypoxia will have even more pronounced impacts on biodiversity	Kelly et al. (2011)	NxCC driven shifts in composition and productivity, possible eutrophication and hypoxia	Kelly et al. (2011)
Streams	River networks may shrink and become less connected with warming and decreasing flow; so less habitat aquatic habitat overall. Reductions in snowpack alter runoff timing. Salmon and other coldwater species will experience additional stresses from temperature. Increases in extreme events such as flooding will also affect biodiversity and trophic structure.	In N-limited systems, eutrophication and subsequent alteration of species composition; hypoxia will have even more pronounced impacts on biodiversity	Rahel and Olden (2008), Baron et al., this issue	NxCC driven shifts in composition and productivity, possible eutrophication and hypoxia	Hobbs et al. (2010), Baron et al., this issue
Estuarine and Near-Coastal Ocean	Changes in flow amount and timing, and estuarine residence time and turnover impact species composition. Ocean acidification. Sea level rise is eroding shorelines. Reduced sea ice in Alaska alters blooms and fish stocks. Displaced marine species and shifts. Changes in currents may increase extent and duration of northern Pacific Dead zone	N drives eutrophication in many coastal systems, affecting structure and biodiversity	Gilbert et al. (2005), Howarth et al. (2011)	NxCC driven eutrophication and hypoxia; eutrophication can increase the susceptibility to acidification	Paerl and Scott (2010), Cai et al. (2011), Howarth et al. (2011)

Changes in growth and increased production from N enrichment are strong predictors of biodiversity decline (Clark et al. 2007). Increases in precipitation may increase ecosystem sensitivity to N deposition by enhancing primary limitation from N, suggesting that future N deposition will have a larger effect over those parts of the US that are likely to experience greater precipitation (Rao et al. 2010). Additionally, impacts from N enrichment could be counterbalanced by elevated concentrations of CO_2, which reduce N cycling in ecosystems and enhance soil water availability through reduced plant transpiration (Luo et al. 2004).

Despite being better-studied than most biomes, empirical evidence is scarce on the interactive effects of different drivers of diversity in grasslands. Generally, experimental N additions to grasslands result in substantial reductions in species diversity and greater losses in areas that are not also limited by other resources such as water (Bobbink 1998; Clark et al. 2007; Bobbink et al. 2010). In an experiment in annual Mediterranean grassland in California, where N, temperature, precipitation, and CO_2 were altered, the effects of these factors were additive, and the total effect led to a large loss of plant species, especially forbs (Zavaleta et al. 2003c). In an experiment in temperate perennial grassland in northern Minnesota where CO_2 and N levels were altered, the reduction in diversity (mostly forbs) due to N addition was partly mitigated by elevated CO_2 because elevated CO_2 reduced soil N and increased soil moisture (Reich 2009). Thus, grassland diversity is likely to be sensitive to changes in N and climate, but the exact nature of these changes can vary from system to system.

Drylands

Plant growth is primarily constrained by water availability in arid systems (Noy-Meir 1973). However, when this constraint is lifted by increased precipitation, N limitation becomes increasingly important (Brooks 2003; Allen et al. 2009; Rao et al. 2010). In Joshua Tree National Park, N addition experiments increased non-native grass biomass and, where non-native grass biomass was high, N decreased native forb species richness (Allen et al. 2009). In areas of the Mojave and Sonoran Deserts in southern California, a series of years with higher-than-average rainfall coupled with increased N deposition from the Los Angeles Basin has promoted the growth of invasive Mediterranean grasses, creating a nearly continuous fuel layer in arid shrublands (Brooks and Minnich 2006; Rao et al. 2010). Fire frequency has increased, as has fire occurrence in areas previously unburned and unadapted to fire (Rao et al. 2010). Native shrubs may not be able to re-establish in these areas, as invasive grasses change the hydrology of the area, removing rainwater from the top layers of the soil thereby preventing its percolation into the root zone of young shrubs (Wood et al. 2006).

Nitrogen can exacerbate drought stress in drylands. In pinyon-juniper woodland of New Mexico, N fertilization decreased mycorrhizae and increased leaf production in pinyon pine, leading to increased drought-induced mortality (Allen et al. 2010).

Wetlands

Changes in N availability and climate may strongly impact species composition and biodiversity in wetlands (Greaver et al. 2011). Nitrogen is the limiting nutrient for plant growth in both freshwater and estuarine wetlands (LeBauer and Treseder 2008). Despite the high biodiversity in wetlands (USDA-NRCS 2009), the effects of N loading are studied in a limited number of plant species. Increased N availability or inputs may preferentially increase the growth of certain species, and since not all species respond equally, this may cause species dominance and composition to change. Sensitivity to N deposition in wetlands is generally thought to follow the pattern: bogs > fens, marshes, swamps > intertidal wetlands, representing the gradient from very low N conditions to very high N conditions. Because bogs receive nutrients exclusively from precipitation, they tend to be most sensitive wetland type to N deposition (Morris 1991). Other wetland types can be vulnerable to anthropogenic N enhancement from deposition as well as agricultural runoff via subsurface or surface waters. A recent study in a brackish marsh in Maryland found that N-induced shifts in biodiversity from C_3 to C_4 species altered the community response to CO_2 (Langley and Megonigal 2010). It has been shown that N loading can increase decomposition rates of organic matter and therefore, C loss, from salt marsh soils (Wigand et al. 2009). This could lead to degradation of the marsh structure and greater susceptibility to sea level increases.

Freshwater systems

Human-driven biodiversity declines are expected to be far greater in freshwater than in terrestrial ecosystems (Sala et al. 2000). Aquatic ecosystems receive water and pollutants from the surrounding catchment, and lose water through landscape-scale withdrawals, and thus are particularly sensitive to anthropogenic change (Dudgeon et al. 2006). Freshwater ecosystems have been described as biological assets that are both disproportionately rich in diversity and disproportionally imperiled (Abramovitz 1996), and the combination of habitat loss, homogenization of flow regimes, and eutrophication has had drastic consequences on native freshwater organisms, including fishes, shellfish, and benthic invertebrates. About 37 % of aquatic animal and 62 % of aquatic plant species are considered at risk in the US (Heinz III 2008; Baron et al. 2002). Climate change has dramatic consequences for freshwaters because dissolved oxygen levels are sensitive to temperature, and flow changes can alter the concentrations and/or fluxes of nutrients. Many of the examples we identified in Table 1 for aquatic ecosystems involve synergistic interactions between N supply and climate change. For example, increases in temperature and changes in the timing and distribution of precipitation may exacerbate eutrophication and hypoxia in many ecosystems, particularly estuaries and coastal receiving waters.

Current levels of N in freshwaters and estuaries are a significant part of the problem by promoting noxious and harmful algal blooms, simplifying food webs, and creating favorable conditions for non-native species (Heinz III 2008). Warming, too, may promote local extirpation or migration of cold-obligate species and invasion of non-native species (Rahel and Olden 2008). Water temperature directly regulates oxygen concentrations, metabolic rates, and associated life processes. The thermal regime influences fitness and the distribution of species in both space (e.g., latitudinal and altitudinal gradients) and time (e.g., seasonal variation at a single location) (Baron et al. 2002). A survey of remote arctic and alpine lakes of North America and Greenland found that diversity of algal diatom assemblages has changed in these regions more significantly in the twentieth century than in the previous 350 years. Hobbs et al. (2010) noted that the greatest changes occurred in areas of most rapid warming (i.e., the Arctic) and areas with N deposition

rates significantly elevated over natural background rates (i.e., alpine lakes), and predicted that diversity in remote lakes will continue to change, particularly in regions where climate change and N deposition interact. Whether from climate change, N availability, or both, the negative effect on biodiversity is expected to continue in the future.

Estuarine and near-coastal systems

Climate change can alter the responses of coastal waters to N pollution in the form of hypoxia, eutrophication, and harmful algal blooms (HABs) toxic to marine fish and wildlife and humans. Coastal ecosystems can become more or less sensitive to N pollution due to climate-driven changes in: (a) water residence time as it affects the time for phytoplankton blooms to occur; (b) ocean currents, as they affect the oxygen levels and nutrient content of water entering estuaries from the ocean; (c) stratification, which is driven by changes in temperature, freshwater discharge, winds and storms; and (d) ecological structure that is driven by temperature or a–c above. Examples of both enhanced and reduced sensitivity to N have been demonstrated for these cases. For instance, New York Harbor estuary has experienced greater occurrences of algal blooms and become much more eutrophic, as water residence times in summer have increased as a result of less winter snowpack in the Adirondack Mountains (Howarth 1998). The St. Lawrence Estuary and Gulf of St. Lawrence have become more sensitive to N-induced hypoxia in recent years, as their bottom waters now come more from the deep Atlantic water, already low in oxygen, and less from the Labrador Current (Gilbert et al. 2005; Howarth et al. 2011). Due to greater stratification, productivity in the Dead Zone area in the Gulf of Mexico has become co-limited by P, causing less N uptake, -cycling, and -loss in coastal environments and greater transport of Nr to deeper waters (Sylvan et al. 2006, Donner and Scavia 2007).

Several aspects of climate change that favor HABs include: longer periods of warm temperatures, increased intensity of vertical stratification, increased salinization, and increased intensity of storms and drought frequency and duration (Paerl and Scott 2010). Storms can increase nutrient loads to coastal zone while droughts increase residence times, retaining nutrients and exacerbating algal blooms. A number

of estuaries have experienced hypoxia and HABs associated with altered nutrient loads during certain key seasonal periods (Howarth et al. 2000; Paerl 2006). Harmful algal blooms can dramatically alter ecosystem biodiversity, and influence recreation, fisheries and a host of other ecosystem services (Compton et al. 2011).

Oceans are also sensitive to atmospheric CO_2 enrichment and climate change, with acidification and coral bleaching affecting coral reefs and other vulnerable ecosystems. Chronic stresses, such as nutrient loading, may make it more difficult for corals to adapt to climate impacts (Scavia et al. 2002). Eutrophication and warming, and associated hypoxia and anoxia, can greatly exacerbate ocean acidification because the respiration that drives oxygen consumption produces high levels of dissolved inorganic C, including CO_2 gas. The resulting acidification harms calcifying organisms such as mollusks and some crustaceans (Howarth et al. 2011).

Evaluating risks from nitrogen enrichment and climate change on biodiversity

In order to evaluate the risks from N enrichment and climate change on biodiversity, we must consider both the exposure and the sensitivity of ecosystems or regions to these two drivers. One tool for evaluating the susceptibility of ecosystems to detrimental effects of elevated N deposition is the critical load (CL). A CL is the deposition below which no harmful ecological effect occurs over the long term, according to present knowledge (UBA 2004). Empirical CLs (i.e., determined from experiments or observations along N deposition gradients) for N have been defined for specific areas, such as national parks (Baron 2006; Bowman et al. 2006; Rao et al. 2010). Empirical CLs have also been defined for ecoregions across the US for various responses including biodiversity or responses which could influence biodiversity (such as shifts in N availability, tissue N concentration, responses to secondary stressors, etc.) (Pardo et al. 2011a, b). Exceedance of the CL indicates regions at risk for detrimental effects from N deposition (Fig. 5). When the CL has been exceeded over many years or by a large amount, initial changes in biodiversity are more likely to have already occurred; the impact of additional N deposition may further alter species composition and biodiversity. When the deposition is near the CL, the risk of initial changes in biodiversity may be highest as was reported in the European Nitrogen Assessment (Dise et al. 2011). The extent, degree, and timing of detrimental impact varies by ecoregion and receptor (i.e., fungi, lichens, herbaceous species), but areas of exceedance occur in each ecoregion for which CLs were reported.

The greatest risks to biodiversity from N and climate change might be expected to occur where exceedance is high, climate change will be greatest, and responses are additive or amplifying. For example, in tundra ecosystems in Alaska where increasing temperature is likely to increase N availability further, impacts on biodiversity are likely to accelerate (Chapin et al. 1995; Chapin and Shaver 1996; Shaver et al. 2001). In addition to increases in temperature and precipitation volume, shifts in seasonal patterns in frequency and intensity of precipitation (including drought) may cause significant interactions with N enrichment and, ultimately, impact biodiversity. Given the complexity both in the types of changes in climate and their interactions with N enrichment in various ecosystems and for multiple species, dynamic modeling will be necessary to assess which ecosystems face the highest the risk of detrimental effects.

Summary of risk by regions to climate–N interactions

This section addresses the risk to biodiversity from climate–N interactions, synthesized by region. The climate information is drawn from the 2009 regional climate impacts section of the National Climate Assessment (NCA 2009). The information on N and climate–N interactions is from Table 1, which presents an overview of the climate, N and climate–N impacts in major ecosystems of the US, with corresponding literature.

Northeast

Forests, lakes, wetlands and a number of estuaries dominate this region, along with a high density of urbanization. Reduced snowpack, longer and more frequent summer droughts, higher mean annual temperatures, higher average total precipitation, and more intense storms are expected for the forest and aquatic ecosystems that predominate the northeastern US
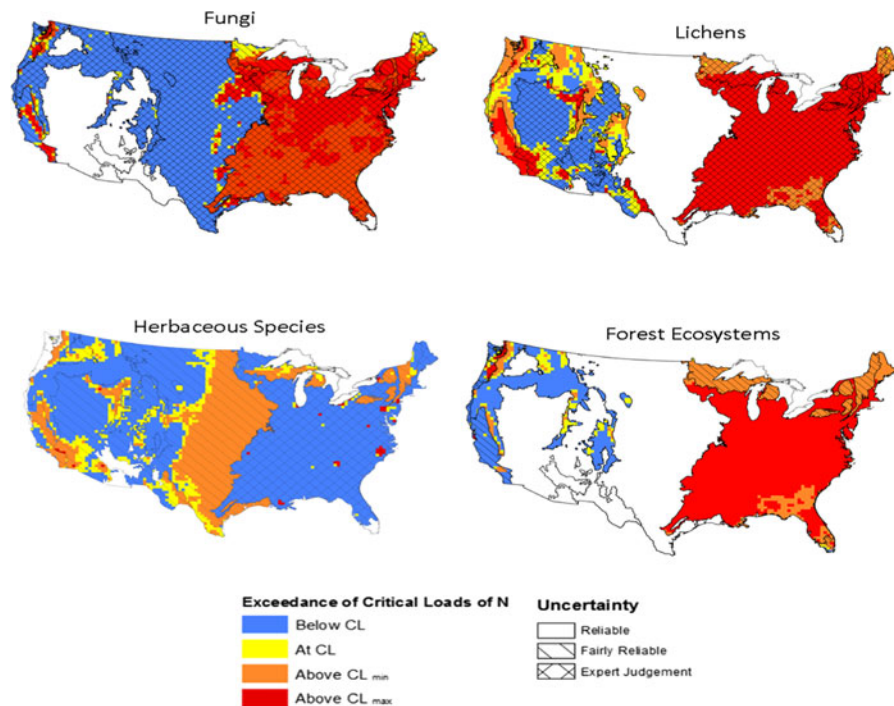
Fig. 5 Map of exceedance of critical load (CL) for nitrogen for mycorrhizal fungi, lichens, herbaceous species and shrubs, and forest ecosystems in the continental US. Exceedance was calculated by subtracting CLs from modeled nitrogen deposition. Exceedance is shown for several categories: (1) no exceedance (below CL), when deposition is lower than the CL range, (2) at CL, when deposition is within ±1 of the CL range, (3) above CL_{min}, when deposition is above the lower end of the CL range, but lower than the upper end of the range, (4) above CL_{max}, when deposition is above the upper end of the CL range. White areas lack data for CL determination. The *hatch marks* indicate increasing level of uncertainty: no *hatch marks* for the most certain "reliable" category, single hatching for the "fairly reliable" category and cross-hatching for the "expert judgment" category (adapted from Pardo et al. 2011b)

(NCA 2009). Fire (which is not common in the Northeast) and pest outbreaks are both expected to increase, impacting species composition. Nitrogen deposition is the highest for this US region due to a higher concentration of transportation and power generation activities. Much of the N deposited is in oxidized rather than reduced form, and remains above the critical load even though N deposition has been declining in recent decades.

Changes in terrestrial biodiversity for this ecoregion are likely slow due to the predominance of trees, but alterations in growth and survival due to N deposition have been reported (Thomas et al. 2010). Changes in understory species and in soil biodiversity due to N deposition may have already occurred in this area (Gilliam 2006; Hurd et al. 1998). Key interactions for the forests in this region include N-driven reductions in freezing tolerance (Schaberg et al. 2002), which will have amplified impacts since the duration

and extent of the protective snow layer is expected to decrease under climate change. Finally, higher and more intense precipitation may exacerbate N-induced nutrient imbalances in terrestrial plants, as more nutrient cations are leached from the rooting zone. Changes in aquatic biodiversity for this ecoregion also have been reported (e.g., Howarth et al. 2011), and will likely continue. Eutrophication of lakes and estuaries will likely be amplified under climate change, with a greater extent and duration of hypoxic events in impacted coastal systems.

Southeast

The Southeastern US is dominated inland by broadleaf and mixed forests that are some of the most diverse in North America, as well as by large coastal wetlands and marshes. Climate in this region is expected to continue to warm especially in the winter, and

continue to get drier especially in the spring and summer months, with more intense storms overall (Karl et al. 2009). Fire, drought, and insect outbreaks are expected to be more prevalent with climate change (NCA 2009). Despite the fact that N deposition levels are lower than in the Northeast, many regions of the Southeast experience N deposition at levels that may affect biodiversity (Pardo et al. 2011a, b).

Nitrogen deposition is more balanced between oxidized and reduced forms compared with the Northeast or Midwest because of the combined influences of industry and agriculture in the Southeast, though the majority still falls as oxidized N. Key interactions for terrestrial ecosystems in this region include a potential increase in susceptibility to drought and pests. Increased aboveground growth in N-limited systems may also make them more prone to fire. The Southeast is not expected to dry to levels more common in co-limited (N and water) environments in the western Great Plains, making N limitation likely to continue, and thus N sensitivity to remain.

Key interactions for aquatic ecosystems include a potential decrease in long-term average N loads from decreased precipitation, punctuated with large synoptic flushes of N from increased storm events and intensities. It is unknown how the impacts from these contrasting factors will play out for aquatic biodiversity. Climate change is expected to result in sea level rise and increased flooding of coastal areas in this region, and the interaction with N may exacerbate eutrophication in these areas. Recent work has also shown that eutrophication may exacerbate coastal acidification in these areas (Cai et al. 2011), illustrating a synergistic interaction between climate and N loads.

Midwest and Great Plains

Rangeland, farmland, and grassland dominate much of this region. Because of the favorable conditions for agriculture, many natural systems have been converted for human use, and only fragmented and dispersed natural habitats remain (Leach and Givnish 1996; Samson and Knopf 1994). The remaining natural ecosystems that are already under stress are anticipated to become warmer and wetter (NCA 2009), which could intensify N limitation and sensitivity to N. Deposition of N in this area is moderate, declining from east to west, and dominated by reduced

forms of N, ammonia (NH_3) and ammonium (NH_4^+), due to the abundance of agriculture. Key interactions for these systems include decreased co-limitation by water and N, and increased preponderance of limitation by N (Clark et al. 2007). This could increase stresses on plant biodiversity from increased plant growth and competition.

Important wetlands and lakes in this region are expected to undergo synergistic interactions between N and climate change, where warmer, wetter conditions could increase nutrient loading to aquatic ecosystems, leading to higher levels of eutrophication and low oxygen conditions. Many wetlands in this region provide important habitats for migrating waterfowl. Forests and alpine systems dominate the western portions of this region in the mountainous areas of Wyoming and Montana. Earlier snowmelt associated with elevated temperatures has been shown to harm some species of wildflowers through increased frost damage (Inouye 2008). Although current N deposition to these regions is generally low, frost damage might be expected to be enhanced with increased N deposition due to increased growth aboveground exposing more tissue to cold stress.

Northwest

Forests generally dominate the Northwestern region with agriculture in many river valleys, and steppe in drylands. Rivers and coastal ecosystems play an important role in the local economy. Elevated temperatures in the Northwest will lead to greater winter precipitation as rain, decreased snowpack, reduced stream flows in the summer, and reduced water availability during peak plant growth periods (Karl et al. 2009). These hydrologic changes are expected to alter aquatic communities and drive declines in fish, especially cold-water species such as salmon. Stream networks are likely to constrict with lower summer water conditions, threatening the integrity of aquatic ecosystems, although increased total precipitation may offset some of these changes.

Inputs of N are lower in the Northwest on average than the Eastern US, though some aquatic and terrestrial ecosystems in the region are stressed in areas dominated by agriculture and industry. For example, increasing N deposition in areas around large cities is already affecting lichen community composition in the Northwest (Geiser et al. 2010). Key

interactions in this region include the increased frost damage from earlier snowmelt combined with N deposition (already observed in the Rockies as described above), greater total precipitation and storm intensities delivering larger amounts of N to aquatic systems, possible shifts in forest tree composition from longer growing seasons and N deposition as observed in the east (Thomas et al. 2010), and increased pest damage from populations feeding on more N-rich tissue in a warmer environment. Changes in climate and in N loading may impact coastal fisheries, although the dynamics of ocean currents play a large role in the coastal ecosystems, and current research indicates that the extent and duration of coastal hypoxic zones are influenced by ocean circulation (Chan et al. 2008). Also, in some Pacific Northwest coastal systems, it has been observed that watershed derived nutrients can acidify coastal waters at a faster rate than atmospheric CO_2 alone (Kelly et al. 2011).

Southwest

Climate change in the forest and desert ecosystems in the Southwestern US is expected to lead to increased temperatures, decreased precipitation, and increased droughts and extreme events (Karl et al. 2009). This will likely make them more susceptible to fire and pests. Nitrogen deposition, although not as extensive by comparison with the east, is high nearer to urban and agricultural areas (Fenn et al. 2003), and will likely contribute to climate-driven increases in fire frequency (through increased grass growth in shrub interspaces) and pest stresses (through increased tissue N). An additional key interaction is air quality, which is already poor in this region. Climate change and increased N will continue to result in high ozone levels in the mountains near large cities in California and other Southwestern cities.

Alaska

Alaska is expected to have large changes in climate, but the changes in N loading are not expected to be significant in the future, except possibly in concentrated areas around cities or ports. The potential impacts related to climate–N interactions are likely to be from alterations of the internal N cycle, for example, increasing decomposition rates, increasing N availability and shifting competitive balances. In

addition, because critical loads are so low for some of these low- biomass systems, small increases in N deposition could result in significant changes (Pardo et al. 2011a, b).

Coasts

Aquatic ecosystems, particularly coastal systems, are at high risk for impacts on biodiversity driven by interacting climate change and N inputs. Warmer conditions and higher nutrients will generally lead to increases in aquatic production, eutrophication and decreased dissolved oxygen levels. Eutrophication of N-limited systems, in turn, will be exacerbated in the warmer conditions with lower water levels. Wetlands and lakes also are at risk for altering biodiversity due to contracting water networks and increased eutrophication. Eelgrass decline has also been associated with high nutrients and eutrophication, and will alter aquatic habitat space and the distribution and abundance of the species that use those areas (Latimer and Rego 2010).

Modeling

Various approaches have been used to estimate changes in biodiversity due to climate change and they typically couple indirect drivers of biodiversity (e.g., population growth, fossil fuel use), direct drivers (e.g., climate, pollution, land-use change), and biodiversity models (e.g., dynamic vegetation models, niche models, and dose–response relationships) (Pereira et al. 2010). Species distribution models (SDMs), that relate field observations to environmental variables, have been widely used to forecast the impacts on biodiversity from a variety of stressors, including climate change. These niche-based models predict the potential distribution of species based on the species' bioclimatic envelope, sometimes integrated with limiting factors of dispersal, disturbance, and resource availability (Guisan and Thuiller 2005). Process-based models, on the other hand, incorporate the underlying mechanisms that influence species response, such as N and C cycling in soils. Some of these models can also simulate changes in ecosystems over time due to changes in temperature and precipitation, making them useful for studying possible responses associated with climate change (Dise et al. 2011).

Linking process-based models to niche-based models may be particularly important for improving forecasts of plant distribution (Keenan et al. 2011). The ForSAFE-VEG model links the dynamic soil biogeochemistry model ForSAFE with the plant response model VEG to forecast changes in plant communities from impact of N deposition and climate change, and has been applied in the EU in Sweden and Switzerland (Sverdrup et al. 2007; Belyazid et al. 2011) and in the US Rocky Mountains (Sverdrup et al. 2012). For a generalized plant community in the US Rocky Mountains, the model suggests that N has exacerbated reductions in biodiversity expected from climate change alone (Fig. 6; Sverdrup et al. 2012). In Britain, the Model of Acidification of Groundwater in Catchments (MAGIC) model (Cosby et al. 2001), which focuses on acid–base relationships but includes an N module, has been linked with a plant niche model to simulate plant community changes with N and climate change (Rowe et al. 2005). Another biogeochemical model, the PnET-BGC (has been used in the US to simulate soil and vegetation dynamics under various scenarios of N and sulfur deposition and climate change (Wu and Driscoll 2010). In addition, the DayCent-Chem (daily version of the CENTURY model) model has been used to simulate daily surface
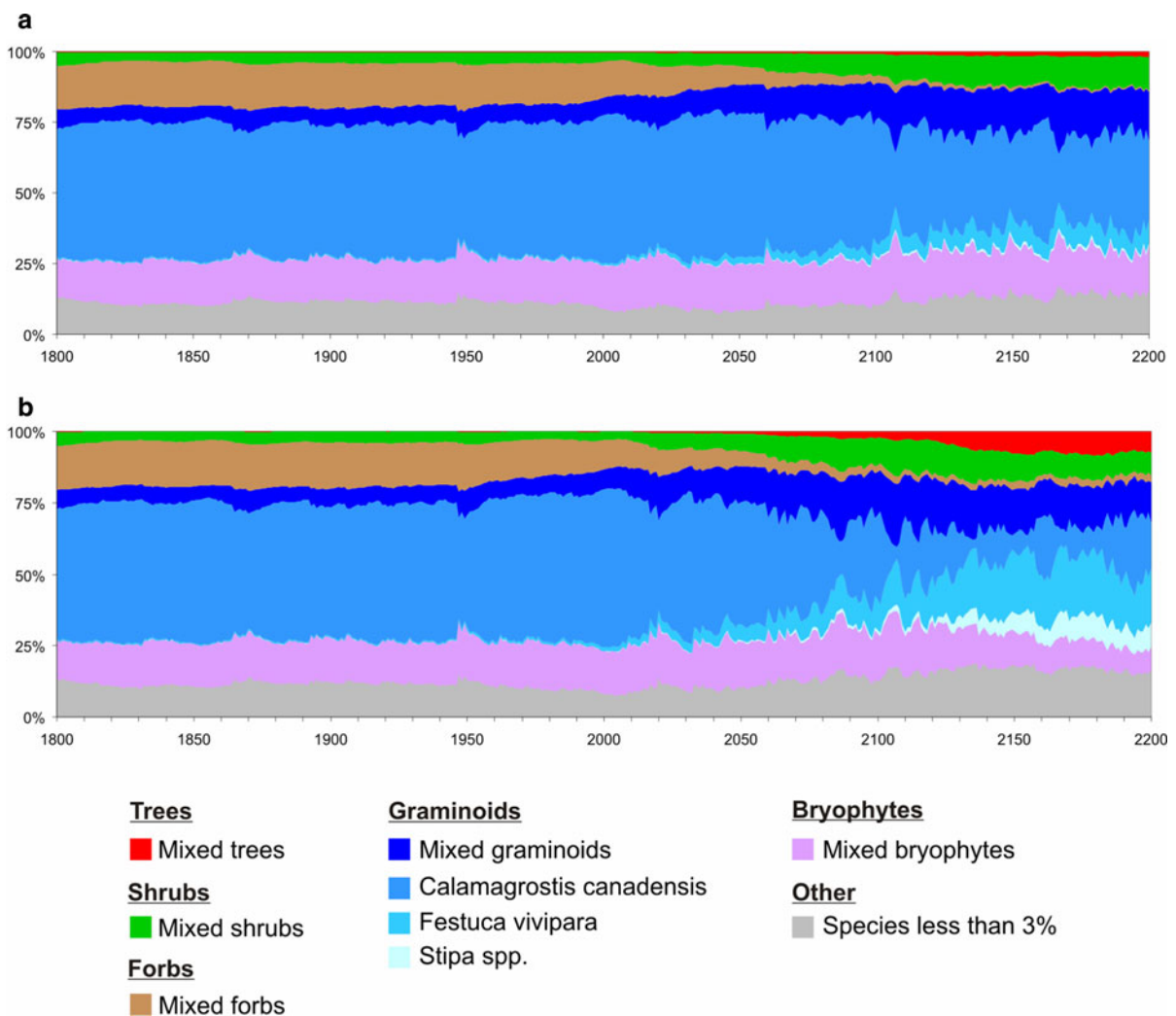
Fig. 6 ForSAFE-VEG model simulations for plant life form coverage based on the IPCC climate change scenario A2 for the Rocky Mountain region and **a** estimated background S and N deposition and **b** elevated future atmospheric N deposition (modified from Sverdrup et al. 2012)

water and ecosystem responses to N and sulfur and climate change (Hartman et al. 2007).

Models are always limited by available data on ecosystem response and by the scale of that data. But ForSAFE-VEG (a model that simulates soil chemistry, C and N cycling, tree growth, geochemistry, and ground vegetation response) and other models show promise as tools to forecast N and climate change interactions, and are likely to be used more widely as the ecosystem response data needed to calibrate the models become available.

Management and policy options for reducing impacts on biodiversity

There are several ways that management and policy may alleviate the interactive effects of climate change and excess N on biodiversity. As a foundation, there must be sufficient understanding of how much and where (1) N is being deposited, and (2) climate is changing. For the former, national monitoring networks (e.g., National Atmospheric Deposition Program—NADP; Clean Air Status and Trends Network—CASTNET) and dynamic atmospheric models (e.g., Community Multi-scale Air Quality—CMAQ), have been developed to generate national estimates of N deposition (Weathers and Lynch 2011These tools are critical in developing action plans to manage impacts on biodiversity. However, there are still significant limitations including sparse coverage nationally especially for remote and mountainous areas, lack of monitoring for some N species altogether (e.g., organic N), and poor sampling or infrequent sampling for some processes (e.g., dry and fog deposition). Other limitations for the models include incomplete process modeling (e.g., cloud deposition, bidirectional N flows) and incomplete calibration (Weathers et al. 2006; Pardo et al. 2011b, Peel et al., this issue). For the latter, the US Global Change Research Program has developed comprehensive reports (in 2000, 2009, and scheduled for 2013) that synthesize the state of knowledge from multiple Agency and non-Agency national and international efforts on how and where climate is changing and expected to change in the future for the US (Karl et al. 2009).

Appropriate actions for managing the interactive impacts on biodiversity from N and climate change depend largely on the dominant mechanism driving biodiversity change. First and foremost is reducing the emissions of N to the environment that are subsequently transported to and deposited on potentially sensitive systems. Several approaches have been proposed (e.g., US EPA 2011) that depend largely on the source of emissions, whether agricultural- or fossil fuel combustion-based. At the other end of the management spectrum are interventions in impacted areas. Reduction of N inputs and the restoration of N and other soil resource conditions will not necessarily guarantee that the original species will return. Species may no longer be present in the degraded habitat or able to disperse there over a fragmented landscape. Seeds of many target grassland species of high biodiversity value are known not to remain viable for more than a few years to a decade in the seed bank (Thompson et al. 1998), suggesting that historical N deposition over the past 50 years could have dramatically altered seed availability to systems thereby necessitating seed addition. This replanting is commonly termed "assisted migration" in the climate literature (IPCC 2007), and may be required for systems where the dominant driver of biodiversity change is climate-induced shifts in range.

In addition to reducing N inputs into ecosystems, several approaches have been proposed to reduce N stores and cycling, including increasing N export through harvesting, turf removal, or fire, increasing N leaching through flushing with aqueous solutions, and decreasing N availability through the addition of C (Bakker and Berendse 1999; Blumenthal et al. 2003; Jordan et al. 2003). Some of these approaches may only redistribute existing Nr rather than removing it such as through denitrification (Galloway et al. 2003). For systems in which N-induced soil acidification dominates, addition of soil amendments (e.g., lime, magnesium) may be used to increase soil pH, inhibit NH_4^+ accumulation, and restore nutrient balances (Bakker and Berendse 1999; Dise et al. 2011). However, aggressive strategies such as biomass removal and soil amendments have limited usefulness because such treatments require periodic application to be effective and are costly and labor intensive, and in some areas may be prohibited because of land protection mandates (e.g., national parks or wilderness) (Fenn et al. 2010).

Because of the significant problems associated with most forms of aggressive intervention management,

reduction of N deposition to ecosystems is the best strategy for long-term success in managing impacts from climate and N deposition on biodiversity (Fenn et al. 2010, 2011; Bobbink et al. 2010). A review of available N mitigation strategies for California concluded that the ideal management option for reducing effects of N excess is to reduce N deposition by improving air quality (Fenn et al. 2010). Reducing N deposition can occur through many policy approaches, including the establishment of critical loads, and through allowing tradable permits for pollution which are slowly removed from the market, thereby reducing total pollution. In many countries including the US, emissions and deposition of nitrogen oxides (NO_x) have decreased dramatically in the past 20 years as a result of regulatory policies (Fenn et al. 2010). However, similar controls for emissions of NH_3 are less prevalent and the proportion of N deposition occurring in reduced forms (NH_x) is increasing in many areas above levels known to have ecological effects on more sensitive taxa (Clarisse et al. 2009; Fenn et al. 2010). This highlights the importance of selecting the appropriate receptor to use when implementing critical loads. The impacts to plant and lichen biodiversity in terrestrial ecosystems occur at lower air pollution levels than impacts on human health, and effects to non-vascular biodiversity occur at lower air pollution levels than effects to vascular biodiversity (Bobbink et al. 2010; Pardo et al. 2011a, b). Thus when air pollution standards are determined primarily or solely by impacts to human health, in many cases sensitive ecosystems and biodiversity will not be effectively protected. Furthermore, the N-induced loss of ecosystem services has serious consequences for human health and well-being (Compton et al. 2011).

Summary and key research needs

Biodiversity is decreasing worldwide and in the US, with serious consequences for ecosystem services including water quality regulation, production of food and fiber, and disease resistance. Although biodiversity losses have been largely driven by land use changes to date, climate change and increases in Nr are recognized as increasingly important drivers of biodiversity. The interactive effects of climate change and N are just beginning to be understood, and effects may vary across ecosystems. In general, N and climate change separately reduce biodiversity in sensitive systems, and together have the potential to cause even greater losses. In summary:

- Nitrogen is a strong driver of biodiversity loss in many types of ecosystems. The effects of climate change are less certain, although there is evidence that changes in precipitation and temperature, increases in drought, floods, and other disturbances can result in simplified, less diverse systems.
- Many areas of the US are now receiving N deposition in excess of critical loads for ecosystem health, including for biodiversity. Some of these areas are also undergoing rapid climate change and are at heightened risk for biodiversity losses from combined N and climate change effects.
- Focused empirical studies are needed to obtain additional response data to changes in N, temperature, precipitation, and CO_2, and the interactions of these stressors in those ecosystems most vulnerable to N and climate change. This response data will improve modeled estimates of future conditions affected by N and climate change interactions.
- Reducing N deposition is likely to be an effective strategy for mitigating climate change impacts on biodiversity.

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