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Nitrogen Pollution Is Linked to US Listed Species Declines

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Nitrogen (N) pollution is increasingly recognized as a threat to biodiversity. However, our understanding of how N is affecting vulnerable species across taxa and broad spatial scales is limited. We surveyed approximately 1400 species in the continental United States listed as candidate, threatened, or endangered under the US Endangered Species Act (ESA) to assess the extent of recognized N-pollution effects on biodiversity in both terrestrial and aquatic ecosystems. We found 78 federally listed species recognized as affected by N pollution. To illustrate the complexity of tracing N impacts on listed species, we describe an interdisciplinary case study that addressed the threat of N pollution to California Bay Area serpentine grasslands. We demonstrate that N pollution has affected threatened species via multiple pathways and argue that existing legal and policy regulations can be applied to address the biodiversity consequences of N pollution in conjunction with scientific evidence tracing N impact pathways.

Keywords: biodiversity, endangered species, eutrophication, nitrogen deposition

Biodiversity loss is a major environmental challenge, with a growing number of recognized drivers that interact in complex ways (Cardinale et al. 2012, Hooper et al. 2012). Habitat destruction, fragmentation, and direct exploitation of species have long been recognized as threats to biodiversity, and most policies for imperiled species (e.g., listed and unlisted species that are in decline) protection are designed with these direct drivers in mind (Sala et al. 2000). Recent climate and atmospheric changes, such as increased temperature, altered precipitation regimes, and increasing nitrogen (N) pollution, have created new threats to biodiversity (Novacek and Cleland 2001, Brook et al. 2008). Establishing the effects of these stressors on vulnerable species and addressing their impacts through existing species protection laws and regulations, such as the Endangered Species Act (ESA), the Clean Air Act (CAA), and the Clean Water Act (CWA), can be challenging. Attribution is hampered by sometimes long and difficult-to-trace chains of causation from climate and atmospheric stressors to impacts on vulnerable species. Nevertheless, it is clear that these emerging threats are contributing globally to ecosystem degradation and affecting a broad array of imperiled species through habitat modification and altered ecological interactions (Vitousek et al. 1997, Porter et al. 2013). Existing laws and policies to protect biodiversity were largely developed before these threats were fully recognized. For example, the ESA was passed in 1973, with major amendments in 1978, 1979, and 1982; the CAA was passed in 1963, with subsequent amendments passed in 1970, 1977, and 1990; and the CWA was passed in 1977. Although the CAA includes both primary standards to protect against adverse health effects and secondary standards to protect against welfare effects, such as damage to crops and vegetation, the secondary standards have historically not been set at levels low enough to protect sensitive plants. The efficacy of existing legal and policy tools (e.g., federal and state regulations, guidance, best management practices, and management strategies) to tackle emerging drivers of imperiled species decline depends on a clear understanding of how and why these emerging threats affect species of concern.

In this article, we focus on establishing the links between N pollution and imperiled biodiversity in the United States. Nitrogen pollution is a prevalent atmospheric and biogeochemical global change driver, with growing effects on terrestrial, aquatic, and coastal ecosystems. Nitrogen pollution and climate change as drivers of species imperilment share characteristics such as complex chains of causation and mechanisms for reducing threats, but climate change has been more explored in the recent literature (Povilitis and Suckling 2010). Moreover, although both are global environmental challenges, N pollution can be more readily addressed within the boundaries of a single nation, region, or watershed, providing opportunities to act on new knowledge within specific areas and with specific benefit to particular species.

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Nitrogen as an emerging biodiversity threat. Nitrogen from human-derived sources is already recognized as a major threat to biodiversity on local, regional, and global scales (Rockström et al. 2009). Agricultural fertilization, the increased production of leguminous crops, and fossil fuel combustion have doubled the amount of global reactive N in terrestrial and aquatic ecosystems (Gruber and Galloway 2008). In the United States, human-derived N inputs are estimated to be fourfold greater than natural N sources (Davidson et al. 2012) and have altered ecosystem productivity, function, and biodiversity (Bobbink et al. 2010, Cleland and Harpole 2010, Baron et al. 2013). The impacts of human-derived N enrichment are ubiquitous in both aquatic and terrestrial ecosystems, and N enrichment is known to affect a wide range of species (Baron et al. 2013, Porter et al. 2013). For example, one-third of US streams and two-fifths of US lakes are moderately to severely affected by excess N inputs (Davidson et al. 2012). Major adverse effects of N enrichment in aquatic systems include harmful algal blooms, hypoxia of fresh and coastal waters, and ocean acidification. At the global scale, increasing N emissions—and subsequently, N deposition—have been projected to occur in most terrestrial regions by 2030 (Dentener et al. 2006), potentially leading to further biodiversity loss in sensitive ecosystems (Sala et al. 2000, Phoenix et al. 2006).

In the past 15 years, understanding has grown of the ecological impacts of human-derived N inputs across taxa and ecosystem types. However, we have limited direct evidence of N pollution as a driver of biodiversity loss (although see Allen and Geiser 2011, Pasari et al. 2011, Chen et al. 2013, Gilliam 2014). Addressing the ecological impacts of and mitigation strategies for N pollution on threatened species requires studies that follow the long chain of causation of the effects of N deposition: the sources of N to ecosystems, the biological responses of organisms to increased N, the changes in ecological interactions in an ecosystem, and the potential for management efforts to minimize the impact on vulnerable species.

In this article, we aim to (a) assess the current threat posed by N to federally protected species in the continental United States and (b) illustrate the complexity in tracing N pollution impacts on federally listed species and the challenges associated with managing such impacts. First, we identify US threatened and endangered species vulnerable to the effects of N pollution by synthesizing federal documentation on the status and threats to species listed or proposed for listing under the federal ESA. We then present a case study of an interdisciplinary approach to tracing the causal chain of N pollution impacts on listed species and addressing the threat of N pollution on a vulnerable ecosystem: California Bay Area serpentine grasslands. As part of this case study, we highlight crucial opportunities for mobilizing existing legal and policy tools to address the N impacts on one listed species and demonstrate how an improved understanding of the ecological mechanisms by which N affects sensitive species could strengthen US policies for controlling N pollution in general.

N impacts on federally listed species

Although the environmental consequences of N pollution in the United States are increasingly well documented (Greaver et al. 2012), many of the direct and indirect effects of N pollution on sensitive species and ecosystems are either poorly understood or insufficiently synthesized for use in decision making. The lists of endangered, threatened, and candidate species protected under the ESA (category definitions found within ESA Section 3), along with associated Fish and Wildlife Service (FWS) and the National Marine Fisheries Service (NMFS) documents detailing the status of and ongoing threats to each of these approximately 1400 species, provide an excellent and internally consistent data set from which to derive and synthesize information about the nature and extent of N pollution impacts on sensitive US biota. For each federally listed species, available knowledge of species biology, habitat needs, and threats are compiled in listing documents, including the petitions for listing, Federal Register notices of proposed and final listing decisions, recovery plans, and five-year review documents. Each of these documents is characterized by relative consistency in the scope of knowledge review for each species and the evidence standard applied in determining whether to include a threat as a factor contributing to species decline.

For a species to be listed as threatened or endangered under the ESA, the species must undergo a detailed accounting of how the species is threatened by one or more of the following mechanisms: (a) the present or threatened destruction, modification, or curtailment of its habitat or range; (b) overuse for commercial, recreational, scientific, or educational purposes; (c) disease or predation; (d) the inadequacy of existing regulatory mechanisms; or (e) other natural or manmade factors affecting its continued existence (ESA Section 4(a)(1), 16 USC 1533). The listing of a species is based on the “best scientific and commercial data available” and is summarized in a required section of the listing documents called “Summary of Factors Affecting the Species,” which provides a detailed review of the impacts on a species within each of the five categories above.

We surveyed the listing documents of all candidate and listed terrestrial and aquatic species (including all vertebrates, invertebrates, and vascular plants) within the continental United States, seeking to determine the extent to which the FWS and the NMFS—the federal agencies in charge of ESA implementation—recognize the effects of N pollution on imperiled species. Specifically, we examined all relevant FWS and NMFS documents available for each listed or candidate species for records of N or nutrient impacts. We gathered the following information for each listed species: species current home range, ecosystem classification, inclusion in a recovery plan, critical habitat designation, cause of species decline, and documentation of N (i.e., atmospheric deposition or aquatic runoff) impacts on species status and designation. We considered a species to be affected by N pollution if the listing documents included one or more of the following words in the “Summary of Factors Affecting the Species": *nitrogen* or any specific form of N (e.g. NH_4, NO_x), *fertilizer* (as long as the documentation did not explicitly mention phosphorus fertilizer), or *eutrophication* (as long as the eutrophication was not explicitly a result of phosphorus pollution). Impacts from factors that may be related to N pollution (e.g., *runoff* or *sedimentation*) but did not explicitly mention N in the documentation were not sufficient to include the species in our list. Furthermore, listing documents tended to describe existing impacts and not potential or projected future impacts on species. Therefore, our estimates are likely conservative, because the number of affected species is likely higher than the ones we identify because of N impacts not reflected in the federal documents, unrecognized indirect impacts of N, and amplifying interactions between N and other environmental factors, such as climate change (Greaver et al. 2012).

We found 78 species formally recognized in federal agency documents as harmed by N loading across aquatic (n = 66) and terrestrial (n = 12) systems within the continental United States (excluding Hawaii and Alaska; tables 1–3, figure 1). Most of the N-affected species are endangered or proposed endangered (n = 55), followed by threatened (n = 20) and candidate (n = 3). Across taxa, most N-affected species are invertebrates (n = 52) such as mollusks and arthropods (table 1), followed by vertebrates (fish, amphibians, and reptiles; n = 18; table 2), and plants (n = 8; table 3). There were no N-threatened mammals mentioned. However, there were species in all taxonomic groups, including mammals, which were noted to be indirectly affected by factors associated with N pollution. For example, the endangered West Indian manatee (*Trichechus manatus*) is affected by harmful red tide algal blooms, which can be a result of inorganic N pollution (Camargo and Alanzo 2006).

We spatially categorized the N-affected species by state within an FWS Region: Pacific Region 1 (Idaho, Oregon, Washington), Southwest Region 2 (Arizona, New Mexico, Oklahoma and Texas), Great Lakes–Big Rivers Region 3 (Illinois, Indiana, Iowa, Michigan, Missouri, Minnesota, Ohio, and Wisconsin), Southeast Region 4 (Alabama, Arkansas, Florida, Georgia, Kentucky, Louisiana, Mississippi, North Carolina, South Carolina, and Tennessee), Northeast Region 5 (Connecticut, Delaware, Maine, Maryland, Massachusetts, New Hampshire, New Jersey, New York, Pennsylvania, Rhode Island, Vermont, Virginia, and West Virginia), Mountain–Prairie Region 6 (Colorado, Kansas, Montana, North Dakota, Nebraska, South Dakota, Utah, and Wyoming), and Pacific Southwest Region 8 (California and Nevada).

The majority of N-affected species are located in the Southeast (n = 53, FWS Region 4), with very few species located in Midwest/Mountain regions (n = 3, FWS Region 6; figure 1). Generally, affected species are not confined to areas with historically high N pollution, such as the Northeast (n = 14, FWS Region 5). This is likely due to several factors, including multiple N impact pathways that are dispersed across large spatial scales and not typically accounted for in recent analyses (Sobota et al. 2013), species that are affected even at relatively low levels of N pollution and therefore not correlated with the magnitude of N pollution, and high concentrations of geographically restricted taxa in US regions with relatively low N pollution.

Pathways of N impact on species

We grouped the nature of N effects on surveyed species into the following four categories: (1) direct toxicity or lethal effects of N, (2) eutrophication lowering dissolved oxygen levels in water or causing algal blooms that alter habitat by covering up substrate, (3) N pollution increasing nonnative plant species that directly harm a plant species through competition, and (4) N pollution increasing nonnative plant species that indirectly harm animal species by excluding their food sources. Here, we highlight specific examples of each N impact pathway on listed species.

Direct toxicity or lethal effects of N. At least nine species in our survey are directly affected by toxic or lethal N effects. This pathway primarily affected species of freshwater mussels (table 1), although direct toxicity was also a potential threat for two amphibian species (*Anaxyrus californicus* and *Eurycea tonkawae*; table 2) and one plant species (*Hackelia venusta*; table 3). Although direct toxicity experiments are rare in the literature, evidence confirms that N deposition can directly harm sensitive species via several mechanisms. Atmospheric N compounds can directly affect plant nutrient-uptake mechanisms, leading to toxicity and negative consequences for growth and photosynthesis in higher plants and lower plants such as mosses (Pearson and Stewart 1993). Inorganic N pollution is also highly toxic to aquatic species such as fish and amphibians, impairing their ability to survive, grow, and reproduce, and may be a contributing factor to the observed global decline of amphibians (Shinn et al. 2008, Johnson et al. 2010). For example, NH_3 toxicity in fish and invertebrates may occur via asphyxiation, reduction in blood oxygen–carrying capacity, disruption of osmoregulatory activity in the liver and kidneys, and repression of the immune system, leading to increased disease susceptibility (Camargo and Alonso 2006, Grizzetti et al. 2011). However, the toxic concentration of NH_3 changes with water pH, water temperature, and the period of exposure. Ammonia in neutral or slightly acidic water is less toxic than when in basic water. Similar toxic effects of nitrite and nitrate have been seen in fishes and crayfishes, although certain freshwater crustaceans, insects, and fishes are more sensitive than seawater organisms because of the ameliorating effects of higher water salinity and chloride ion concentration. The toxicity of these pollutants is also dependent on the period of exposure and chloride concentration (Camargo et al. 2005).

A recent US Environmental Protection Agency report (EPA 2013) reviewed acute and chronic ammonia toxicity data for numerous fish, invertebrate, and amphibian species, with emphasis on freshwater unionid mussels and nonpulmonate snails. The report recommended that a single

Table 1. A list of the federally listed invertebrate species documented as impacted by reactive nitrogen (N).

Scientific name	Common name	Status	Taxonomic group	FWS region	N impact pathway
Euphydryas editha bayensis	Bay checkerspot	T	IV (insect)	8	5
Pseudanophthalmus paulus	Nobletts Cave beetle	C	IV (insect)	4	2, 3
Acropora cervicornis	Staghorn coral	T	IV	4	3
Acropora Palmata	Elkhorn coral	T	IV	4	2, 3
Alasmidonta heterodon	Dwarf wedgemussel	E	IV	5	2, 3
Campeloma decampi	Slender campeloma	E	IV	4	2, 3
Cumberlandia monodonta	Spectacle case	E	IV	3, 4, 5	1, 2, 3
Cyprogenia stegaria	Fanshell	E	IV	3, 4, 5	2
Elimia crenatella	Lacey elimia	T	IV	4	2, 3
Elimia melanoides	Black mudalia	C	IV	4	2
Elliptio chipolaensis	Chipola slabshell	T	IV	4	2
Elliptio steinstansana	Tar River spinymussel	E	IV	4	2, 3
Elliptoideus sloatianus	Purple bankclimber	T	IV	4	1, 2
Epioblasma brevidens	Cumberlandian Combshell	E	IV	4, 5	1, 2, 3
Epioblasma capsaeformis	Oyster mussel	E	IV	4	1, 2
Epioblasma florentina curtisi	Curtis pearlymussel	E	IV	4	2, 3
Epioblasma obliquata perobliqua	White catspaw	E	IV	3	2
Epioblasma othcaloogensis	Southern acornshell	E	IV	4	2, 3
Epioblasma penita	Southern combshell	E	IV	4	2, 3
Epioblasma torulosa gubernaculum	Green blossom	E	IV	4, 5	1, 2, 3
Fusconaia burkei	Tapered pigtoe	T	IV	4	2, 3
Fusconaia cuneolus	Finerayed pigtoe	E	IV	4, 5	2, 3
Fusconaia escambia	Narrow pigtoe	T	IV	4	2, 3
Fusconaia rotulata	Round ebonyshell	E	IV	4	2, 3
Hamiota australis	Southern sandshell	T	IV	4	2, 3
Lampsilis altilis	Finelined pocketbook	T	IV	4	2, 3
Lampsilis higginsii	Higgins eye	E	IV	3	1, 2, 3
Lampsilis powellii	Arkansas fatmucket	T	IV	4	2
Lampsilis virescens	Alabama lamp mussel	E	IV	4	2
Lanx sp. 1	Banbury Springs limpet	E	IV	1	2, 3
Leptodea leptodon	Scaleshell mussel	E	IV	3, 4, 6	2, 3
Leptoxis ampla	Round rocksnail	T	IV	4	2, 3
Physa natricina	Sanke River physa snail	E	IV	1	2
Plethobasus cicatricosus	White wartyback	E	IV	4	1
Plethobasus cooperianus	Orangefoot	E	IV	3, 4, 5	2
Plethobasus cyphyus	Sheepnose	E	IV	3	2, 3
Pleurobema clava	Clubshell	E	IV	3, 4	2
Pleurobema curtum	Black clubshell	E	IV	4	3
Pleurobema marshalli	Flat pigtoe	E	IV	4	2, 3
Pleurobema pyriforme	Oval pigtoe	E	IV	4	2
Pleurobema strodeanum	Fuzzy pigtoe	T	IV	4	2, 3
Pleurobema taitianum	Heavy pigtoe	E	IV	4	2, 3
Pleurocera foreman	Rough hornsnail	E	IV	4	2, 3
Popenaias popeii	Texas hornshell	C	IV	2	2
Ptychobranchus jonesi	Southern kidneyshell	E	IV	4	2, 3
Pyrgulopsis ogmorhaphe	Royal marstonia	E	IV	4	2, 3
Pyrgulopsis pachyta	Armored snail	E	IV	4	2
Quadrula cylindrica	Rabbitsfoot	E	IV	3, 4, 5	1, 2, 3
Quadrula intermedia	Cumberland	E	IV	4, 5	2, 3
Villosa choctawensis	Choctaw bean	E	IV	4	2
Villosa fabalis	Rayed bean	E	IV	3, 5	1, 2, 3
Villosa perpurpurea	Purple bean	E	IV	4, 5	1, 2, 3

Note: The pathways of N impacts to species are grouped into the following five categories: 1, direct toxicity or lethal effects of N; 2, eutrophication lowering dissolved oxygen levels; 3, eutrophication causing algal blooms that alter habitat by covering up substrate; 4, N pollution increasing nonnative plant species, directly harming a species through competition; and 5, N pollution increasing nonnative plant species, indirectly harming species by excluding their food sources. The listed species-status categories include candidate (C), endangered (E), proposed endangered (PE), and threatened (T). The US Fish and Wildlife Service (FWS) Regions include the Pacific Region (1), the Southwest Region (2), the Great Lakes Big River Region (3), the Southeast Region (4), the Northeast Region (5), the Mountain Prairie Region (6), the Alaska Region (7), and the California and Nevada Region (8).

Table 2. A list of the federally listed vertebrate species documented as impacted by reactive nitrogen (N).

Scientific name	Common name	Status	Taxonomic group	FWS region	N impact pathway
Anaxyrus californicus	Arroyo toad	E	A	8	1
Eurycea tonkawae	Jollyville plateau	PE	A	2	1
Acipenser oxyrinchus	Atlantic sturgeon	E	F	4, 5	2, 3
Chasmistes brevirostris	Shortnose sucker	E	F	1, 8	2, 3
Chasmistes cujus	Cui-ui	E	F	8	2
Cottus sp. 8	Grotto sculpin	PE	F	3	2
Crystallaria cincotta	Diamond darter	PE	F	5	2, 3
Deltistes luxatus	Lost River sucker	E	F	1, 8	2
Etheostoma chermocki	Vermilion darter	E	F	4	3
Etheostoma etowahae	Etowah darter	E	F	4	2, 3
Etheostoma moorei	Yellowcheek darter	E	F	4	2, 3
Gasterosteus aculeatus williamsoni	Unarmored threespine stickleback	E	F	8	2
Notropis buccula	Smalleye shiner	PE	F	2	3
Notropis girardi	Arkansas River shiner	T	F	2, 4, 6	2
Noturus placidus	Neosho madtom	T	F	2, 3, 6	2
Percina aurolineata	Goldline darter	T	F	4	2
Chelonia mydas	Green turtle	E	R	1, 4	5
Gopherus agassizii	Desert Tortoise (Sonoran population)	T	R	2	5

Note: The abbreviations for pathways of N impacts to species, listed species categories, and FWS Regions are defined in table 1.

Table 3. A list of the federally listed plant species documented as impacted by reactive nitrogen (N).

Scientific name	Common name	Status	Taxonomic group	FWS region	N impact pathway
Arenaria paludicola	Marsh sandwort	E	P	8	3
Astragalus tener var. titi	Coastal dunes milk-vetch	E	P	8	4
Clarkia franciscana	Presidio clarkia	E	P	8	4
Hackelia venusta	Showy stickseed	E	P	1	1, 4
Halophila johnsonii	Johnson's sea grass	T	P	4	2, 3
Helonias bullata	Swamp pink	T	P	4, 5	4
Paronychia chartacea	Paper-like whitlow wort	T	P	4	4
Potamogeton clystocarpus	Little aguja pondweed	E	P	2	2

Note: The abbreviations for pathways of N impacts to species, listed species categories, and FWS Regions are defined in table 1.

national acute and a single national chronic water-quality criterion should be applied to all US waters. Surveyed species identified as most sensitive in the acute data set included the oyster mussel (*Epioblasma capsaeformis*) and Higgins eye (*Lampsilis higginsii*), both federally endangered (table 1). The federally endangered Lost River sucker (*Deltistes luxatis*) was identified as a sensitive species in both the acute and chronic data sets (table 2).

Eutrophication (lower dissolved-oxygen levels, algal blooms, and habitat alteration). The large majority of N-affected species on the ESA list are threatened by eutrophication-related factors (n = 67), such as low dissolved-oxygen levels, algal blooms leading to habitat alteration, or both (tables 1–3). Freshwater ecosystems are particularly vulnerable to these indirect effects of N deposition. Increased N leads to shifts in species composition of primary producers, increased producer biomass and organic matter sedimentation, and reductions in dissolved oxygen, water clarity, and light availability that alters the habitat and trophic dynamics of aquatic species (Smith 2003, Camargo and Alonso 2006). The limited dispersal ability of freshwater invertebrates such as mussels and crustaceans makes them particularly vulnerable to these impacts from nutrient deposition (Master et al. 2000, Camargo and Alonso 2006). Particular species traits are often associated with vulnerability to specific drivers (Zavaleta et al. 2009), and it appears that dispersal ability may influence species vulnerability to the harmful effects of N deposition in both terrestrial and aquatic ecosystems.

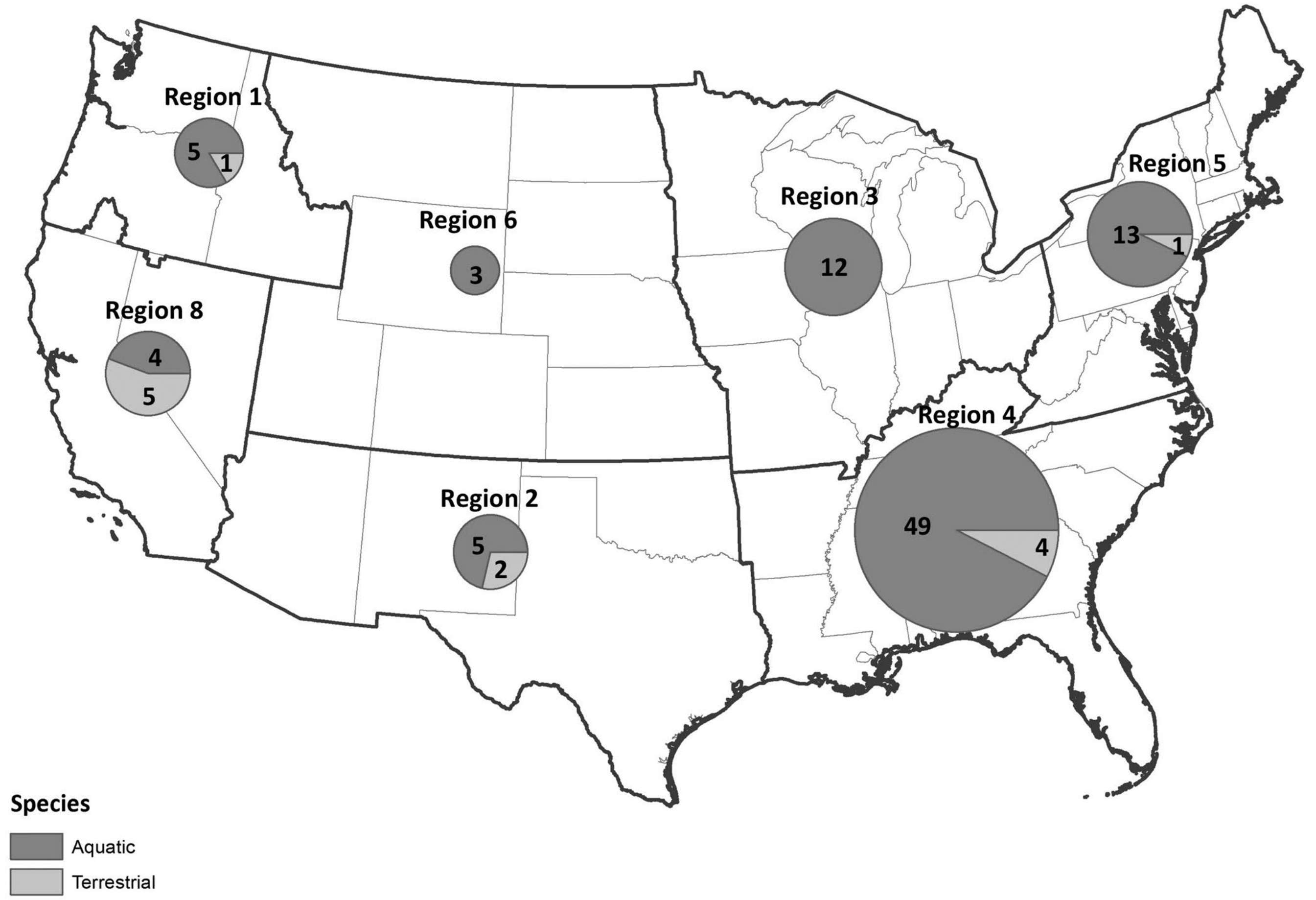

Figure 1. A Fish and Wildlife Service (FWS) Regional Map of the continental United States, with the relative magnitude and distribution of federally listed plant and wildlife species (terrestrial versus aquatic) documented as impacted by nitogen (N, from atmospheric deposition or aquatic runoff).

N pollution increasing nonnative plant species, directly harming a species through competition. Five federally listed plant species (*Astragalus tener var. titi*, *Clarkia franciscana*, *Hackelia venusta*, *Helonias bullata*, and *Paronychia chartacea*) were directly harmed through competition with a nonnative species (table 3). For example, *C. franciscana* is a native species in California serpentine grasslands that, like many native serpentine plants, is outcompeted by nonnative annual grasses (box 1; Harrison and Viers 2007). Increasing levels of N pollution in many nutrient-limited ecosystems may affect native species via several mechanisms, including interspecific competition and changes in interactions with herbivores and pathogens (Gilliam 2014). These community alterations can transform species composition by creating environmental conditions more favorable for faster-growing plants, such as exotic grasses, than for native plants that are adapted to nutrient-deficient soils (Bobbink et al. 2010, Gilliam 2014). Such a shift in resource availability may be the primary mechanism controlling invasive establishment and persistence in many ecosystems (Davis and Pelsor 2001, Ochoa-Hueso et al. 2011). Researchers have investigated the effects of N pollution on competition between native and exotic species in a wide variety of systems (Grime 1973, Pennings et al. 2005, Pfeifer-Meister et al. 2008, Abraham et al. 2009, Bobbink et al. 2010, Vallano et al. 2012). However, both the role of N pollution and the mechanisms underlying the successful invasion of exotic plant species require more study to reveal the full extent of N impacts on invasion-mediated species declines.

N pollution increasing nonnative plant species, indirectly harming native animal species by excluding their food sources. Although only three listed species—the Bay checkerspot butterfly (*Euphydryas editha bayensis*), green turtle (*Chelonia mydas*), and desert tortoise (*Gopherus agassizii*)—were documented as harmed by a loss of food availability as a consequence of competitive exclusion, this pathway is also the most indirect and difficult to assess. For example, short-term experimental studies have documented N limitation and N effects on food availability for the Bay checkerspot butterfly and native–exotic plant competitive outcomes in Bay Area serpentine grasslands (box 1; Huenneke et al. 1990, Weiss 1999, Vallano

Box 1. Is N deposition damaging critical habitat for a listed butterfly? Understanding and addressing indirect N threats to protected biodiversity.

The diversity of the nitrogen (N) impact pathways, affected habitats, and life-history characteristics of vulnerable species makes it difficult to generalize about the effects of N on vulnerable species and ecosystems. The most challenging cases, however, involve the indirect effects of N on whole ecosystems over long time scales and ultimately habitat alteration for a protected species.

Nitrogen deposition due to increasing fossil-fuel emissions in the San Francisco Bay Area contributes to the recent invasion of nutrient-poor, edaphically defined serpentine grasslands by nonnative annual grasses (e.g., *Festuca perennis*, *Bromus hordeaceus*; Weiss 1999). These invaders are in turn displacing rare native and endemic plant species, including the larval host plants and adult nectar sources for the federally listed Bay checkerspot butterfly (BCB; *Euphydryas editha bayensis*; Weiss 1999).

The chain of causation linking N deposition to declines in the butterfly is long and complex. However, its establishment is crucial for understanding how to conserve threatened species and provides the basis for effective action. The demonstration of harm to the BCB requires evidence linking regional increases in atmospheric N pollution to local inputs in serpentine systems, to accumulation in those systems, to changes in plant species composition and biomass, to declines in the host plant, and finally—and crucially for conservation and policy strategy—to declines in BCB populations (figure 2).

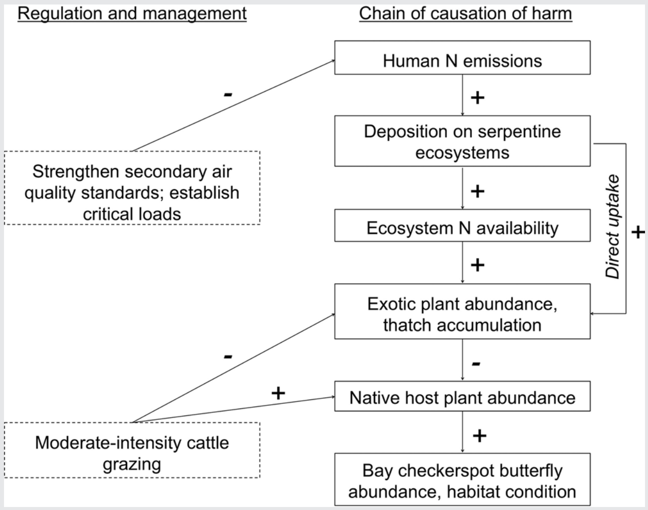

Figure 2. The chain of causation of nitrogen (N) emissions on the federally threatened Bay checkerspot butterfly (BCB), including the existing management strategies and necessary regulatory changes to mitigate the impacts of N on the BCB. Plus and minus signs denote the direction of the response of each component of the system to changes in the previous component.

1. Evidence of increasing N in serpentine grasslands

The San Francisco Bay Area generally experiences chronic low levels of atmospheric N deposition but includes several hotspots of elevated N deposition in areas located downwind of large and expanding urban centers (Fenn et al. 2003). Although contributions from NO_x emissions have declined in recent years, increased NH_3 emissions from combustion and agricultural operations are likely having a more substantial impact on ecosystems (Bishop et al. 2010).

2. The effects of N on current BCB habitat

The effects of N additions in serpentine grasslands are fairly well documented in field fertilization studies. The impacts of high levels of N fertilization include declines in the abundance of *P. erecta*, the BCB's host plant (Koide et al. 1988), increases in invader aboveground biomass (Koide et al. 1988, Huenneke et al. 1990), and increases in invasion and biomass leading to the dominance by exotics of formerly native-dominated patches (Huenneke et al. 1990). Realistic increases in N have also led to differences in microbial activity and N cycling (Esch et al. 2013). Likewise, Vallano and colleagues (2012) documented increases in invader biomass and invader competitive dominance over *P. erecta* under N addition in a controlled growth-chamber study.

3. The efficacy and consequences of management strategies

Grazing by cattle is the dominant management strategy implemented to mitigate the effects of exotic species on BCB habitat (Weiss 1999). Moderate intensity grazing has been shown experimentally to be an effective management tool for reducing invasive grass cover under current levels of N deposition (Pasari et al. 2014, Beck et al. 2015). Grazing reduced exotic cover and increased the stability of native species richness and cover across years, maintaining a more consistent food supply for the BCB in this inherently heterogeneous system (Beck et al. 2015). However, the impacts of grazing were not universally positive for all native species. Some native species (primarily native grasses) were negatively affected by grazing, and variability in grazing intensity influenced the community and ecosystem response to grazing within years (Esch et al. 2013, Pasari et al. 2014). Grazing is clearly the best management tool currently available to manage serpentine ecosystems and has been used to successfully maintain BCB habitat for over three decades. However, because grazing only addresses the proximate impacts of increased N deposition, it is an incomplete solution to the problem. Policy interventions are necessary to curb N emissions and therefore reduce the impact of N on threatened species in this system to levels below established critical loads.

Tzankova and colleagues (2011) demonstrated that the documented chain of causation of the effects of N on BCB reproduction brings a legal ability to argue that N deposition is causing ESA-prohibited harm, take, and jeopardy of federally listed wildlife. In the BCB case, this effectively means that the species-protection provisions of the ESA might be used to trigger an otherwise unlikely rethinking of the current federal and state ambient air–quality standards and emission-control decisions that determine the amount of reactive N deposited on the BCB's serpentine grassland habitat—the kind of rethinking necessary to ensure protection of the BCB and other threatened species.

et al. 2012), but recent studies have also begun to reveal long-term N accumulation via deposition to serpentine plants and soils, as well as to quantify the fates and effects of this additional N on species loss, biodiversity, and ecosystem processes (box 1; Ochoa-Hueso et al. 2010, Esch et al. 2013, Pasari et al. 2014, Beck et al. 2015). The extent of the impacts of N accumulation on species interactions is likely greater than currently recognized, and additional research is needed to determine how N deposition impacts trophic relationships in threatened and endangered species.

Addressing the threat of N pollution

We show that the recognized threat to federally protected species from N pollution is substantial (at least 78 listed taxa harmed), geographically widespread, and posed by a variety of pathways linking N to direct organismal harm in some cases and habitat alterations leading to population decline in many others. Given the existence and nature of both federal protections for listed biodiversity and regulatory standards for N as a pollutant, an opportunity and a need exist to update pollution thresholds to fulfill the federal regulatory mandate to protect listed animals and plants.

We next provide an example of how even in cases with the most indirect links between N pollution and species decline, a chain of causation can be established through literature review combined with targeted experimental and observational studies on a timescale of one to a few years and used as the basis for effectively leveraging regulatory tools (see box 1). The links from N deposition to declines in a listed species, the Bay Checkerspot butterfly, are complex but possible to substantiate through a range of investigations at the atmosphere–ecosystem interface and the intersections of ecosystem, community, and population ecology, involving both historical and comparative approaches.

For instance, both quantitative and qualitative knowledge of the sensitivity of listed species and their habitat to additional N deposition are required for the calculation of ecosystem critical N loads where listed plant and wildlife species are found. The concept of identifying a “critical load” (defined as the level of input of a pollutant below which no harmful ecological effect occurs over the long term; Pardo et al. 2011) and setting thresholds for ecosystems is increasingly used to assess the status of vulnerable ecosystems in response to atmospheric N deposition. To date, critical loads have been designated for many ecosystems, but the links between these identified thresholds and habitat alteration are uncertain (Fenn et al. 2010, Pardo et al. 2011). The potential loss of biodiversity is highly sensitive to the degree to which ecosystems respond to N deposition (Clark et al. 2013). Therefore, accurate assessments of critical loads are necessary to ensure protection of biodiversity.

Thresholds for both atmospheric and aquatic N inputs need to be set in sensitive ecosystems on the basis of integration of observational, experimental, and modeling studies on N pollution at realistic levels (chronic low N inputs) combined with observations on N loading and accumulation along multiple scales and management conditions (Bobbink et al. 2010, Davidson et al. 2012, Baron et al. 2013). For example, in California serpentine grasslands, the current estimated *CL* (defined as the level above which nonnative grasses invade and replace native forbs) is 6 kilograms N per hectare per year (Weiss 1999, Fenn et al. 2010), approximately half the rate of current levels of N deposition found in the habitat of the threatened Bay Checkerspot Butterfly (Weiss 1999). The body of knowledge needed to make this determination included the synthesis of several scientific studies across disciplines (atmospheric chemistry, ecology, and biogeochemistry), scales, and techniques. Ecological knowledge regarding species impacts of N inputs, including population and possibly individual-level impacts of the habitat modifications caused by excessive N loading, is necessary for accurately updating N thresholds, effective conservation, and science policy (box 1).

Nitrogen pollution is only one widespread form of environmental change that interacts with other long-standing and emerging stressors, such a climate change, with a high likelihood of exacerbating declines in populations of threatened species. A need persists to look comprehensively at other drivers and the interactions among them, because many more species and ecosystems, both listed and not, are likely affected both by N pollution itself and its interactions with other threats. Interdisciplinary science-policy efforts are more necessary than ever to tackle these more complex—but very widespread—challenges to biodiversity conservation and ecosystem stewardship.

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