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CONCEPTS, REVIEWS AND SYNTHESSES

Ecological consequences of the expansion of N₂-fixing plants in cold biomes

Erika Hiltbrunner · Rien Aerts · Tobias Bühlmann · Kerstin Huss-Danell · Borgthor Magnusson · David D. Myrold · Sasha C. Reed · Bjarni D. Sigurdsson · Christian Körner

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Abstract Research in warm-climate biomes has shown that invasion by symbiotic dinitrogen (N₂)-fixing plants can transform ecosystems in ways analogous to the transformations observed as a consequence of anthropogenic, atmospheric nitrogen (N) deposition: declines in biodiversity, soil acidification, and alterations to carbon and nutrient cycling, including increased N losses through nitrate leaching and emissions of the powerful greenhouse gas nitrous oxide (N₂O). Here, we used literature review and case study approaches to assess the evidence for similar transformations in cold-climate ecosystems of the boreal, subarctic and upper montane-temperate life zones. Our assessment focuses on the plant genera *Lupinus* and *Alnus*, which have become invasive largely as a consequence of deliberate

introductions and/or reduced land management. These cold biomes are commonly located in remote areas with low anthropogenic N inputs, and the environmental impacts of N₂-fixer invasion appear to be as severe as those from anthropogenic N deposition in highly N polluted areas. Hence, inputs of N from N₂ fixation can affect ecosystems as dramatically or even more strongly than N inputs from atmospheric deposition, and biomes in cold climates represent no exception with regard to the risk of being invaded by N₂-fixing species. In particular, the cold biomes studied here show both a strong potential to be transformed by N₂-fixing plants and a rapid subsequent saturation in the ecosystem's capacity to retain N. Therefore, analogous to increases in N deposition, N₂-fixing plant invasions must be deemed significant threats to biodiversity and to environmental quality.

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E. Hiltbrunner (✉) · T. Bühlmann · C. Körner
Department of Environmental Sciences, Institute of Botany,
University of Basel, Schönbeinstrasse 6, 4056 Basel, Switzerland
e-mail: erika.hiltbrunner@unibas.ch

R. Aerts
Department of Ecological Science, VU University Amsterdam,
De Boelelaan 1085, 1081 HV Amsterdam, The Netherlands

K. Huss-Danell
Department of Agricultural Research for Northern Sweden,
Swedish University of Agricultural Sciences,
90183 Umeå, Sweden

B. Magnusson
Icelandic Institute of Natural History, Urriðahóltsstræti 6-8,
212 Garðabær, Iceland

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D. D. Myrold
Department of Crop and Soil Science, Oregon State University,
Agric Life Sci Bldg 3017, Corvallis, OR 97331-7306, USA

S. C. Reed
U.S. Geological Survey, Southwest Biological Science Center,
2290 S. West Resource Blvd, Moab, UT 84532, USA

B. D. Sigurdsson
Agricultural University of Iceland, Hvanneyri, 311 Borgarnes,
Iceland

N₂-fixing invaders in cold climate ecosystems

Atmospheric nitrogen (N) deposition originating from agricultural and industrial sources, and as a by-product of fossil fuel burning, has been a matter of significant ecological concern from the 1950s onwards (e.g., Sutton et al. 2011). High anthropogenic N inputs result in declines in biodiversity, increases in soil acidification, eutrophication, and nitrate in drinking water (e.g., Magill et al. 2004; Stevens et al. 2004; Brookshire et al. 2007; Pardo et al. 2011). Currently, on a global scale, there is more reactive N created and released by humanity than the total amount of biologically-fixed N (Vitousek et al. 1997; Galloway et al. 2004, 2008; Vitousek et al. 2013), and the highest amounts of deposition occur in densely populated industrialized countries with intensely managed agriculture (Galloway et al. 2004). The effects of this increase in N are evident from the tropics (Hietz et al. 2011) to the poles (Holtgrieve et al. 2011). However, there is less awareness regarding high N inputs into ecosystems resulting from the invasion of either non-native N₂-fixing plants or from expansion of native N₂-fixing species into ecosystems that experienced unsustainable land use.

Here, we use the term ‘invasive’ as a more neutral ecological characterization (sensu Colautti and MacIsaac 2004; Lockwood et al. 2013). We define invasion as an extraordinary range expansion, irrespective of the origin of a taxon. A highly invasive species rapidly becomes widespread and dominant, and suppresses the species of the invaded community. Other non-indigenous species also become established, but remain localized and numerically rare, mainly due to environmental and/or community interactions (e.g., lacking freezing resistance, pollinators, etc.) and are categorized as non-invasive. Invasive species are considered a major threat to the environment, because they alter habitats, negatively affect ecosystem functions and services, and cause substantial economic losses in agriculture, forestry, fisheries, etc. (McGinley 2012). Thus, we propose here that invasive species moving or expanding into areas where they were previously absent or rare do not necessarily need to originate from other continents or regions to represent an invasion threat. As will be shown, even species native to a given region may become invasive in the above sense under certain conditions. ‘Invasion’ also does not inevitably imply an early successional stage such as river banks, but refers to a rapid and massive, regularly monospecific ‘take over’ of an ecosystem. By all measures, such invasions are directly or indirectly caused by anthropogenic drivers and are not considered part of a natural succession process.

The effects of invasion by N₂-fixing plants can be equivalent to a large, consistent source of N deposition, and the impact of these invasions can be similar or even larger than that of massive atmospheric N deposition, with significant

threats to biodiversity (McQueen et al. 2006; Scherer-Lorenzen et al. 2007). Symbiotic N₂ fixation can introduce very large amounts of reactive N into terrestrial ecosystems. For example, N₂ fixation rates of >100 kg N ha⁻¹ year⁻¹ have been suggested for multiple biomes (Cleveland et al. 1999). Nevertheless, to our knowledge, synthetic assessments of N₂-fixer invasions and their ecological consequences have been performed only for warmer climates. Indeed, awareness of the negative impact of invasive N₂-fixing species largely originates from (1) the publicity surrounding the introduced N₂-fixing actinorhizal plant *Myrica faya*, which is potentially destroying native Hawaiian *Metrosideros* forests (Vitousek et al. 1987); (2) the legume *Ulex europaeus* expansion, originally deliberately brought to New Zealand (Magesan et al. 2012); and (3) invasions by symbiotic N₂-fixing *Acacia* in warm-temperate to subtropical rangelands around the globe (Richardson et al. 2000). However, there are substantial expansions of native N₂-fixing species and invasion issues associated with introduced N₂-fixing species in cooler climates of the Holarctic.

Species of genera such as *Alnus*, *Hippophaë*, *Myrica* and *Lupinus* have either been introduced and become invasive or are native and have started a large-scale expansion in many parts of the temperate, boreal and subarctic world (David 2010; Fremstad 2010; Magnusson 2010). In part, this success relates to the common presence of compatible symbiotic bacteria (*Rhizobium*, *Frankia*) in these cool habitats. Richardson and co-workers (2000) showed that *Alnus* (alder) nodulated wherever transplants were grown throughout the world, suggesting that *Frankia* bacteria compatible with alder are cosmopolitan. N₂ fixation is clearly not restricted to warm environments, and it seems that there are few habitats where symbiotic N₂ fixation cannot take place (Bordeleau and Prévost 1994). Thus, while some incubation data show that cooler temperatures can reduce N₂ fixation rates in the laboratory (Houlton et al. 2008), the success and high fixation rates of symbiotic N₂-fixing plants observed in the field underpin that N₂ fixation is common in cold environments. For instance, vascular plant taxa, such as *Dryas drummondii* and *Hippophaë rhamnoides*, and certain species of *Alnus* and *Myrica*, are N₂-fixers in cold habitats. Genera such as *Trifolium*, *Lupinus* and *Astragalus* are also found to have high N₂ fixation activities at high elevation (Johnson and Rumbaugh 1986; Jacot et al. 2000a, b; Olsen et al. 2013) and, overall, arctic and alpine life conditions seem quite favourable for symbiotic N₂ fixation. In addition, free-living N₂-fixing cyanobacteria are commonly associated with certain boreal, montane and lower alpine feather mosses, such as *Hylocomium splendens* and *Pleurozium schreberi* (DeLuca et al. 2002), and many N₂-fixing cyanobacterial lichens are typically found in cold climates (Kershaw 1985).

Ecosystem responses to N_2 fixation and anthropogenic N inputs can vary depending on extant N demand, stocks and cycling (e.g., Aber et al. 1989). Typically, annual net primary production (NPP) in late successional, largely unmanaged ecosystems is driven almost completely by the internal N cycle, requiring relatively little N_2 fixation as long as N losses (e.g., via leaching, erosion and denitrification) are low (Chapin III 2002). Hence, over the course of ecosystem succession, an ecosystem builds up N stocks from initially small annual rates of N_2 fixation and N deposition (Walker and Syers 1976; Crews et al. 2001; Belnap and Lange 2003); both symbiotic and free-living N_2 fixation rates vary significantly over the course of ecosystem development (Vitousek 1994; Crews et al. 2001; Menge and Hedin 2009), with free-living rates contributing 5–63 % to the total N_2 fixation (Reed et al. 2011). However, with N_2 -fixer invasion and anthropogenic N deposition, N inputs can become decoupled from demand and induce a suite of ecosystem consequences related to excess N availability.

In this review, we set out to build a contemporary understanding of (1) how and why N_2 -fixers are invading cold climate ecosystems, and (2) the ecosystem consequences of this invasion into cool temperate, boreal, arctic and alpine regions. We explore whether these ecological consequences are exclusively due to the N_2 fixation, and, thus, due to N-related mechanisms or if, instead, they are mediated by other effects, such as disturbance regime and/or altered land management. We first recall the nature of symbiotic N_2 -fixation and ask where these invasions occur and why; then, we discuss ecological consequences largely assembling case studies for *Lupinus* and *Alnus*, with special reference to gaseous N losses, nitrate leaching and soil properties. We will close with a section assessing effects on biodiversity and the implications for these results within a climate warming context.

Symbiotic N_2 fixation, where, why?

Symbiotic N_2 fixation in angiosperms occurs in all terrestrial ecosystems. However, it is still an open question why this mode of N_2 acquisition by angiosperms had relatively limited evolutionary success (Sprent 2009). *Lupinus* and *Alnus* both belong to the group of N_2 -fixing plants that has evolved the ability to accommodate N_2 -fixing bacteria intracellularly. This symbiosis develops novel root organs, so-called nodules, which are mainly root-derived (Pawłowski and Sprent 2008). Nitrogen-fixing endosymbiosis predominately occurs in two forms: (1) actinorhizal hosts that belong to three eurosid orders (Fagales, Cucurbitales and Rosales) and that nodulate with Gram-positive actinobacteria of the genus *Frankia* (Swensen and Benson 2008), and (2) legumes (order Fabales) that enter specific

interactions with members of a diverse group of Gram-negative bacteria, called rhizobia (Benson et al. 2011).

Actinorhizal and many rhizobial plant symbioses typically colonize less-developed soils such as glacial tills, sandy soils and even dry dunes. Actinorhizal N_2 fixation is largely realized under disturbed, pioneer type of life conditions, including those created by human land use (e.g., land degradation). Among the likely reasons why actinorhizal plants and some legume species are more abundant on less-developed soils is their relatively high demand for mineral nutrients other than N, such as phosphorus and molybdenum, their high light requirement, and also their need for adequate soil moisture (Uliassi and Ruesch 2002). A recent study on N_2 -fixing trees (U.S. forest inventory data) indicates that phylogenetic constraints are not the reason why N_2 -fixing trees are relatively abundant in early successional, but rare in late-successional, temperate forests (Menge et al. 2010). The pattern apparently emerges in large part because N_2 -fixers are less shade tolerant. The concept of carbon and energy exerting limits to N_2 fixation (e.g., Gutschick 1978) has been questioned by experiments showing that internal plant N concentration in the form of amino acids regulates nodule growth and activity. As amino acids contain both C and N, data in several older studies, where photoassimilates were considered to be regulating nodule activity, could be interpreted as regulation by amino acids (Parsons et al. 1993).

Because of their pioneer performance, many of these N_2 -fixing taxa—both native and non-native—have been used in re-vegetation programmes aiming to rehabilitate degraded soils. However, after their introduction, they often spread to the surrounding areas in an uncontrolled manner. A typical example is *Lupinus*, where North American species (*L. polyphyllus*, *L. arboreus*, *L. nootkatensis*, *L. perennis*) have become invaders in Scandinavia (Fremstad 2010), Iceland (Magnusson 2010), northern Eurasia (Thompson et al. 1995), New Zealand and Australia (Harvey et al. 1996; Goulson and Rotheray 2012). At a large scale, the two most significant cool climate woody taxa that perform actinorhizal N_2 fixation are *Alnus* (Betulaceae) and *Hippophaë* (Elaeagnaceae), both associated with early succession, often in relatively wet habitats.

In contrast to legumes, alder is exhibiting an obligate N_2 -fixing pattern largely insensitive to soil N supply (Menge et al. 2009). However, under experimental conditions, and using liquid culture techniques, nodule growth was inversely related to added nitrate concentrations in *Alnus viridis* (Benecke 1970) and also to added ammonium nitrate in a pot experiment with young *A. maritima* trees (Laws and Graves 2005). Applied N concentrations in such experimental trials often surpass N concentrations in natural soil solution; thus, the application of these results to natural conditions is limited. Interestingly, irrigation

with N-free water after N addition in the above-mentioned experiment induced a resurgence of the N₂-fixing activity in nodules of *A. maritima*. It is well known from experiments and agricultural practice that additional N fertilization or high levels of mineral N in the soil, in particular, high nitrate concentrations, drastically suppress rhizobial N₂ fixation (Streeter 1988; Marschner 1995; Richter 2005).

The natural distribution of *Alnus* and *Lupinus* species covers much of the terrestrial land area outside the tropical and subtropical lowlands (see supplementary material, Fig. S1). During the past decades, the range of *Lupinus* has been extended substantially beyond its natural range, and both taxa exhibit clearly invasive characteristics (Fig. S2). The invasive behavior of *Alnus viridis* shrubs has been documented for the Alps (Anthelme et al. 2007; Wiedmer and Senn-Irlet 2006; David 2010; named *A. viridis* ssp. *sinuata* in North America), as well as for *A. fruticosa* in Alaska (Myers-Smith et al. 2011; Tape et al. 2012), Siberia (Frost and Epstein 2014), and NW Canada (Mackenzie River valley and delta; Lantz et al. 2010, 2012). *Alnus incana* colonizes the youngest part of land-uplift seashores, forming an alder belt along the Gulf of Bothnia in northern Sweden (e.g., Svensson and Jeglum 2003) and is often accompanied by *M. gale* and/or *H. rhamnoïdes*. *Hippophaë*, which can be found dominating any river flat across central Asia and in parts of Europe and temperate East Asia (Fig. S2). The neophytic, both wanted and unwanted, role of *Lupinus* has also been shown in central Europe (Volz and Otte 2001; Otte and Maul 2005), Iceland (Magnússon et al. 2003, 2004; Magnusson 2010) and northern Sweden and Norway (Huss-Danell and Lundmark 1988; Fremstad 2010). Some of these monospecific stands are most likely natural (most of *Hippophaë* and *Myrica*), but many follow from massive human disturbance.

As explained above, both native and exotic N₂-fixing taxa can become invasive under conditions of abrupt changes in land use or by a combination of soil destruction and regional availability of invasive taxa (via active introductions or by spreading from regionally available populations). The regional availability alone of such taxa is often not sufficient (cf. environmental filters by Colautti and MacIsaac 2004), and different species of N₂-fixers vary in their invasiveness and the conditions required for their success.

Lupinus nootkatensis was first introduced to Iceland in 1885, and an additional seed source came in from Alaska in 1945 (Magnússon 1995). Individuals of this perennial species can get over 20 years old, but stands often thin with time and commonly are replaced by graminoids or forbs, but sometimes by other non-native species such as *Anthriscus sylvestris* (Magnusson 2010). Furthermore, *L. nootkatensis* forms a persistent seed bank that may contain up to 2,900 seeds m⁻². Seeds can germinate even after

numerous decades, and germination is easily activated by ecosystem disturbance (Sigurdsson and Magnússon 2004).

In parts of central Europe and in New Zealand, the uncontrolled spreading of *Lupinus* spp. is considered a nuisance weed. In the Swiss central Alps, the Black Forest, and in the eastern Austrian Alps, perennial lupins were used for the stabilization of road embankments even above tree-line elevation (Gigon and Weber 2005; Volz 2003). These populations, particularly of *L. polyphyllus*, have repeatedly persisted at high elevation and spread into adjacent pastures at a slow rate, but remained vigorous and dominant over decades once established (Fig. S2). In Switzerland, *L. polyphyllus* is currently listed on the so-called watch list, underpinning that the species has a potential to become invasive, and that future spreading needs to be observed (Gigon and Weber 2005).

The dominant reason why alders (mainly various ssp. of green alder, *Alnus viridis* ssp.) became so invasive in large parts of the Holarctic and high elevation temperate zone seems to be the abrupt opening of land in the immediate vicinity of the natural habitat. Under natural conditions, *A. viridis* ssp. is confined to wet ravines, river embankments or avalanche tracks, unable to invade the adjacent forest. Commonly, green alder has a lower distributional limit at 1,200–1,100 m a.s.l., as long as adequate moisture is provided, and grows frequently at the alpine treeline (Körner 2012). However, when forests are burned, undergo windthrow or mudflow, or when erosion opens new terrain, alders establish faster than the late successional tree taxa (conifers). Similarly, when millennium-old sustainably used grassland on previous montane forest terrain is abandoned or less intensively used (e.g., light grazing instead of regular mowing), the local *Alnus* populations are released from constraints by land use pressure, and thus there is nothing to stop this species from invading the adjacent open land. For instance, within 40 years of reduced grazing, a large fraction of former montane pasture land has become overgrown in the upper Reuss valley (Ursern valley, Swiss central Alps; 56 % increase in alder shrubland from 1965 to 2005; Wettstein 1999, van den Bergh et al., unpublished). In the Ursern valley, the cutting of the alder wood for heating purposes contributed to the restriction of its spreading until the 1950s (Wunderli 2010). During the last decade, shrubland mainly formed by *Alnus viridis* increased by 12,000 ha in the Swiss Alps, exceeding the rate of current forest expansion about three- to fourfold (Brändli 2010).

In contrast to low elevations, where tall and more vigorous deciduous tree taxa can outcompete *Alnus* spp. (e.g., *A. incana*, *A. glauca*, *A. rubra*), *A. viridis* becomes so dominant at higher elevations that the typical montane conifers such as *Picea abies*, *Pinus cembra*, *Pinus mugo* and *Larix decidua* cannot establish, and their seedlings are also unable to outgrow the lush herbfields facilitated by the N

supply in the *Alnus viridis* understory (Körner 2012). *Hippophaë* and *Myrica* also become invasive and dominant in cool regions (Isermann et al. 2007). Once established through seeds, the success of these invasive woody taxa is also related to their clonal expansion.

It was formerly thought that these *A. viridis* thickets may open for forest succession after half a century (Körner and Hilscher 1978; Körner et al. 1978), but soil N has a long residence time in such high elevation ecosystems (Körner 2003; Gerzabek et al. 2004). This results in the continuation of lush, tall herb fields beyond the timeline of potential shrub collapse, which has significant long-term ecological consequences. In the Swiss Ursern valley, some alder stands were described in 1748 (cf. Oechslin 1927) and, even more than 250 years later, such stands are still dominated by green alder at the very same locations, demonstrating that this species is capable of persisting for centuries (E. Hiltbrunner, unpublished).

Ecological consequences

The transformation of cold climate ecosystems by a high abundance of N₂-fixing actinorhizal plants or legumes is associated with the following four core issues (all are related to higher N availability mediated by the N₂-fixers).

1. Species diversity: the suppression of non-N₂-fixing, cold-adapted taxa of lower stature by competitive exclusion (biodiversity consequences, invasion syndrome).
2. Changing the N cycle: N₂ fixation affects the N cycle in ecosystems, especially in those with a naturally slow N cycle (e.g., low N mineralization rates). As a higher soil N pool becomes established, N₂ fixation may slow down (depending on the N₂-fixing species); however, enriched soil N pools and nitrophilous vegetation persist over a very long time [N retention/storage; biodiversity effects as in (1)].
3. N₂ fixation induces N losses: due to the massive N enrichment, N losses occur in the form of nitrate leaching and NO_x, N₂O, and N₂ gas. Incomplete denitrification leads to emission of the greenhouse gases N₂O and NO.
4. Alterations to N and C storage: in many systems, N inputs increase N and C storage in soils (via SOM accumulation), but in the case of alder expansion, the succession toward late-successional forest is blocked. Because C stocks are substantial in montane and boreal forests, this obstruction toward late-successional stages and the expansion and persistence of alder shrubland actually represents a reduction in the landscape C storage potential (diminished C sequestration).

In the following, we will review the evidence for these assertions and will use data from case studies in *Lupinus* and *Alnus* to illustrate the current knowledge.

The *Lupinus* example from Iceland

In subarctic Iceland (63–66°N), three-quarters of the land presently perform at far lower net primary production (NPP) than one would naturally expect at such latitudes and climate: 45 % of the total surface is completely barren (devastated) or covered by degraded heathland terrain (Aradóttir and Halldórsson 2011). As much as 10 % (corresponding to c. 500,000 ha) of this land is found below 400 m a.s.l. with a favorable climate for high plant production. This area was formerly occupied mainly by a boreal downy birch (*Betula pubescens*) forest with an estimated NPP of 1,000 kg C ha⁻¹ year⁻¹, but NPP is currently only few g C m⁻² (Kardjilov et al. 2006). On such land, perennial lupins are able to produce 4,000–8,000 kg C ha⁻¹ year⁻¹ during their thicket stage, which is very similar to a wheat crop in the temperate zone. In this environment that would naturally receive 1–2 kg N deposition ha⁻¹ year⁻¹ (Gíslason et al. 1996), there are only seven native N₂-fixing vascular plant species and they are all rare, except one (*Trifolium repens*). On such almost bare land, the introduced *L. nootkatensis* can fix 260 kg of N ha⁻¹ during 7 years, of which 83 kg N can be recovered from above-ground plant biomass, 18 kg N resides in organic debris, and the rest is tied to soil organic matter (Pálmason et al. 2009). Interestingly, even barren, eroded terrain shows some N storage in old soil organic matter (SOM) from the previous historic vegetation.

The net N accumulation in SOM on the barren areas in Iceland goes hand in hand with C accumulation, which may increase from 0.5–1 to 2–4 % soil organic carbon (SOC) in 30 years (Magnússon et al. 2001). Another study found an annual SOC accumulation of 330 kg C ha⁻¹ year⁻¹ in a 40-year chronosequence study on *L. nootkatensis* in Iceland (Arnalds et al. 2000). At a fairly constant soil pH of 6.6, the presence of lupins reduces the C/N ratio from 18 to 14 on such sites within ca. 30 years (Magnússon et al. 2001). Remarkably, that C/N ratio remains lower even after lupins disappear. Another interesting aspect is that these volcanic soils are sulfur (S)-deficient in some places, so that PKS fertilization can enhance *L. nootkatensis* productivity five- to sixfold (NPP rising from 300 to c. 1,700 kg C ha⁻¹ year⁻¹; Björnsson 2007).

In boreal Sweden, the impact of *L. nootkatensis* on the N cycle was similar to the situation in Iceland. During the first 20 years after establishment, the net N accumulation was on average 39 kg N ha⁻¹ year⁻¹, assuming that N losses were zero and increases of N in some few *Betula pendula* growing in the lupin plot were negligible (Myrold

and Huss-Danell 2003). This compares to *L. nootkatensis* fixing on average $37 \text{ kg N ha}^{-1} \text{ year}^{-1}$ in the study by Pál-mason et al. (2009). *L. nootkatensis* had, however, almost completely disappeared some 30 years after establishment in the Swedish study, leaving only the few birches and some sparse ground vegetation (Huss-Danell, unpublished data), which is a different successional trajectory than typically experienced in Iceland.

The *Alnus* example in the Alps

Alnus viridis often expands on stable, well-developed soils with relatively high total SOC concentrations, which become substantially and rapidly enriched in N (Podrazskya and Ulbrichova 2003; Uri et al. 2011). The soil solution collected beneath the main rooting horizon in green alder stands showed increased nitrate and to lesser extent higher ammonium concentrations (T. Bühlmann, unpublished). Other studies have observed an alder-induced increase in soil ammonium (Rhoades et al. 2001). Differences in the form of inorganic N that accumulates in the soil may depend on soil factors (e.g., C/N ratio, clay content, pH, soil moisture, microbial community composition). Nitrate is easily leached and, in order to maintain the ion-balance, base cations are leached together with the nitrate ions (Fig. 1). In addition, during nitrification and plant uptake of ammonium, protons are released and high N input to the soil is commonly linked to soil acidification. For example, along a chronosequence of green alder stands, ranging from c. 15- to c. 90-year-old stands, drop in soil pH was substantial when alder stands reached an age of c. 25 years (Caviezol et al. 2014). In the study of Podrazskya and Ulbrichova (2003), a tendency of lower soil pH in planted green alder stands was already noticed after 9 years, and in *A. incana* stands soil, pH (0–10 cm depth) dropped by 1.3 units during a 14-year period (Uri et al. 2011).

Nitrate leaching rates should be related to the ecosystem capacity to retain N (invested in different pools: soil, plant biomass), but also to current atmospheric N deposition rates. Seasonal nitrate leaching rates in the green alder stands studied in the Swiss Alps (encroaching former pastures) amounted to $15 \text{ kg N ha}^{-1} \text{ season}^{-1}$, yielding annual rates up to c. $25 \text{ kg N ha}^{-1} \text{ year}^{-1}$, which is c. 100 times more than the nitrate leaching rates in neighboring, grazed pastures (ongoing works by T. Bühlmann et al.). N input by atmospheric N deposition for the same study region varied between 10 and $15 \text{ kg N ha}^{-1} \text{ year}^{-1}$ (modeled values; BAFU/BFS 2011).

In early successional stages of the expansion of N_2 -fixing plants, N losses may commence rapidly after 10–20 years, whereas for older stands a decline in N losses has often been assumed, partly through inhibitory effects of accumulated soil N on the N_2 -fixing activity. Decline

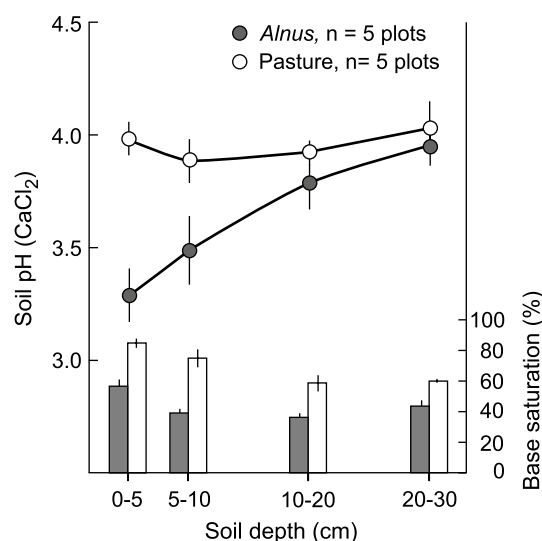


Fig. 1 The consequence of the establishment of *Alnus* shrubs on former pasture land in the Swiss central Alps on soil pH and base saturation across the soil profile. Dark symbols *Alnus* shrub, open symbols adjacent grassland (T. Bühlmann, unpublished)

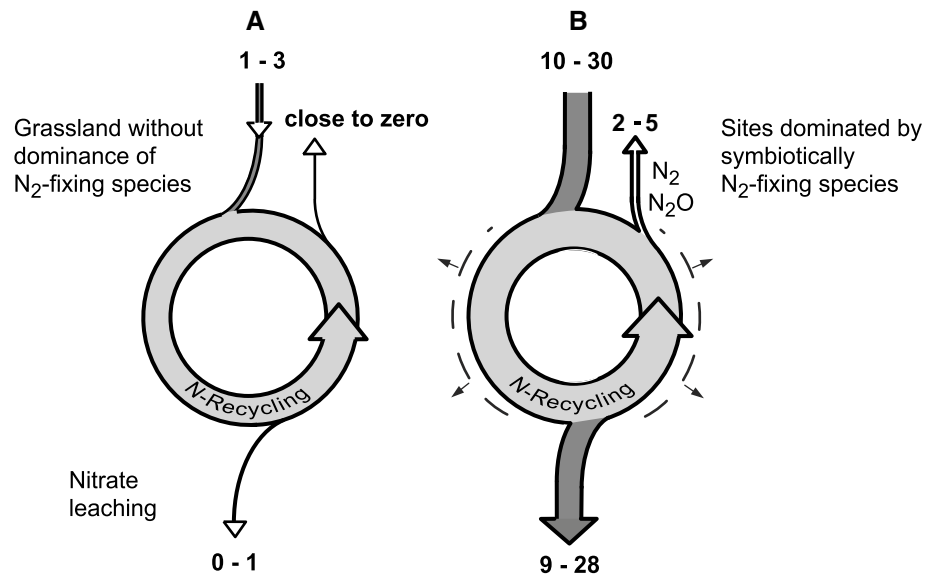
in N_2 -fixing capacity has repeatedly been observed under increased nitrate supply in rhizobial symbiosis but to lesser extent in actinorhizal symbiosis (Vessey and John Waterer 1992; Marschner 1995). For instance, the nitrate concentration in the soil solution below the rooting zone in >30-year-old (up 100 years old) green alder stands was on average only slightly lower than in younger stands (15–30 years old), indicating that old green alder stands may still fix substantial amounts of N_2 (T. Bühlmann, unpublished).

Southern hemisphere actinorhizal species in cool regions also have the potential to fix significant amounts of N_2 and thereby influence soil N cycling with the consequences of enhancing N availability to associated plant species or for losses of N from ecosystems. For instance, Chaia and Myr-old (2010) used differences in the natural abundance of ^{15}N in actinorhizal *Ochetophila* and *Discaria* relative to non- N_2 -fixing *Rosa* and *Berberis* in Patagonia to demonstrate that most of the actinorhizal plants were obtaining almost all of their N from N_2 fixation, and were enriching these ecosystems with N.

Induced gaseous N losses

According to the N saturation hypothesis (Aber et al. 1989), N losses occur when an ecosystem's capability to retain N is exceeded, including the demand for biomass production, incorporation in microbial mass and/or soil pools. Nitrate leaching to the groundwater mainly occurs under medium and high atmospheric N deposition loads. Thimonier et al. (2010) reported nitrate leaching in forest stands subjected to N deposition levels $>10 \text{ kg ha}^{-1} \text{ year}^{-1}$, and MacDonald

Fig. 2 A schematic illustration of N dynamics in systems with **a** ‘normal’ versus systems with **b** increased N input through N_2 -fixing plants in cold biomes. With N inputs in ‘normal’ systems, we refer to N_2 fixation by free-living cyanobacteria and deposition of mainly oxidized forms of N from lightning or wild fires, disregarding atmospheric N deposition. Numbers (in $\text{kg N ha}^{-1} \text{ year}^{-1}$) represent a combination of values obtained from the literature (Körner 2013b) with results from the field measurements



et al. (2002) observed losses in forests at N deposition rates of $> 25 \text{ kg N ha}^{-1} \text{ year}^{-1}$. However, gaseous losses (N_2O , NO , NH_3) reveal much more variable patterns among ecosystems and across temporal and spatial scales (Butterbach-Bahl and Gundersen 2011). Whether through N_2 fixation or N deposition, as N inputs increase, the amount of N cycled within the ecosystem and N released in leachates and to the atmosphere increase (Fig. 2).

Data from an ongoing project (cf. Bühlmann et al. 2013) show that, in green alder stands at 1,600 m a.s.l. in the Swiss Alps, $4.1 \text{ kg N}_2\text{O-N ha}^{-1}$ were emitted during the growing season (mid-May until late October), which was 35 times the rate assessed in adjacent pastures. Accounting for the long dormant period with wet, cold soils, the annual N_2O emissions are potentially more than twice as high, yielding c. $10 \text{ kg N}_2\text{O-N ha}^{-1} \text{ year}^{-1}$. At higher elevation (1,900 m a.s.l.), N_2O emission was lower, at $1.1 \text{ kg N}_2\text{O-N ha}^{-1}$ during the shorter growing season. Using the identical chamber method in an *A. incana* stand, lower N_2O emission rates were measured (Caprez 2012), which was mainly explained by differences in stand structure (*A. incana* was forming c. 30-m-tall trees) and higher water drainage at the *A. incana* site. Small N_2O emission rates of $0.5 \text{ kg N}_2\text{O-N ha}^{-1} \text{ year}^{-1}$ were reported for *A. incana* stands by Uri et al. (2011); however, in this study, most of the annual N losses were in the form of N_2 ($73.8 \text{ kg N ha}^{-1} \text{ year}^{-1}$), indicating complete denitrification. Preliminary N_2O data for *L. nootkatensis* stands in Iceland (measured directly in the soil air and not as emitted gas), however, did not differ between sites with lupin and non- N_2 -fixing plants (M. Maljanen unpublished). Overall, due to the power of the greenhouse gas, such N_2O releases from alder stands in the range of 5 to $10 \text{ kg N}_2\text{O-N ha}^{-1} \text{ year}^{-1}$ largely outweigh their benefits as C sinks in a Kyoto Protocol context.

N storage and immobilization in soil, effects on C storage

Soils in late successional ecosystems with high C/N ratios of >25 or high organic matter have been shown to immobilize substantial quantities of soluble N input (Butterbach-Bahl and Gundersen 2011 and citations therein). ^{15}N -labeled N fertilizer added to an alpine grassland, dominated by *Carex curvula* at 2,300 m a.s.l., was rapidly incorporated into SOM, with 84 % stored in the same year and c. 45 % recovered after 27–28 years (Gerzabek et al. 2004), underpinning the high N storage capacity of organic soils. In this experiment, added ^{15}N fertilizer corresponded to $100 \text{ kg N ha}^{-1} \text{ year}^{-1}$ and consisted of ammonium sulfate. It is well known that ammonium ions can be ‘stored’ in clay–humus complexes for long periods and/or N becomes incorporated into different humic and fulvic acids. Soil varied in pH from 4.6 to 6.0 and the ^{15}N recovery was higher in the more acidic soils (55 vs. 34 %; Gerzabek et al. 2004). Organic N inputs from former cattle resting places in montane and alpine areas are well known to translate into long-lasting fingerprints in vegetation with tall, nitrophilous forbs, partly the same as found as beneath *Alnus* bushes (Körner 2003).

It remains unresolved to what extent increased N inputs would enhance (or reduce) the long-term C sequestration to soils. It has been argued that, because of the increase in forest growth across Europe during the last 50 years, which was partly explained as an effect of N deposition, N deposition is assumed to stimulate C sequestration. Nadelhoffer and co-workers (1999) emphasized that the contribution of N deposition to C sequestration may be only small, since most of the N is retained in soils at a high C/N ratio of approx. 30. By assembling data from various studies, De Vries et al. (2008, 2009) noticed values for soil

C sequestration in the range between 5 and 35 kg C per 1 kg N deposition. However, due to stoichiometric constraints, growth is only fostered by a particular resource (e.g., N) as long as other resources are not limiting and plant productivity is commonly not directly related to ecosystem C storage (Körner 2013a).

Nitrogen-fixing tree species have consistently been reported in association with higher SOC concentrations or stocks in a range of studies (e.g., Johnson 1992; Cole et al. 1995; Cools et al. 2014). Based on a meta-analysis, Johnson and Curtis (2001) reported that the presence of N₂-fixing species (e.g., red alder *Alnus rubra* and black alder *A. glutinosa*) caused a marked, positive change in the C concentration of A horizon (mineral soils) in temperate and boreal forests. However, when N₂-fixing green alder stands persist at the same locations for centuries (see above), the succession toward montane forests does not take place (Bischof 1984). Since montane forests store far more C than alder shrublands, the net result is a C stock far below the potential one.

Effects on the water cycle and on water chemistry

Estimated water use in *Alnus glutinosa* stands was found higher than in neighboring beech (*Fagus sylvatica*) stands, although the estimated LAI in the alder stands were not significantly higher (4.8 vs. 4.5 in beech; Herbst et al. 1999), presumably a result of higher rates of transpiration per unit leaf area (associated with higher leaf nitrogen concentration and, thus, higher photosynthetic capacity) in *Alnus*. Ongoing research in the Swiss Alps indicates a mean increase of evapotranspiration by at least 20 % on bright summer days from *A. viridis* shrubs compared to adjacent pastures, causing proportional reductions in runoff and catchment discharge throughout the growing season (T. van den Bergh, unpublished).

A recent study on 25 headwater streams in Alaska revealed that variation in stream N was best explained by alder cover (0–28 % cover; different alder species: *A. viridis*, *A. viridis* ssp. *sinuata* and *A. incana*) and not by other physiographic watershed variables (Shaftel et al. 2012). Compton and co-authors (2003) found a strong, positive relationship between alder cover, predominantly by *A. rubra*, and nitrate and dissolved organic nitrogen (DON) concentrations in 26 streams of the Oregon coast range. Depending on red alder cover, total annual N export of the streams varied between 2.4 and 30.8 kg ha⁻¹ year⁻¹ and nitrate accounted for 92 % of the total dissolved N. The higher nitrate concentrations in Oregon streams than in the Alaskan study is mainly explained by higher alder cover (>50 % compared to maximum cover of 28 % in the Shaftel et al. 2012 study). Increased nitrate concentrations were also observed in small streams passing *A. viridis* in

the central Alps after autumnal leaf shedding (Bühlmann et al. 2013). In contrast to most other deciduous trees and shrubs, alder sheds its leaves green and hardly retranslocates N from the leaves during autumnal senescence (Pallardy 2008).

Relating net anthropogenic N inputs into catchments to river N export has become a popular approach to assess the contribution of atmospheric N deposition to riverine or coastal N export (NANI calculations, e.g., Hong et al. 2011, 2012). In most NANI studies, covering different catchments sizes and various land cover categories (from forest dominated to agricultural watersheds), c. 25 % of the N input anthropogenic sources was exported to rivers (Eriksson Hägg et al. 2012; Howarth et al. 2012); thus, 75 % of the N input remained within the catchment area (e.g., as soil organic N) or left the catchment as gaseous loss due to denitrification or in form of feed and food. Nitrogen fixation in legume crops or pastures was partly included as an input variable in these N input–export calculations, but not N₂ fixation from invasive/expanding taxa as discussed here (e.g., Kopacek et al. 2013). In the above-mentioned alder-dominated catchments, the N export was occasionally higher than has been reported based on the NANI approach, regardless of the atmospheric N deposition.

Biodiversity effects and long-term ecosystem consequences

Initially, most of the fixed N₂ is incorporated in the biomass of the N₂-fixing plants; later on, the soil N pool becomes enhanced, and also non-N₂-fixing, nitrophilous plants beneath or adjacent to the N₂-fixers ‘profit’ from the increased N availability. This ecosystem-scale nitrophilization leads to a reduction in plant species richness (Anthelme et al. 2007), in the extreme case, to almost monospecific alder and lupin stands (Fig. S2). In the study of Anthelme and co-authors (2007), when assessing 243 vegetation plots in three regions which differed in precipitation, their results showed that plant species richness was halved when the alder cover (*A. viridis*) reached 50 %, irrespective of soil type and precipitation input. A tall, dense plant cover reduces soil heat flux, thus creating a cooler microclimate, explaining, beside the increased N availability, the loss of most grassland/heath taxa of lower stature. As plant productivity becomes enhanced, plant diversity declines, and with it, insect and bird diversity may be affected. In dense alder stands, Hymenoptera, Coleoptera and Orthoptera decreased, whereas Diptera somewhat increased (Anthelme et al. 2001) and a few other taxa became dominant (Uhlir et al. 2011). Different bird species may respond differently, depending on their habitat and food species demands.

However, when N_2 -fixing taxa invade barren land (as is often the case with lupins in Iceland), a net stimulatory effect on both vegetation succession (Magnússon et al. 2004) and bird biodiversity (Gunnarsson and Indridadóttir 2009; Davíðsdóttir 2013) was noticed. But when such invasions occurred on sparsely vegetated range, or in heathland with full ground cover, plant species richness sharply decreased, with the long-term, successional trajectory still unclear (Magnússon et al. 2003, 2004).

A ‘take-over’ and long-term dominance by N_2 -fixing plants will always interfere with the natural course of succession. In the case of the montane or boreal bioclimatic zone, the natural late-successional vegetation is a closed coniferous or birch forest. Most of the forest taxa in these cold regions (*Picea*, *Pinus*, *Abies*, *Betula*) produce tiny seeds and depend upon open regeneration niches, the opposite of what a nitrophilous ground cover by tall herbs resembles. Hence, unless major disturbances come into play (either natural or by active human intervention), it may take several hundreds of years for trees to return and re-establish a forest, for reasons largely related to competitive exclusion and regional absence of appropriate seed sources (Huber and Frehner 2012). In the case of *Alnus viridis*, first signs of canopy opening in closed stands were observed after 60 years (Körner and Hilscher 1978), and certain fungal diseases may induce the needed canopy fragmentation. However, the clonal growth of *A. viridis* and its high reproductive success allows it to close gaps rapidly. Should the shrub canopy open, the tall clonal herbs, facilitated by decades of high N input, will continue to remain an obstacle for tree seedling establishment.

Whether such a dominance of N_2 -fixing species and subsequent inhibition of forest succession will occur seems to be site dependent. On young soils, and on soils on slopes that receive regular input of fresh mineral sediments from upslope, canopy openings and successional shifts seem more likely. On poor, degraded soils, even intended plantations of both *Alnus* sp. and *Lupinus* failed in the long run, as evidenced by a re-examination of old experimental plots in northern Sweden (Huss-Danell 1986; Huss-Danell and Lundmark 1988; Myröld and Huss-Danell 2003; K. Huss-Danell, unpublished data from 2012). Thirty-three years after planting *A. incana* and *L. nootkatensis*, both species had essentially disappeared from degraded pine forests, but the top humus layer was clearly thicker and the cover by mosses had increased at the expense of lichens where N_2 -fixing plants had been planted, particularly when *A. incana* plantations had received a starter dose of lime and/or NPK fertilizer. The location in northern Sweden where lupins survived, and, in fact, had built and retained 80-cm-tall thickets even after 33 years, was a test area that had been deeply ploughed before sowing. Planted *Pinus sylvestris* appeared to have profited from the continued presence

of *Lupinus* in that case (K. Huss-Danell, unpublished). In comparison, the introduction of *L. nootkatensis* to the vast degraded landscape in lowland Iceland, with topsoils eroded after many centuries of forest clearing and overgrazing, led to a naturalization of lupins and to their dominance over large areas during several decades.

The long-term consequences of planting alder into conifer forests have been explored extensively in the Pacific Northwest of North America. The presence of red alder (*Alnus rubra*) on a site (for instance, with Douglas-fir, *Pseudotsuga menziesii*) increased total N and N availability (Tarrant and Miller 1963; Bormann et al. 1994; Cromack et al. 1999; Rothe et al. 2002; Lavery et al. 2004) and sometimes had a beneficial effect on overall site productivity, particularly on relatively nutrient poor sites (Miller and Murray 1978; Binkley and Greene 1983; Binkley 2003; Radosevich et al. 2006). Interestingly, although alder-based N_2 fixation ($50\text{--}200\text{ kg N ha}^{-1}\text{ year}^{-1}$) augmented the soil N inventory by 20–50 % over 50 years, the rate of N turnover increased several-fold (Binkley et al. 1992, 1994). In this context, Hart et al. (1997) showed that the presence of red alder increased both gross rates of N mineralization and N immobilization and that gross NO_3^- immobilization correlated well with NO_3^- production. The net effect is that there are often persistent increases in long-term losses of nitrate from red alder compared to Douglas-fir stands (van Miegroet and Cole 1984).

N_2 -fixers in a warmer climate

Higher temperatures are likely to enhance or accelerate both the natural N cycle as well as rates of N_2 fixation (e.g., Thomas et al. 2006; Schaeffer et al. 2013). For instance, a 2 K higher soil temperature in Iceland has been found to double annual litter decomposition rate (Oddsdóttir et al., unpublished), which could translate into enhanced N mineralization rates, but also greater N immobilization (coupling to the C cycle). In a simulated summer warming by 1 K, fluxes of soil organic N and ammonia nearly doubled in arctic peat soils over the growing season (Weedon et al. 2012).

Current investigations show that young *A. viridis* stands at 1,900 m elevation in the Swiss Alps released one-fourth as much nitrate into the soil solution than comparable stands at 1,550 m elevation, whereas in adjacent pastures soil water was almost free of soluble N at both elevations (T. Bühlmann, unpublished). This elevational distance corresponds to a c. 2.5 K difference in growing season temperature. Hence, a relatively small climatic warming is likely to substantially enhance N_2 fixation, but would likely also lead to higher N losses in the alder system. Unless competition by warmer adapted trees or pathogen infections (e.g., Rohrs-Richey et al. 2011) come into play at the lower edge

of the *Alnus viridis* range, such effects on enhanced nitrate leaching are likely to become effective within the next 50–100 years.

Conclusions

Our study shows that symbiotic N_2 -fixing species exert great invasive potential in cold climates, irrespective of whether they are native to a region or introduced. The subsequent changes to the N cycle are so substantial that these systems are subjected to a kind of large-scale ‘natural experiment’, similar to or larger than has been observed with continuous atmospheric N deposition rates. Such eutrophication of terrestrial ecosystems may be periodically beneficial in greatly degraded situations, but in many cases it incurs N loads that contribute both to strong declines in biodiversity, increases in nitrate leaching to discharge water, and to elevated N_2O emissions to the atmosphere. However, perhaps the most dramatic consequences are those for natural forest succession by competitive exclusion of seedlings of the dominant small-seeded tree taxa typical for montane and boreal environments. In this case, N_2 -fixing, invasive species exert long-lasting ecosystem consequences by preventing forest regeneration. The extent of human alteration to the global N cycle has been discussed in many scientific, political and social venues, with a particular focus on the effects of N deposition. Although global N deposition is undoubtedly an important threat to ecosystems and human well-being, we advocate an additional, and thus far less recognized, avenue of ‘N pollution’ that also results in significant and lasting effects on ecosystem structure and function in cold regions; namely, the invasion by and expansion of N_2 -fixing plants. Such invasions cause marked alterations to the regional C and N cycles, increasing water consumption and air pollution, and severely threatening biodiversity.

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