Chapter 4
Alteration of Nitrogen Cycling as a Result of Invasion

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Abstract The invasion of ecosystems by non-native species may alter the nitrogen (N) cycle through different nonexclusive mechanisms. Dramatic alterations occur in an ecosystem when the invasive species possesses a new strategy to acquire this nutrient, such as N_2 fixation ability. Gradual alterations are caused by changes in the utilisation of N with respect to dominant natives, such as changes in N allocation patterns, which affect the chemical composition of tissues and therefore the decomposition and mineralisation processes. Changes in the disturbance regime mediated by plant invasion, and alteration of the trophic structure caused by the invasion of non-native animals, may also have profound effects on the N cycle. Published synthesis studies suggest that, altogether, plant invasions tend to increase N pools and to accelerate N fluxes of the invaded ecosystems. However, particular impacts are highly dependent on the context and therefore difficult to predict. A critical review of these syntheses shows that the available literature on invaders' impacts is highly biased in the selection of species, impact metrics, and ecosystem types. These biases suggest that, in spite of great advances in understanding the impacts of invaders on the N cycle, more information is needed on the impacts of many invaders so far ignored, on how invaders change the net ecosystem gains and losses of N, and on the role of the context.

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4.1 Introduction

Nitrogen (N) is the fourth most abundant element in living tissues, only behind oxygen, carbon and hydrogen. It forms part of proteins, DNA, chlorophyll, etc. Although N is very abundant on Earth, particularly in the atmosphere where it appears as N_2, it is not accessible for most plants in this form. This N_2 remains inaccessible to plants until specific microorganisms break down the bonds between the N molecules, thereby freeing N atoms that can then bond with hydrogen or oxygen to form accessible inorganic compounds (mainly ammonia NH_4^+ or nitrate NO_3^-). This N fixation is an important biological process and is primarily mediated by living organisms (microbes), although some N fixation can also occur in the atmosphere using the energy of lightning discharges without the involvement of living organisms. Once N has been converted to accessible inorganic forms, it enters the biological pathways of the N cycle (Fig. 4.1), where it cycles between organic and inorganic compartments. A relevant part of N gets locked up in the soil organic matter, which must be decomposed by microorganisms before being available for most plants. Given the bottlenecks of N fixation and organic matter mineralization, N becomes in one of the major limiting factors of primary production controlling the functioning and structure of many ecosystems.

Similar to other nutrient cycles, the N cycle is considered as a supporting ecosystem service that is necessary for the maintenance of other services. For instance, the production of plant-derived goods (food, wood, fibre, etc.) depends on primary production, which in turn depends on N availability. Water quality is largely mediated by plants growing in floodplains, estuaries, or marshlands and their influence on nutrient cycling, while climate regulation is linked to the N cycle both directly, because of the greenhouse power of some N oxides that are emitted in the combustion of organic matter, and indirectly, by controlling the growth of plants and phytoplankton, which are the major sinks of CO_2.

We are deeply aware of the strong alterations that certain human activities have caused to the N cycle and the associated ecosystem services (Vitousek et al. 1997; Galloway et al. 2004; Shibata et al. 2015). Humans have dramatically increased the annual N_2 fixation by the industrial production of N fertilizers. By extending the amount of land devoted to the cultivation of N_2-fixing plants (mainly those of the Fabaceae family), humans have additionally contributed to a substantial increase of biotic N_2 fixation. The burning of forests, grasslands, or wood liberates N from long-term biological storage pools, and the burning of fossil fuels does the same with long-term geological storage. In both cases, the N is released in the form of N oxides (NO and N_2O) into the atmosphere, where the oxides may contribute to greenhouse warming (NO), stratospheric ozone depletion (NO), and acid rain (N_2O). Human activities have also increased nutrient inputs to aquatic ecosystems: 2.2 fold for nitrate and 4 fold for ammonia (Goudie 2006). Overall, these alterations contribute to increasing the stocks of biologically available N and to speeding up the N transfers among different storage forms (Vitousek et al. 1997; Galloway et al. 2004; Shibata et al. 2015).

The alteration of the N cycle by non-native species has been less well studied. This topic started to receive the attention of scientists and land managers at the end of the 1980s. Given that some invasive plants differ from the natives in N uptake strategy and/or N utilisation, they have the potential to alter the N cycle. In addition, some aquatic invasive animals may alter the N cycle increasing the concentration of growth-limiting nutrients and accelerating transformations. This chapter reviews the mechanisms by which invasions by non-native species may alter the N cycle in terrestrial and in aquatic ecosystems, and explores whether there are general trends on the impact of invaders on the N cycle.

4.2   Mechanisms of N Cycle Alteration by Invasions

Non-native invasive species may alter the N cycle, either by changing the size of N storage in different compartments of the ecosystem (diamonds in Fig. 4.1) or by changing the rate at which N is transferred (arrows in Fig. 4.1). Based on Vitousek
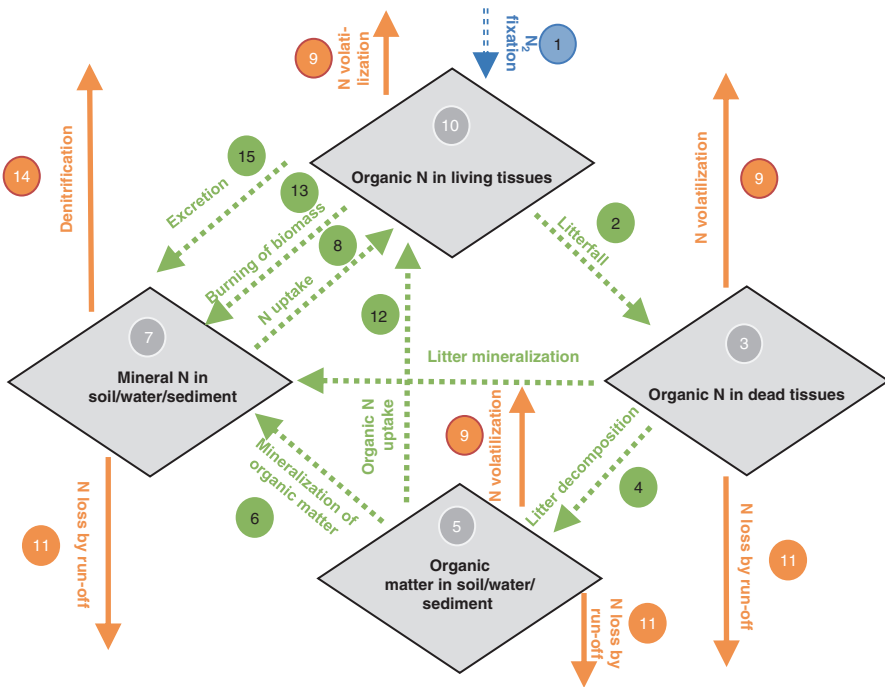

Fig. 4.1 Schematic representation of the nitrogen (N) cycle. *Diamonds* indicate N pools in different chemical forms and ecosystem compartments. *Dashed arrows* indicate N fluxes between different pools, *solid arrows* represent ecosystem N losses, and the *double-dashed arrow* indicates ecosystem N inputs. *Numbers* identifying each pool or flux are mentioned throughout the text and in Tables 4.1 and 4.2

(1990), we suggest four types of nonexclusive ways by which invaders can change ecosystems: by differing from natives in the strategy of (1) N acquisition or (2) N utilisation; (3) by altering the disturbance frequency or intensity; and (4) by altering the trophic structure of the community. This section reviews each of these mechanisms, using examples to illustrate them.

4.2.1 Changes in the Strategy of N Acquisition

Ecosystems can change dramatically when newly introduced non-native species have access to N sources that are not available to native species within that ecosystem. In contrast, gradual alterations occur when non-natives differ from natives in the magnitude of any functional trait controlling the rate of N transfer across ecosystem compartments (Chapin et al. 1996). This section considers dramatic changes resulting from new strategies of N acquisition; gradual alterations are addressed in the next section.

The best known mechanism of dramatic N cycle alteration by invasive species is the introduction of plants with mutualistic N_2-fixing microorganisms in ecosystems lacking such symbioses. The additional N input is first stored in the plant biomass, but it rapidly cycles within the ecosystem, increasing the size of one or more N pools. Higher N availability in the soil may also stimulate metabolic reactions of decomposers, along with their population growth, leading to a faster processing of organic matter. This alteration was first illustrated by the actinorhizal N_2-fixing shrub, *Moreya faya*, invading young N-poor volcanic soils in Hawaiian islands in the late 1800s. Given the lack of N_2-fixers in this early-succession rainforest, the invasion of *Moreya* quadrupled the input of fixed N_2 in the ecosystem and enhanced N mineralisation, making this extra N available to plants (Vitousek and Walker 1989). This seminal study on the scientific community launched the search for other case studies, where N_2-fixing non-native plants also invaded N-poor systems, with similar impacts (Table 4.1).

Another potential new strategy of N acquisition might be the ability of non-native plants to uptake N in organic form in communities with no or little ability to do so, which would lead to a shortcut in the N cycle (see path 12 in Fig. 4.1). This mechanism was suggested to explain the changes on soil properties caused by invasive *Hieracium pilosella* in heavily grazed tussock grasslands in New Zealand. Soils beneath this invader showed increased organic N and C accumulation, as well as C mineralisation. However N mineralisation was decreased in the invaded soils. The suggested explanation for this pattern was that *Hieracium*—thanks to the high levels of polyphenols in its leaves—inhibits N mineralisation and leads to the accumulation of organic N in the soil. At the same time, *Hieracium* would be able to take up organic N, benefiting from its own soil transformation (Saggar et al. 1999). However, no other evidence of this mechanism has been found in the literature, and further research is needed to check the extent to which this mechanism impacts the N cycle.

Table 4.1 Summary of mechanism of N cycle alteration by non-native species and examples reported in the literature

Mechanisms	Examples	References	Reported effect[a]	Affected pool/flux
Invasive plants support symbiotic N$_2$ fixers	Invasion of young volcanic soils of Hawaii by *Moreya faya*	Vitousek and Walker (1989)	N fixation + N mineralisation + soil mineral N +	(1/6/7)
	Invasion of South African fynbos by *Lupinus luteus* and *Acacia saligna*	Yelenik et al. (2007)	Soil mineral N +	(7)
	Invasion of Portuguese coastal dunes by *Acacia longifolia*	Marchante et al. (2008)	Soil N +	(5/7)
Changes in dominant life/growth form	Invasion of perennial-dominated short-grass steppe of Colorado by the annual *Kochia scoparia*	Vinton and Burke (1995)	N mineralisation +	(6)
	Invasion of perennial-dominated Californian grasslands by non-native annuals	Parker and Schimel (2010)	Soil ammonium + nitrification +	(7/6)
	Invasion of New Zealand broadleaf forests by the perennial herb *Tradescantia fluminensis*	Standish et al. (2004)	Litter decomposition + soil mineral N +	(4/7)
	Invasion of New Zealand tussock grasslands by conifers	Harding (2001)	Plant N uptake +, plant biomass +	(8/10)
Changes in tissue quality	Invasion of Californian serpentine annual grasslands by the annual *Aegilops triuncialis*	Drenovsky and Batten (2007)	Plant biomass + litter decomposition −	(10/4)
	Invasion of a mixed forest in Wisconsin by the shrub *Frangula alnus*	Stokdyk and Herrman (2014)	N mineralisation +, soil mineral N +	(6/7)
	Invasion of NW Spain forests by *Eucalyptus globulus*	Castro-Díez et al. (2012)	Litter decomposition − Nitrification −	(4/6)

Table 4.1 (continued)

Mechanisms	Examples	References	Reported effect[a]	Affected pool/flux
Changes in disturbance regime	Fire increase by African grasses invasion in Hawaii *Metrosideros* forests	Ley and D'Antonio (1998)	N_2 fixation −	(1)
	Soil disturbance by *Sus scrofa* invasion in the Monte Desert biome (Argentina)	Cuevas et al. (2012)	N mineralisation +, soil mineral N +	(6/7)
Altered trophic structure	Invasion of NE-US forests by earthworms of the genus *Amynthas*	Burtelow et al. (1998)	Soil organic matter − Mineralisation + denitrification +	(5/6/14)
	Invasion of the American red swamp crayfish (*Procambarus clarkii*) in floodplain wetlands	Angeler et al. (2001)	N in water column +	(5/6)
	Invasion of lake Erie by the freshwater mussels *Dreissena polymorpha* and *D. bugensis*	Conroy et al. (2005)	N excretion +	(15)

The last column indicates the impacted N pool or flux according to Fig. 4.1
[a]+ and − mean that the invasion increases and decreases the pool or flux, respectively

4.2.2   Changes from a Different Utilisation of N

Plant functional properties, such as growth rate, plant/leaf longevity, or growth form, largely determine the properties of the N cycle. Slow-growth plant species tend to produce long-lasting tissues by prioritizing investment in defence and support over growth; these tissues decompose at a slow rate, leading to a slow N cycling and to a high proportion of N locked up in organic forms. By contrast, fast-growth plant species tend to produce N-rich tissues by prioritizing production over defence and support. These tissues rapidly decompose and mineralise, leading to a fast N cycling. Similarly, annual plants invest their entire annual N budget in growth and reproduction, whereas perennial plants may divert part of their budget to storage, slowing down the N cycle. Also, large growth forms, such as trees, must invest more resources in long-life support tissues than smaller growth forms, such as herbaceous plants. Accordingly, when a non-native plant differs in growth rate, longevity, or growth form those prevailing in the native community, the plant tissue quality may change and the N cycle may be altered. As already explained, this type of alteration may be considered as "gradual," so that the magnitude of these impacts

would increase with the functional difference between the invader and the natives in the recipient ecosystem.

The addition of fertiliser in short-grass perennial-dominated steppe sites in Colorado promoted the invasion by the annual non-native grass *Kochia scoparia*. The litter properties of the annual invader increased the N cycling in soils of invaded sites (Vinton and Burke 1995). Similarly, in a podocarp-broadleaf forest in New Zealand, litter decomposition rate and N availability were found to be larger in soils beneath the invading perennial herb *Tradescantia fluminensis* than beneath uninvaded forests, where the vegetation is dominated by trees and shrubs (Standish et al. 2004). In New Zealand tussock grasslands, invasive conifer trees, which are much taller and have much deeper roots than native grasses, take up and hold more nutrients than the native community, presumably through increased mineralisation of the soil organic matter or through nutrient transfer from deeper soil horizons (Harding 2001).

Even if there is no change of the dominant life form or growth form after invasion, the tissue quality and quantity of the new dominant plant may be different from most natives in the recipient ecosystem, altering the N cycle. For instance, the non-native annual grass *Aegilops triuncialis*, which invades Californian serpentine annual grasslands, increases aboveground biomass twofold and produces a litter with higher lignin:N and C:N ratios, which decomposes less rapidly than litter from non-invaded plots (Drenovsky and Batten 2007). Litter produced by the non-native tree *Eucalyptus globulus* decomposes at a lower rate and drastically declined nitrification as compared with coexisting native trees in northwest Spain, probably because of its low N and high content of soluble polyphenols (Castro-Díez et al. 2012). Many species of the *Pinus* genus, naturalised mainly in the Southern Hemisphere, tend to decline the quality of the litter, which is often poorer in N and richer in lignin and secondary compounds than that of coexisting native trees. Consequently, pine introduction has been often found to deplete nutrients from upper mineral soil layers and to accumulate them in the overlying organic layer, and also to decrease N mineralisation as a result of its negative effects on soil bacteria (Simberloff et al. 2010; Scholes and Nowicki 1998). Further examples of changes to the N cycle by changes in the utilisation of N can be found in Table 4.1.

4.2.3 Alterations Mediated by Disturbances

Disturbances are widely recognised as key factors influencing the structure of plant communities, soil microbial activity, and therefore the N cycle (Pourreza et al. 2014; Bond et al. 2005). Given that some invaders may alter disturbance regimes, they may indirectly modify the N cycle.

Fire is one disturbance that may change upon invasion (Rabitsch et al. 2017). Invasive plants may alter the quality and quantity of fuel load and therefore the frequency and intensity of fires (Levine et al. 2003; D'Antonio 2000). Altered fire regimes may trigger a myriad of cascade effects on the structure and function of the

ecosystem, including changes in the N cycle. The combustion the organic matter (biomass, litter, or soil organic matter) represents a sudden mineralisation, that is, the liberation of mineral forms of N and other nutrients (paths 6, 9, and 13 in Fig. 4.1). Part of this inorganic N may be lost to the atmosphere as N oxides or leached by water runoff. The inorganic N remaining in the soil after the fire may be easily taken up by the first pioneer plants able to establish after the fire, which may include non-native opportunistic species. Therefore, an increased fire frequency by non-native plant invasions may increase the net loss of N from the ecosystem, accelerate the N fluxes, and change the balance between labile inorganic N and more durable organic N. Unfortunately, most studies reporting changes of the fire regime upon plant invasions (Rabitsch et al. 2017) do not directly address the impacts on the N cycle.

Changes of fire regime may also have indirect consequences on the N cycle. A remarkable example is that of the African grasses introduced in Hawaii, which promoted fire and declined native populations of fire-sensitive trees, such as *Metrosideros polymorpha*. The litter of this native tree is home to non-symbiotic N_2-fixing bacteria, which in turn do not develop in the litter of non-native grasses. Consequently, this change in the plant community leads to a reduction of N_2 fixation and therefore a decrease in N content in the invaded soils (Ley and D'Antonio 1998).

Certain non-native species may cause biotic disturbances previously absent in the recipient ecosystem. One such case is the wild boar, *Sus scrofa*, introduced in South America for hunting purposes. To obtain food, wild boars overturn extensive areas of soil, leaving behind areas bare of vegetation. In the Monte Desert biome of Argentina, the wild boar was found to enhance N mineralisation, probably because of increased soil moisture and oxygenation and the incorporation of litter into the soil (Cuevas et al. 2012). The increased mineral N and decreased vegetation cover may lead to a higher loss of soil N by runoff or volatilisation.

4.2.4   Alterations Caused by Changes in the Trophic Structure

Changes in the uppermost level of a trophic pyramid may have ecosystem effects disproportionate to the amounts of biomass involved. Animal invasions are particularly disruptive in oceanic islands, where the lack of certain trophic groups makes some species particularly vulnerable to introduced non-native species (Vitousek 1990). Addition of pigs, goats, or cattle on islands lacking large herbivores may lead to a catastrophic decline of primary producers. Given that plants are responsible for a great part of mineral N uptake from the soil, a drastic reduction of plant biomass will dramatically decline the proportion of N moving between the soil and the living organisms. The reverse effect may occur when a non-native predator is introduced to an island that has previously lacked predators capable of declining the populations of herbivores. Unfortunately, these types of studies rarely document impacts on the N cycle.

Invasion of non-native organisms belonging to existing trophic levels may also alter the N cycle by unbalancing the trophic structure. For instance, formerly glaciated regions of the northeastern United States have few native earthworm species, so the invasion of Asian earthworms decreased soil organic matter and increased N fluxes (Burtelow et al. 1998). The golden apple snail, *Pomacea canaliculata*, dramatically decreased aquatic plant populations in wetlands of Southeast Asia, which led to the dominance of planktonic algae, increasing N in water (Carlsson et al. 2007). The inordinate proliferation of the non-native freshwater mussels *Dreissena polymorpha* and *D. bugensis* in Lake Erie (USA) increased the ammonia excretion rate and reduced N turnover time (Conroy et al. 2005). The worldwide invader, the Pacific oyster, *Crassostrea gigas*, can establish dense populations that monopolize shorelines. In a field experiment, this species increased total oxidized N in the sediment and NH_4^+ in the pore water (Green et al. 2012). In a Spanish floodplain wetland, the extreme proliferation of the benthic omnivorous American red swamp crayfish, *Procambarus clarkii*, reduced the submerged vegetation and periphyton-grazing snails. As a consequence, N previously bound to sediments passed to the water column, becoming available for algae (Angeler et al. 2001). A similar effect is caused by the common carp, *Cyprinus carpio*, a fish invasive worldwide.

4.3 Are There General Trends on the Impact of Invaders on the N Cycle?

The diversity of impacts reported by different case studies (see Table 4.1) raises the question of whether there is a prevalent type of impact upon invasion by non-native species. This question began to be addressed for plant communities at the beginning of the twenty-first century and still continues to be explored, thanks to the growing number of studies available in the literature. The first major review was performed by Ehrenfeld (2003), who identified 79 papers comparing pools and fluxes of N, C, and water under non-native plants and under co-occurring or displaced natives. Ehrenfeld (2003) followed a vote-counting approach where, for each selected variable, the direction, but not the magnitude, of the change was noted. The main generalisations emerging from this seminal study were that invasive non-native species, as compared with associated natives, tend to have higher standing biomass and primary production; to produce litter that decays faster; and have soils beneath them that tend to have higher mineralisation rates and microbial N mass than noninvaded soils.

The publication of additional studies and the development of meta-analytical techniques allowed Liao et al. (2008) to revisit Ehrenfeld's conclusions. Using 94 studies, they quantified the changes of C and N pools and fluxes as the ratio of the mean value of a concerned variable in the invaded and in the uninvaded ecosystem. Moreover, this study posed the question of how impacts vary depending on the

attributes of recipient ecosystems (forest, grassland, or wetland) and of the invaders (life form and N_2 fixation ability). This analysis confirmed most of Ehrenfeld's previous conclusions (i.e., plant invasion increases N pool sizes in plants, soils, and microbes, as well as primary production and rates of litter decomposition and soil N mineralisation). For most of the reported N pools and fluxes, the impact of woody and N-fixing invaders was greater than that of herbaceous and non-N fixing invaders, respectively. However, the impact was similar among forests, grasslands, and wetlands.

Three years later and using the same meta-analytical approach, a new synthesis of 199 articles on the impacts of non-native plants across different levels of ecological complexity, including variables related to the N cycle, was published (Vilà et al. 2011). Again, the question of how an attribute of the recipient ecosystems (island vs. mainland) and of the invaders (N_2-fixing ability) modulate the impact was addressed. Some of the reported impacts coincided with those previously described (increase of plant production and mineral N), but impacts on other variables did not significantly differ from zero (N mineralisation, litter decomposition). These discrepancies suggest that the variability of responses across studies is too great to derive generalisations. A small part of this variability was explained by the fact that N_2-fixing invaders increased N pools and N nitrification more than non-N_2-fixing invaders, but not by the insularity of the invaded ecosystem.

Pyšek et al. (2012) adopted a new approach to perform a global assessment of invasive plant impacts on the ecosystems by using classification trees. This tool allowed the authors to examine complex interactions among impact, the invaders' traits (those that might facilitate recruitment, competition and resistance to generalist herbivores), and environmental properties (the invaded region, biome, and habitat). Based on a total of 287 publications, this study found, among other results, that N content in plant tissues and soils, along with litter decomposition rate, were more often reported to increase than to decrease upon invasion. In contrast to previous studies, plant productivity was more often found to decrease. This study also revealed that taller species (>1.2 m) have more chances to impact plant productivity. Unfortunately, no pattern of plant traits and site characteristics was found for impacts on soil nutrient content.

The issue of the variability of impacts of plant invaders on the N cycle across studies was specifically targeted by a more recent meta-analysis (Castro-Díez et al. 2014). Based on 100 published articles and 345 case studies, the authors tested whether the impact size on N pools and fluxes depends on properties of the invaded site (disturbance, residence time, climate, insularity, or biome) or on functional and phylogenetic distinctiveness between the invader and the native species. This synthesis, along with previous ones, provided strong evidence that, overall, invasion by non-native plants increase total N pools and speed up N fluxes (Table 4.2). Again, a large variability of impacts across studies became evident, highlighting the relevance of the invasion context. Climate was found to be a relevant factor explaining variability: the invader's impact on N fluxes was greater under warm and moist conditions. This finding was attributed to the fact that the enzymatic reactions

Table 4.2 Number of case studies quantifying the impacts of plant invasions on the N pools and fluxes represented in Fig. 4.1 in four published meta-analyses

Pool/Flux	Code in Fig. 4.1	Liao et al. (2008)	Vilà et al. (2011)	Pyšek et al. (2012)[a]	Castro-Díez et al. (2014)
N-pools					
Plant/microbial biomass	10	49 (+)	–	60 (+)	47 (+)
Litter mass	3	–	–	–	54 (+)
Soil organic matter	5	83[b] (+)	26 (=)	–	36 (=)
Soil mineral N	7	88[c] (+)	47 (+)	436[d] (+)	45 (=)
N fluxes					
N₂ fixation	1	–	–	–	–
Litterfall	2	–	–	–	–
Litter decomposition	4	58 (+)	13 (=)	25 (+)	71 (=)
N mineralisation	6	58 (+)	11 (=)	–	23 (+)
Plant N uptake	8	42 (+)	90 (+)	105 (−)	69 (+)
N volatilization	9	–	–	–	–
N loss by runoff	11	–	–	–	–
Organic N uptake	12	–	–	–	–
Burning of biomass	13	–	–	–	–
Denitrification	14	–	–	–	–

The +, − or = sign in parentheses beside each figure indicates whether the variable measured in the invaded sites was on average greater, smaller, or not significantly different from the noninvaded sites

[a]This study only reports the number of cases where the variable was reported to increase or decrease upon invasion, with no statistical analysis to test whether any response was more frequent than the other. We show the most frequent response

[b]Number of case studies reporting soil carbon pool

[c]Number of cases reporting soil N pools, with no distinction between organic and inorganic N

[d]Number of cases reporting pools of any nutrient (not only N) on soils

involved in the N cycle are generally faster at higher temperatures, particularly if water availability is not limiting. This study also found stronger impacts on N pools when the invasive plants were N₂ fixing, tall, annual, or deciduous and the natives possess the reverse traits, according to the classic hypothesis that invaders that are functionally more different from natives have greater impacts on ecosystem properties (Chapin et al. 1996; D'Antonio and Corbin 2003). Other tested factors (residence time, whether the study was experimental or observational, or if the impact was mediated by disturbance) failed to explain impact variability, perhaps because some of them have effects only at a local scale.

Overall, considering several hundred field studies, the general trend of nonnative plants to increase N pools and accelerate N fluxes within the ecosystem is strongly supported. Yet, there is also strong evidence of the wide variability and context dependency of the impacts. Finally, there is insufficient knowledge to derive general trends of how invaders alter the net ecosystem gains and losses of N (solid and double-dahsed arrows in Fig. 4.1).

4.4 Limitations of Current Knowledge and Future Research

The best knowledge we have so far on the impacts of non-native species on the N cycle is based on the syntheses of published field studies. But does this information reflect what happens in nature? Several authors have warned about the tendency of scientists to select case studies where dramatic impacts are more likely (Levine et al. 2003; Hulme et al. 2013). In fact, Castro-Díez et al. (2014) found that N_2-fixing species (those with higher potential to alter the N cycle) accounted for 21 % of the 345 reviewed case studies, although the average proportion of N_2-fixing invaders across different databases worldwide is 15 %. Hulme et al. (2013) highlighted that only a small proportion of non-native plants causing impacts worldwide have been the target of robust quantitative assessments and that scientists tend to select species already studied. Accordingly, only 9 and 12 species accounted for one-third of the case studies reviewed by Hulme et al. (2013) and by Castro-Díez et al. (2014), respectively. The selection of variables accounting for impacts on the N cycle is also biased. On average, impacts on N pools are more studied than impacts on fluxes. Only 3 of the 10 N fluxes of Fig. 4.1 (litter decomposition, N mineralisation, and plant N uptake) were covered by any of the four syntheses (Table 4.2). Terrestrial ecosystems have been explored much more frequently than aquatic ecosystems in the available reviews. Only Liao et al. (2008) explicitly included impacts on wetlands, but the number of case studies was only 5 % to 17 % of the total (table S2 of Liao et al. 2008). Castro-Díez et al. (2014) specifically targeted terrestrial ecosystems, and Vilà et al. (2011) and Pyšek et al. (2012) were not explicit about the inclusion or non-inclusion of aquatic ecosystems. Finally, we are not aware of any review addressing the impacts of non-native animals on the N cycle. Therefore, to have a complete and unbiased picture of the overall impacts of invasions on the N cycle, future research should explore the impacts of non-native animals, address more N-cycle variables (particularly net ecosystem gains and losses of N, see Table 4.2 and Fig. 4.1, solid and double-dashed arrows), and include more case studies from aquatic ecosystems.

From an applied perspective, a relevant challenge to prioritize the management of non-native species at a particular site is to know whether the impact of non-native species can be predicted from the knowledge of previous impacts in other sites, or even from other regions. Evidence suggests that impacts of the same species may largely vary in magnitude and even in direction across different contexts. Part of this variation may be explained by climatic factors and by the functional novelty of the invasive species, but another great part of the variation is the result of local and historical factors, such as community structure, soil properties, disturbance, or residence time. Hulme et al. (2013) demonstrated that the variability of a given impact increases with the number of studies, and emphasised that results from single studies at single locations or years might not be widely generalisable. Unfortunately, according to the data collected by Castro-Díez et al. (2014), the number of invasive species in which the impacts on the N cycle have been quantified several times by independent studies in different locations is very low. In summary, in addition to increasing the number of explored species, variables and ecosystem types, more information is needed on the impacts of the same species across different sites and times.

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