



Review

Nitrogen deposition effects on Mediterranean-type ecosystems: An ecological assessment

Raúl Ochoa-Hueso^{a,*}, Edith B. Allen^b, Cristina Branquinho^c, Cristina Cruz^c, Teresa Dias^c, Mark E. Fenn^d, Esteban Manrique^a, M. Esther Pérez-Corona^e, Lucy J. Sheppard^f, William D. Stock^g

^a Department of Plant Physiology and Ecology, Centro de Ciencias Medioambientales, Consejo Superior de Investigaciones Científicas, C/Serrano 115 Dpto., 28006 Madrid, Spain

^b Department of Botany and Plant Sciences and Center for Conservation Biology, University of California, Riverside, CA 92521, USA

^c Universidade de Lisboa, Faculdade de Ciências, Centro de Biologia Ambiental, Campo Grande, Bloco C4, 1749-016 Lisboa, Portugal

^d US Department of Agriculture (USDA) Forest Service, Pacific Southwest Research Station, 4955 Canyon Crest Drive, Riverside, CA 92507, USA

^e Department of Ecology, Faculty of Biology, Universidad Complutense de Madrid, C/José Antonio Novais 2, 28040 Madrid, Spain

^f Centre of Ecology and Hydrology, Bush Estate, Penicuik EH26 0QB, UK

^g Centre for Ecosystem Management, School of Natural Sciences, Edith Cowan University, 100 Joondalup Drive, Joondalup, Perth, WA 6027, Australia

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ABSTRACT

We review the ecological consequences of N deposition on the five Mediterranean regions of the world. Seasonality of precipitation and fires regulate the N cycle in these water-limited ecosystems, where dry N deposition dominates. Nitrogen accumulation in soils and on plant surfaces results in peaks of availability with the first winter rains. Decoupling between N flushes and plant demand promotes losses via leaching and gas emissions. Differences in P availability may control the response to N inputs and susceptibility to exotic plant invasion. Invasive grasses accumulate as fuel during the dry season, altering fire regimes. California and the Mediterranean Basin are the most threatened by N deposition; however, there is limited evidence for N deposition impacts outside of California. Consequently, more research is needed to determine critical loads for each region and vegetation type based on the most sensitive elements, such as changes in lichen species composition and N cycling.

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1. Introduction

Fertilizer production (Haber–Bosch reaction), intensification of agricultural production and fossil fuel combustion have increased inputs to and losses from the global nitrogen (N) cycle. The outcome is a host of environmental problems such as eutrophication and acidification of terrestrial and aquatic ecosystems (Gruber and Galloway, 2008). Nitrogen deposition impacts on the biodiversity of major terrestrial ecosystems worldwide have been recently revisited and critical loads for these effects have been re-evaluated and revised (Bobbink et al., 2010); changes in species richness in European temperate acidic grasslands have also been described along current and historical N deposition gradients (Stevens et al., 2004; Duprè et al., 2010). In addition, long-term field fertilization experiments within temperate Europe and Eastern US have tested

the hypothesis that N is a key driver of ecosystem structure and function (Bobbink et al., 1998, 2010). However, the potential ecological effects of N deposition on Mediterranean climate areas have been investigated less (Bobbink et al., 2010), even though they are usually recognized as hot-spots of biodiversity (Myers et al., 2000). This represents a big gap in our knowledge, as the understanding gained from ecosystems where wet deposition dominates, depositing relatively low-N doses at high frequency, will be of limited value to understanding how systems that are seasonally water-limited, where dry deposition is cumulative, and where fires occur naturally and are frequent, will respond to enhanced reactive N deposition.

Despite the predicted increase in N inputs to the Mediterranean Basin, from $\sim 7 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ in mid-1990s to $\sim 12 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ in 2050 on average, (following estimates in Phoenix et al., 2006), a recent synthesis (Bobbink et al., 2010) only identified one publication addressing the potential effects of N deposition on the biodiversity of Mediterranean ecosystems, in this case a semi-natural Italian grassland (Bonanomi et al., 2006). Shrublands and

* Correspondence author.

E-mail address: raul.ochoa@ccma.csic.es (R. Ochoa-Hueso).

woodlands of the Mediterranean Basin (matorral, monte bajo, garrigue, macchia, phrygana) are, consequently, poorly investigated with regard to the potential effects of elevated anthropogenic N (Bobbink et al., 2010; Ochoa-Hueso and Manrique, 2010b). Other Mediterranean ecosystems are even less studied (for example, Chilean matorral, South African fynbos and renosterveld or Australian kwongan and mallee) even though N deposition is also predicted to increase in these areas, although to a lesser extent (Table 1; Phoenix et al., 2006).

Currently, most of the research on the impacts of N deposition on Mediterranean ecosystems has been conducted in California (Table 1; Fenn et al., 2000, 2003a, 2008, 2010; Takemoto et al., 2001; Allen et al., 1998, 2005). These Mediterranean-type ecosystems (mixed conifer forest, chaparral, coastal sage scrub, etc.) have received chronic N inputs exceeding recently determined empirical N critical loads ($3\text{--}17\text{ kg N ha}^{-1}\text{ yr}^{-1}$) for various ecosystem parameters (Fenn et al., 2008, 2010, *in press*). Evidence for such critical loads has come from field fertilization experiments or gradient-based studies (Fenn et al., 2008, 2010, *in press*) and are based on different indicators (e.g., shifts in lichen community, exotic grass invasion, decrease in native plant species and forb richness, nitrate leaching losses, etc.) (Fenn et al., 2008, 2010, *in press*).

A general critical load of $\sim 10\text{ kg N ha}^{-1}\text{ yr}^{-1}$ (based on N leaching) has been defined for temperate and boreal ecosystems of Europe (Dise and Wright, 1995), and lower critical loads $<7.5\text{ kg N ha}^{-1}\text{ yr}^{-1}$ have been reported for these ecosystems based on sensitive organisms such as lichens (Britton and Fisher, 2010). However, critical loads for Mediterranean ecosystems of Europe have only been rarely identified (Pinho et al., 2009 Table 1). Because of the scarcity of data, critical loads or levels for N deposition effects are not available for any of the other three Mediterranean regions, i.e., excluding Europe and California. Moreover, the significantly greater research database for California has led to the adoption of this region as a model to predict N deposition impacts on other areas with Mediterranean climate. However, despite similarities, there are a wide range of differences in climate and soils among these areas (see below) potentially conditioning effects of increased N inputs and of other global change factors (Table 1).

The main purpose of this article is to review current knowledge about N deposition impacts on natural and semi-natural Mediterranean-type ecosystems. When possible, discussion focuses on areas other than California as reviews are already available for this region (Bytnerowicz and Fenn, 1996; Fenn et al., 1999a,b, 2003a,b,c, 2008, 2010, *in press*; Takemoto et al., 2001). The article has been divided into sections addressing the following aims:

1. Demonstrate the importance of taking into account the impacts caused by N deposition on Mediterranean-type ecosystems (Section 2. Mediterranean ecosystems).
2. Summarize the estimated N deposition loads to the different Mediterranean regions (Section 3. Nitrogen deposition estimates in Mediterranean Regions).
3. Demonstrate how N dynamics in Mediterranean-type ecosystems are/could be altered by N deposition (Section 4. Natural and altered-N cycling in Mediterranean ecosystems).
4. Demonstrate the role of water and other nutrients (mainly P) in ecosystem responsiveness to N deposition (Section 5. Water and P availability condition response to N deposition).
5. Review what is known about N deposition impacts on different groups of organisms, i.e., cryptogams, higher plants, animals, mycorrhizae and soil microbial communities, forming part of Mediterranean ecosystems (Section 6. Experimental evidence of N deposition impacts on Mediterranean ecosystems).
6. Discuss potential interactions of N deposition with other global change drivers, such as climate change, biotic invasions, land-

use change and ozone, co-occurring in Mediterranean regions (Section 7. Likely interactions of N deposition with other global change drivers).

7. Highlight current strategies to manage/mitigate N deposition impacts (Section 8. Mitigation strategies) and suggest future research lines to improve our current understanding of N deposition impacts on Mediterranean ecosystems (Section 9. Future work and conclusions).

Our final aim is to stimulate ongoing debate, encourage research, and to create a common framework to determine critical thresholds, and also to identify early-warning signals before these thresholds are reached, for different Mediterranean-type ecosystems (Scheffer et al., 2009).

2. Mediterranean ecosystems

2.1. What is a Mediterranean-type ecosystem?

Mediterranean-type ecosystems are found in five regions of the globe: California, central Chile, Mediterranean Basin, southern Cape region and south western and southern Australia, between 40° and 32° latitude, and where land is influenced by cold offshore ocean currents (Fig. 1; Cody and Mooney, 1978). The flora of the Mediterranean areas is one of the richest in the world, and annual grasslands, shrublands, dry woodlands and forests are typical (Archibald, 1995; Cowling et al., 1996). The climate is highly seasonal and characterized by warm, dry summers, i.e., by a seasonal-drought, and cool, rainy winters. Spring and autumn are usually the growing seasons.

2.2. Soils in Mediterranean regions

Soils are rather variable (even within the same region), usually rich in bases when compared to more mesic systems. Consequently, acidification impacts as consequence of N deposition are predicted to be less important than those caused by eutrophication (Bobbink et al., 2010). Acidification has, however, been reported in soils from forests (Breiner et al., 2007) and shrublands (Vourlitis et al., 2009) of semi-arid California and in soils in Spain subjected to N fertilization (Ochoa-Hueso and Manrique, 2010a).

Soils in South Africa and Australia are geologically older and nutrient-poor (especially P) when compared with those of the Mediterranean Basin, Chile and California, which are younger and more fertile (Kruger et al., 1983). Mediterranean-type ecosystems are frequently reported as N-limited but primary production and responsiveness to extra N are mostly limited by water and conditioned by P (Kruger et al., 1983; Xia and Wan, 2008).

2.3. What are currently the main threats for Mediterranean-type ecosystems?

The Mediterranean Basin and California are the most populated, and thus impacted, areas with Mediterranean climate (Table 1). However, the outskirts of Cape City in South Africa and Perth in SW Australia have also seen unprecedented rates of growth during the last years, with consequent impacts on the environment. Therefore, together with land-use change, i.e., loss of natural and semi-natural habitats, and climate change, N deposition is predicted to increase in these regions and to have a major impact on their biodiversity (Sala et al., 2000; Phoenix et al., 2006).

Dry deposition is usually the main form of atmospheric input (up to 90% depending on the regional climate, vegetation type and orography but usually between 30 and 70%, Fig. 2) in Mediterranean systems and N frequently accumulates in soil and

Table 1

General characteristics of the different Mediterranean-type ecosystems and what we know concerning ecological effects of N pollution.

	Australia	Cape region	Mediterranean basin	California	Chile
Main vegetation types ^a	Forests; woodlands; mallee; heath; kwongan; reed swamps; halophytes	Forest and thicket; karroid and renoster shrubland; grassland and grassy shrubland; fynbos	Broadleaved-evergreen forest; coniferous forest; oak woodlands; savanna; matorral; steppe/grassland; semi-desert	Coniferous forest; broadleaved-evergreen forest; oak woodland/savanna; riparian woodland; chaparral; coastal sage scrub; grassland	Matorral; espinal (savanna); hygrophilous forest
Soils ^{a,c}					
Siliceous	++++	++++	++	++	–
Argillaceous and mafic rocks	+	+++	+	++++	++++
Calcareous	+	++	++++	+	–
Phosphorus ^a	Low	Low	Medium	Medium-high	High
Fires	Natural	Natural	Natural	Natural	Non-natural
Predicted average increase in kg N ha ⁻¹ yr ⁻¹ by 2050 ^b	~(1→1)	~(3→10)	~(7→12)	~(3→4)	~(2→5)
Area (%) receiving > 10 kg N ha ⁻¹ yr ⁻¹ by 2050 ^b	n.a.	41,7	68,9	15 (Estimated from current value of 13%; Fenn et al., in press)	n.a.
Estimated critical loads or critical levels	n.a.	n.a.	Epiphytic lichens (1 µg m ⁻³ NH ₃ ; Pinho et al., 2009)	Epiphytic lichens (3–5 kg N ha ⁻¹ yr ⁻¹ ; Bobbink et al., 2010; Fenn et al., 2008); Nitrate leaching (14–17 kg N ha ⁻¹ yr ⁻¹ ; Fenn et al., 2008, 2010); Invasive species in coastal sage scrub (8–10 kg N ha ⁻¹ yr ⁻¹ ; Fenn et al., 2010); Invasive species in serpentine grassland (6 kg N ha ⁻¹ yr ⁻¹ ; Fenn et al., 2010)	n.a.
Bio-indicators	n.a.	Increase of ephemeral species in fynbos (Witkowski, 1989a); Moss tissue N and C:N ratio (Wilson et al., 2009)	Moss and lichen tissue and plant litter N and C:N (Fratl et al., 2007; Peñuelas and Filella, 2001; Dias et al., unpublished); extracellular ammonium and functional diversity of lichens (Pinho et al., 2009; Branquinho et al., 2010); N fixation by cyanobacterial crust in semi-arid sites (Ochoa-Hueso and Manrique, unpublished)	Increase in exotic grasses and decrease in native species; changes in mycorrhizal and epiphytic lichen communities and lichen tissue N concentrations (Bobbink et al., 2010; Fenn et al., 2010, in press)	Increase in European herbs (Holmgren et al., 2000)
Main type of pollutant	n.a.	NO _x around the Metropolitan Cape region (Wilson et al., 2009)	Livestock (e.g., Segovia and Catalonia) and crops (e.g., Murcia and Almería) are sources of NH ₃ ; urbanization and major transport networks (highways, shipping routes, etc.) are the main sources of NO _x (Theobald et al., 2010). Dry deposition is dominant but this also depends on topographic effects	Motor vehicles are the main emitters of NO _x (Fenn et al., 2003a); NH ₃ from agriculture and from cars equipped with 3-way catalytic converters is also a widespread problem. Sulfur deposition has historically been and continues to be much lower than N deposition.	n.a.
Physical forms of atmospheric deposition	n.a.	n.a.	Dry deposition is dominant but this also depends on topographic effects	Dry deposition dominates, although in many areas fog or cloudwater inputs are significant inputs for N	n.a.
Level of current concern ^d	+	+++	++++	++++	+
	N and P pollution are possibly leading to an increase in the grassiness of the systems which in turn could alter the fire cycle (William Stock, personal observation)		Nitrophilous plants (both grasses and forbs) are becoming more dominant, especially in wet years.	Major effects are eutrophication responses causing changes in vegetation communities, with implications for the fire cycle; altered plant root:shoot ratios; and forest susceptibility to bark beetles. Soil acidification has also occurred in the most polluted sites.	

^a Modified from Hobbs and Richardson (1995).^b Phoenix et al. (2006).^c Relative frequency.^d Based on expert judgment.

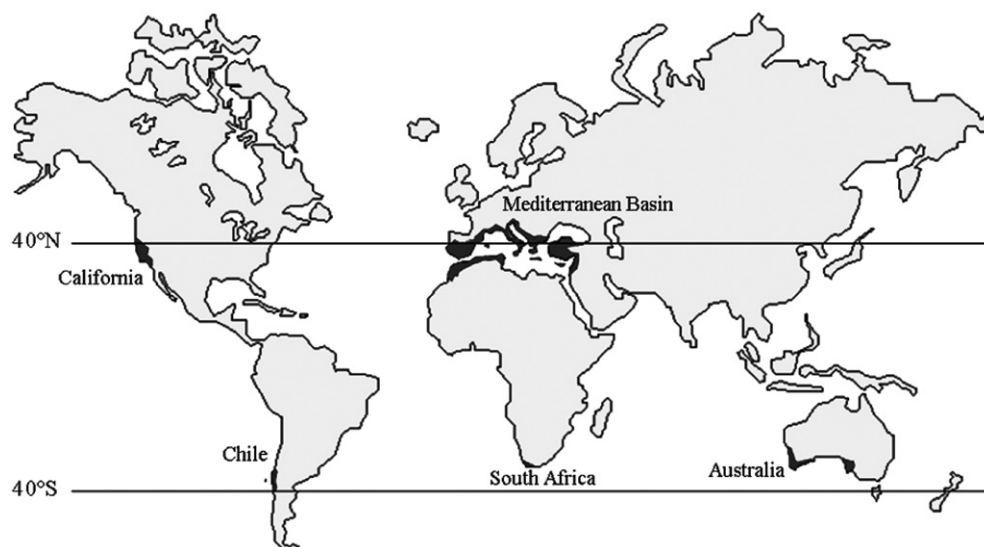


Fig. 1. The five regions of the world with a Mediterranean climate.

on plant surfaces during dry periods, becoming available as high-N concentration pulses with rainfall events (Bytnerowicz and Fenn, 1996; Fenn et al., 2003a,b,c). These anthropogenic N inputs, together with the introduction of alien species from other equivalent Mediterranean regions, are currently amongst the main threats to Mediterranean ecosystems, as they usually lead to altered fire cycle and loss of native species as a consequence of competitive exclusion (Stock and Lewis, 1984; Allen et al., 1998; Holmgren et al., 2000; Lambrinos, 2000; Minnich, 2008; Fisher et al., 2009).

Rural abandonment in the Mediterranean Basin, coupled with increasing N deposition, is compromising the existence of semi-natural grasslands subjected to periodic N loss in biomass removal (Hobbs and Richardson, 1995; Bonanomi et al., 2006). Habitat fragmentation in Mediterranean areas also separates wildlife populations and provides a point of entrance for non-native and often invasive and N-loving plant and animal species, threatening the native biodiversity (Fisher et al., 2009). For example, Sharma et al. (2010) have shown a significant decrease in cover of the invasive grass *Avena fatua* L. from the edges to the interior of South

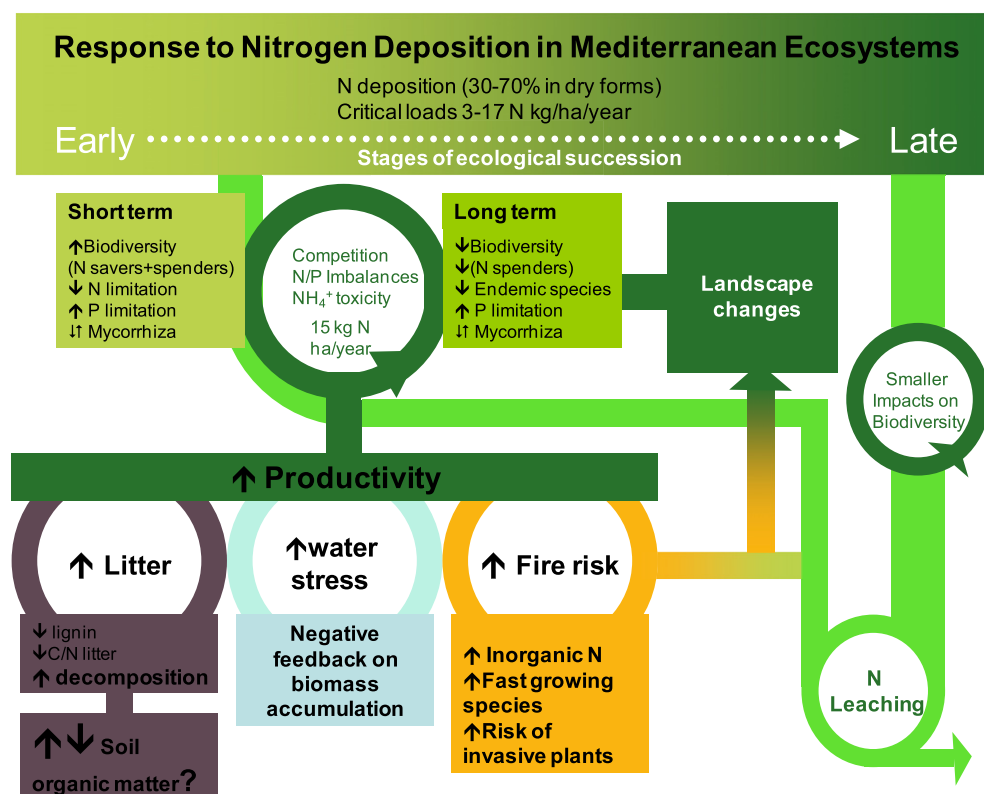


Fig. 2. Mechanisms involved in the response of Mediterranean ecosystems to N deposition and functional and structural consequences.

African renosterveld habitat fragments, a response probably regulated by lower N availability in the interior.

2.4. What is the role of fire in Mediterranean ecosystems and how N deposition can alter the fire cycle?

Fire is a natural element in Mediterranean ecosystems (except in the Chilean matorral) that governs nutrient dynamics and energy pathways (Aschmann and Bare, 1977). Fire frequently leads to transient flushes of N (as high as 66 kg N ha^{-1}) and P availability in recent post-fire conditions (Stock and Lewis, 1986a; Vourlitis et al., 2007a). As these ecosystems are adapted to fire, there is a suit of herbaceous “fire-followers”, as well as seeder and re-sprouter shrubs, that appear soon after a fire event. Then, “N-savers” tend to replace “N-spenders” as soil N levels decrease along the ecological succession.

In semi-arid Mediterranean sites, herbaceous productivity in late-successional stands is usually very limited and shrubs are frequently disconnected in a low-productivity matrix. However, elevated soil fertility caused by N deposition favors dry biomass accumulation, frequently of grasses and nitrophilous forbs such as thistles, etc., i.e., of highly flammable fuel, during the dry season; abandonment of traditional agricultural practices (such as shepherding, mowing, etc.) also leads to biomass accumulation. This accumulation of fine fuel connecting otherwise isolated shrubby patches, frequently coupled with climate alteration, especially when particularly wet springs and hot/dry summers co-occur, is able to alter the fire regime and its severity (Lavorel et al., 1998; Lloret, 2004; Bonanomi et al., 2006) by creating a continuum of flammable material (Fig. 2). The consequence of this is a dramatic change in the landscape and, when fires occur close to populated areas, the impact of N pollution on herbaceous productivity can be also considered as very important for the human well-being and the economy.

3. Nitrogen deposition estimates in Mediterranean regions

As a consequence of the dominance of dry N deposition, up to 90%, in Mediterranean ecosystems (Bytnerowicz and Fenn, 1996; Anatolaki and Tsiouridou, 2007) and the general lack of appropriate monitoring networks, N deposition estimates in most Mediterranean areas remain quite uncertain (Fenn et al., 2009, 2010; EMEP, 2010).

3.1. California

The best estimates for N deposition rates in Mediterranean areas are those available for Californian ecosystems. The highest rates occur to forests in the more exposed regions of southern California (30 to over $70 \text{ kg N ha}^{-1} \text{ yr}^{-1}$). However, vast areas of forests, woodlands, shrublands and grasslands receive only low atmospheric N inputs ($\sim 2\text{--}5 \text{ kg N ha}^{-1} \text{ yr}^{-1}$) (Fenn et al., 2008, 2010). Deposition of reduced forms of N (NH_x) is of increasing importance in ecosystems of California, in areas influenced by either urban or agricultural emissions (Fenn and Poth, 2004; Fenn et al., 2003b; Mark Fenn, unpublished data). Fog has also been described as an important source of N in these systems, e.g., providing 33% of total N deposition in the San Bernardino Mountains, to the east of Los Angeles (Fenn et al., 2000); however, this form is usually ignored because normal wet and dry samplers fail to capture it (Fenn and Poth, 2004). Fog-derived N deposition has not been estimated for any other Mediterranean region, but the importance of its contribution to the total N inputs is expected to be generalized as most regions have fog.

3.2. Europe

In general, only a few and geographically scattered studies estimating N deposition loads are available for the Mediterranean Basin (e.g., Rodà et al., 2002; Sanz et al., 2002; Ávila et al., 2010). The EMEP (European Monitoring and Evaluation Program under the Long-range Transboundary Air Pollution) model provides modeled estimates of N deposition loads for this region. However, the scarcity of monitoring stations across southern Europe, together with dry deposition underestimation, means that these estimates have large uncertainties (EMEP, 2010). For airborne total nitrate (NO_3^-) and ammonium (NH_4^+), the spatial coverage is slightly better in the western Mediterranean (Spain and Portugal have several stations) than in eastern regions (EMEP, 2010).

In the particular case of Spain, and like most of European countries, the spatial distribution of emissions is not homogeneous. Reduced N emissions mainly originate from agricultural activities and the main hot-spots are in Catalonia (pig farms), Segovia (pig farms) and Murcia (horticulture) whereas hot-spots for oxidized N emissions surround major cities (e.g., Madrid and Barcelona), industrial areas, power stations and shipping routes (Theobald et al., 2010). For example, wet inorganic N deposition has been found to range from $\sim 4\text{--}7 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ across five rural sites in Catalonia, NE Spain; however, if estimates of dry deposition are included, total annual N deposition rises to $10\text{--}20 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ (Ávila et al., 2010). At the national level in Portugal there are approximately 70 air quality monitoring stations for NO_x that run continuously in urban, suburban and rural areas. However, there are no NH_3 monitoring stations at the national level. Thus, air quality and the deposition of NH_3 are only based on statistical information and air deposition models and not validated with flux measurements to the appropriate vegetation (Martins-Loução, in press). Knowing that most of the Iberian (both Portuguese and Spanish) Natura 2000 Network is located in rural areas with high agriculture and livestock activities, assessment of the impact of NH_3 with high spatial resolution on biodiversity and ecosystem function must be a priority for this region.

Similarly, bulk N loads of $\sim 13 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ have been measured in high elevation northern Italian forests, with organic N constituting 17% of the flux (Balestrini and Tagliaferri, 2001). Deposition as high as $15\text{--}18 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ were measured in the same study as throughfall inputs, 40% being organic N (Balestrini and Tagliaferri, 2001), suggesting the importance of this form of N in deposition; although it has to be said that throughfall does represent interaction with the canopy (both uptake and leaching) and may not be wholly representative of deposition. In Greece, Michopoulos et al. (2004) have found bulk N deposition values of $\sim 15 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ in Aleppo pine stands close to Athens; throughfall was much higher, indicative of dry deposition capture, reaching values of $\sim 38 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ (Anatolaki and Tsiouridou, 2007) have also measured similar N deposition values ($\sim 15 \text{ kg N ha}^{-1} \text{ yr}^{-1}$) at an urban site in the center of Thessaloniki, Greece, with dry forms accounting for 70–90% of total N inputs.

3.3. Australia

There are no estimates of atmospheric N deposition available for SW Australia; however, the Department of Environment and Conservation of Western Australia has 10 stations monitoring NO_2 and other pollutants in the Perth metropolitan region (DEC, 2005, 2006). In 2005, all stations registered averaged values below 0.12 ppm (over 1 h) and 0.03 ppm (over 1 year), which are the NEPM (National Environment Protection Measures) standards for this pollutant (DEC, 2005). Most of the region is, however, unpopulated and based on the low NO_x data we may conclude that anthropogenic N inputs are low.

3.4. South Africa

The number of vehicles in the Cape Metropolitan Area has increased by 80% over the past 20 years which has resulted, together with the rapid urbanization and industrialization, in increased N deposition; current estimates in the Cape Town Metropolitan area range from 6 to 13 kg N ha⁻¹ yr⁻¹ (Wilson et al., 2009). In contrast, estimated atmospheric N deposition at unpolluted fynbos sites located more than 60 km from Cape Town was <2 kg N ha⁻¹ yr⁻¹, with a significant proportion of the total N input being of organic origin (Stock and Lewis, 1986b).

3.5. Chile

Dry deposition in central Chile has been estimated at 0.8 kg NO₂-N ha⁻¹ yr⁻¹ and 1.0 kg NH₃-N ha⁻¹ yr⁻¹ with 0.4 kg NO₃-N ha⁻¹ yr⁻¹ and 0.8 kg NH₄-N ha⁻¹ yr⁻¹ in wet deposition, providing in total 2.8 kg N ha⁻¹ yr⁻¹ (Godoy et al., 2003 and references therein). Dry gaseous NH₃, as result of intensification of agriculture is, consequently, the main atmospheric N input to the Chilean matorral (Godoy et al., 2003). However, as was the case for Australia, N deposition across most of the Chilean territory is predicted to be low.

4. Natural and altered-N cycling in Mediterranean ecosystems

4.1. Nitrogen dynamics and climate seasonality

Natural nutrient (including N) cycling and N deposition in Mediterranean-type ecosystems are highly seasonal processes conditioned by the Mediterranean climate (Bonilla and Rodà, 1992; Gallardo et al., 2000). This is because nutrient cycling is primarily affected by water availability and soil organic matter (soil C content and C:N ratio) during the annual cycle rather than by plant community type (Rutigliano et al., 2009).

Net N mineralization and nitrification frequently peak in spring and summer and contribute, with N deposition, to increase the N concentration in soils to unusually high levels at the end of these seasons. Net N mineralization and nitrification are at their lowest in autumn when microbial biomass production usually contributes to N immobilization (Bonilla and Rodà, 1992; Gallardo et al., 2000). In sites where litter accumulation is very low or where soils become severely moisture-limited, N mineralization and nitrification rates can also decrease dramatically in summer (Castaldi and Aragosa, 2002). Extractable NO₃⁻ and NH₄⁺ are consequently higher early in the wet season (Vourlitis et al., 2007a), although their availability can also be altered by tree/shrub canopy cover (depending on litter inputs, moisture retention, allelopathic effects and also on exchange processes influencing throughfall N deposition) (Gallardo et al., 2000), demonstrating the role of vegetation spatial heterogeneity on soil N (Cruz et al., 2008). In Mediterranean shrublands (Carreira et al., 1994; Vourlitis et al., 2007a,b) and forests (Fenn et al., 2005), net nitrification usually dominates over denitrification, the latter being restricted by soil water content, and can be either increased or reduced by atmospheric N inputs depending on the level of N limitation, N toxicity (mainly NH₄⁺) and production of nitrification inhibitors (Ochoa-Hueso et al., unpublished manuscript). In California chaparral and forest stands the soils actively nitrify N that is mineralized so inorganic N in soil is predominantly as NO₃⁻ (Vourlitis et al., 2007a,b; Vourlitis and Zorba, 2007).

Increased mineral N in soils is frequently attributed to (i) drying and rewetting periods leading to microbial cell lysis (Austin et al., 2004), (ii) net N mineralization (iii) fires and, (iv) dry deposition of N (Bytnerowicz and Fenn, 1996; Fenn et al., 2009; Padgett et al., 1999) and, when co-occurring, these processes can lead to

extremely high inorganic N concentrations in soil. Summer dry deposition (as aerosols or particles) is favored by thermal inversions, atmospheric washout with rains also being important for nutrient (including N) and particle inputs after rainless periods.

In the Mediterranean Basin, Saharan dust transported by northward winds provides an additional major seasonal contribution to N inputs, mainly NO₃⁻, to aquatic and terrestrial ecosystems (Moulin et al., 1997; Goudie and Middleton, 2001). Saharan dust is also highly enriched in calcium carbonate, which contributes to neutralize rain acidity thus reducing the likelihood of soil acidification (Ávila and Rodà, 1991).

Nitrogen loss from soils occurs as: (i) NO₃⁻ leaching during and after rain events, (ii) plant and microbial uptake (during the favorable growing season), (iii) NH₃ volatilization and, (iv) denitrification (Carreira et al., 1994). The relative importance of these processes depends on the soil texture and aeration, pH and the dominant vegetation type (Vourlitis et al., 2007a). Soil NO₃⁻ (coming from both N deposition and mineralization and nitrification) is highly soluble, being mobilized in high flow rain events (Bernal et al., 2002; Fenn and Poth, 1999a,b), causing pulses of inorganic N availability from which levels progressively decline to spring (Fig. 2; Carreira et al., 1994). The limited capacity of soils to retain N inputs is conditioned by a decoupling between N flushes and plant demand (Vourlitis et al., 2009), which is also dependent on the post-fire successional stage (Carreira et al., 1994). Consequently, runoff solute concentrations frequently peak after drought periods although solute exports are maximal during large rainfall events (Bernal et al., 2002; Butturini and Sabater, 2002). In southern California chaparral and forested catchments, where N deposition has been elevated for 60 years, ca. 40% of streamwater NO₃⁻, following storm events, originate from atmospheric sources that have moved through the watershed without any prior biological assimilation (Michalski et al., 2004). This suggests that during peak flows a substantial proportion of chronic N deposition is being lost from Mediterranean catchments due to poor retention capacity; this N can eventually reach drinking water sources. By contrast, N cycling in some sub-humid Mediterranean forested catchments appears to be very tight, with almost complete retention of N deposition loads of 15 kg N ha⁻¹ yr⁻¹ (Ávila et al., 2002; Rodà et al., 2002). Likewise, in mixed conifer forests in California, incipient NO₃⁻ leaching during peak runoff periods has only been observed with N deposition of >17 kg N ha⁻¹ yr⁻¹ (Fenn et al., 2008, 2010).

Forest canopies, and particularly those with sclerophyllous evergreen leaves, which are typical in the Mediterranean, are very effective at accumulating dry deposition (Bytnerowicz et al., 1987; Rodà et al., 2002), which can be removed by precipitation (foliage washing) and provide significant N inputs to soil. However, net N retention in canopies is also common, presumably largely due to canopy uptake of dry-deposited gaseous N via stomata and the cuticle, at low to moderate N deposition forested sites (Rodà et al., 2002). For this reason, measuring N deposition in Mediterranean ecosystems as throughfall after prolonged dry periods can underestimate it by as much as 50% (Fenn et al., 2000).

5. Water and P availability condition ecosystem response to N deposition

Water availability is the main factor limiting plant production and microbial/animal activity in Mediterranean ecosystems and thus the likelihood of response to reactive N deposition; i.e., without water, no N deposition impact would be expected. However, extended dry periods would also lead to higher N accumulation in soil and plant surfaces and so to potentially more negative effects (such as toxicity) as soon as water becomes available. Besides N and water, soil P fertility also plays a key role in

Mediterranean ecosystems (Kruger et al., 1983; Hobbs and Richardson, 1995; Fanelli et al., 2008) and ecosystem responsiveness to N pollution is likely to be tightly linked to ecological stoichiometry, particularly to soil N:P ratios (Vitousek et al., 2010).

Soil fertility (including P availability) and nutrient ratios can be modified by various processes, including mechanical disturbance of habitats, animal activity, fire and also N pollution (e.g., through positive or negative effects on mineralization rates). For example, fertile patches can be created and maintained by animals, which have implications for natural annual plant communities as well as for alien plant invasion (Holmgren et al., 2000; Brooks et al., 2006; James et al., 2009). In this sense, rabbit latrines and partridge feeders in semi-arid central Spain game reserves create patches enriched in P where plant biomass (mostly nitrophytic Brassicaceae) is extremely large during the growing season compared to the adjacent and low P unproductive matrix, even when this is experimentally N-fertilized (Ochoa-Hueso and Manrique, personal observation). Phosphorus availability also increases after a fire (Kutiel and Inbar, 1993) which together with N deposition could be helping to maintain plant communities in the early stages of the ecological succession (i.e., dominated by nitrophilous plants) and precluding re-colonization by late-successional shrubs. Similarly, Fanelli et al. (2008) have demonstrated that soil N:P ratios may reflect an index of disturbance severity, with ruderality (frequently regarded as synonymous with nitrophily) increasing with P availability. This evidence may help to explain why the invasion of exotics in Californian Mediterranean ecosystems appear to result from the interactive effects of moderately-high levels of soil P availability and increased N pollution and why high competition and altered fire regimes preclude return to desirable pre-invaded stages (Fig. 2). In South Africa, however, and despite P limitation, increased soil N has also enabled alien grasses to naturalize, reducing the biodiversity of indigenous communities and altering ecosystem processes (Milton, 2004).

Plant tissue stoichiometry (N:P) also depends inherently on the type of Mediterranean ecosystem and on seasonal-drought strategies (Margaris et al., 1984), with leaves of evergreen sclerophyllous shrubs having low-N concentration compared to seasonally dimorphic or deciduous species, such as those in coastal sage or phrygana stands. Thus responses to N deposition are expected to be highly ecosystem-specific as well as modified by the frequency of drought events, as they have been demonstrated not only to reduce water, but also P availability (Sardans and Peñuelas, 2004).

Overall, these examples demonstrate that alterations in soil nutrient stoichiometry, particularly with regard to those nutrients that limit plant growth such as N and P, and water availability, are important for understanding and predicting structural and functional responses to anthropogenic N enrichment. Similar observations have been made in temperate ecosystems (Pilkington et al., 2007; Phoenix et al., 2003) and reported in communities where cryptogams are common (Carfrae et al., 2007; Arróniz-Crespo et al., 2008).

6. Experimental evidence of N deposition impacts on Mediterranean ecosystems

There is a limited amount of data from N fertilization experiments outside California. The majority, especially the field studies, have used high doses of NPK (Grünzweig and Körner, 2003; Pardos et al., 2005) or urea (e.g., Mamolos et al., 1995; Mamolos and Veresoglou, 2000), serving primarily to show the potential for physiological or ecosystem response to N. However, responses to high-N are not always a reliable proxy for responses to low annual N additions in the long-term (Bobbink et al., 2010) and consequently more research is still needed.

6.1. Nitrogen deposition effects on cryptogams

Epiphytic lichens and mosses have been widely used to evaluate the impacts of chronic N inputs as they are usually the most sensitive elements of the ecosystem and respond rapidly to changes in atmospheric chemistry (Bobbink et al., 2010). Their usefulness as early-warning ecological indicators has already been demonstrated in Mediterranean as well as in many other areas (Fenn et al., 2010; Pinho et al., 2008, 2009). Cryptogams are particularly useful in this respect as they can accumulate N before they show negative symptoms of toxicity (Branquinho et al., 2010). In arid and semi-arid Mediterranean sites, terricolous lichen and moss communities forming part of biological soil crusts are also important for ecosystem function and nutrient cycling (including N) (Maestre et al., 2005; Castillo-Monroy et al., 2010) but their sensitivity to anthropogenic N deposition is poorly understood (Ochoa-Hueso and Manrique, 2010b).

Three approaches to monitoring atmospheric N pollution using lichens have been described: (i) assessment of variations in species diversity and/or abundance (e.g., Cepeda Fuentes and García Rowe, 1998; Frati et al., 2007; Pinho et al., 2008, 2009); (ii) measurement of variations in physiological responses such as tissue N and pigment content (e.g., Sánchez-Hoyos and Manrique, 1995) or Fv/Fm and, (iii) quantification of N accumulation in transplanted lichen thalli (Branquinho et al., 2010). Monitoring studies combining these approaches should be routinely undertaken throughout most of the Mediterranean territories to substitute the absence of proper monitoring stations.

Using the first approach, Pinho et al. (2009) defined a threshold, i.e., concentration of atmospheric NH_3 , from which an alteration of lichen diversity in a Portuguese Mediterranean site was expected to occur; this threshold has also been used in the re-evaluation of the European critical NH_3 level for epiphytic lichens from the previously defined $8 \mu\text{g m}^{-3}$ down to $1 \mu\text{g NH}_3 \text{ m}^{-3}$ (Cape et al., 2009).

Lichen pigment concentration can also reflect N deposition, such studies being common within the Mediterranean Basin and California; e.g., Sánchez-Hoyos and Manrique (1995) reported increased photosynthetic and photoprotective pigment content in *Ramalina capitata* (ACH.) Nyl. (an epiphytic lichen from the Mediterranean Basin) when treated with NO_3^- -N but not with NH_4^+ -N, whereas Riddell et al. (2008) demonstrated that the Californian related species *Ramalina menziesii* Taylor experiences a significant decline in total chlorophyll content and C assimilation capacity when fumigated with nitric acid vapor, a major reactive N compound in photochemical smog. Other studies have demonstrated different physiological responses between nitrophytic and oligotrophic epiphytic lichen species exposed to a combination of reduced and oxidized N (NH_4NO_3) (Gaio-Oliveria et al., 2005); namely, oligotrophic species took up more N and their greater NH_4^+ accumulation was correlated with a reduction in ergosterol, implying detrimental effects on the fungal partner; in contrast, the nitrophytic species accumulated NO_3^- without adverse effects on the ergosterol or chlorophyll *a* (related to the algal partner) content (Gaio-Oliveira et al., 2005). Additionally, Ochoa-Hueso and Manrique (2010b) found increased photosynthetic and photoprotective pigment content in *Cladonia foliacea* (Hudson) Willd., a typical species of soil crusts in semi-arid shrublands in central Spain, in response to $50 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ as NH_4NO_3 ; by contrast, Fv/Fm was reduced by this N treatment and the mismatch between pigment synthesis and Fv/Fm was interpreted as a consequence of luxury N consumption (Ochoa-Hueso and Manrique, 2010b). Interestingly, *C. foliacea* appears to be more tolerant of N deposition than other *Cladonia* species from temperate Europe (Ochoa-Hueso and Manrique, 2010b).

Finally, the usefulness of transplants as bio-monitors of atmospheric NH_4^+ concentration has been demonstrated using common

epiphytic lichens from the Mediterranean Basin (e.g., *Usnea filipendula* Stirton and *Evernia prunastri* (L.) Ach.) (Branquinho et al., 2010; Frati et al., 2007). In the case of *U. filipendula*, several N-related variables including intercellular, extracellular, and bound fractions of NH_4^+ , total N, and C:N ratios related well to the distance from an NH_3 source (Branquinho et al., 2010). Equilibration between lichen N concentrations and atmospheric N inputs can be achieved quite rapidly: <15 days for bound NH_4^+ , whereas 35-day transplants can double tissue N concentration and reach up to 72% of the extracellular NH_4^+ concentrations of *in-situ* lichens (Branquinho et al., 2010). In the case of *E. prunastri*, Frati et al. (2007) have demonstrated a parallel increase of tissue N content with a reduction in chlorophylls and total carotenoids in response to NH_3 deposition.

In the particular case of mosses, increases in tissue N concentration (% dwt) during the 20th century has been demonstrated in studies using herbaria samples of terricolous species from South Africa (Wilson et al., 2009) and Spain (Peñuelas and Filella, 2001). Peñuelas and Filella (2001) also found less negative $\delta^{15}\text{N}$ values in vascular plants and bryophytes, which suggest that additional anthropogenic $\delta^{15}\text{N}$ -depleted inputs are being retained in Spanish ecosystems. Such depleted $\delta^{15}\text{N}$ values have also been measured in polar and alpine cores (Freyer et al., 1996) and in N-fertilized soils from semi-arid Mediterranean shrublands in California (Vourlitis et al., 2007a). In addition, $\delta^{15}\text{N}$ values may be used to infer the source of the N deposition; Gerdol et al. (2002) found a more positive $\delta^{15}\text{N}$ signature in mosses along an urban-to-rural gradient in northern Italy, which was attributed to a greater oxidized than reduced N contribution in the N deposition, as a result of emissions from the transport sector.

6.2. Nitrogen deposition effects on higher plants

The response of Mediterranean-type ecosystems to increased N availability depends on where the ecosystem sits with respect to ecological succession (Fig. 2), being possibly faster and more dramatic in the early stages following a disturbance (fire, soil removal, etc.) when “fire-followers” and nitrophilous plants dominate (Aber et al., 2003; Vourlitis et al., 2007a). For instance, Cruz et al. (2003) demonstrated that certain early successional plants have evolved a preference for NO_3^- , most likely as a consequence of the post-fire pulse and a related peak of N mineralization, while showing sensitivity to increased NH_4^+ availability. Later successional plants tend to be more NH_4^+ tolerant (Cruz et al., 2003). However, this could also depend on particular soil properties, such as soil pH (conditioning the dominant form of mineral N in soil, NH_4^+ in acidic and NO_3^- in basic soils), and, consequently, on the main strategies of native plants to acquire N and on their tolerance to different N forms.

Under increased N availability, ‘N savers’ (plant species adapted to low-N) tend to be replaced by ‘N spenders’ (Emmett, 2007). Several mechanisms contribute to this shift (Fig. 2), namely (i) competition (‘N savers’ inherently grow slowly and are progressively out competed by faster growing ‘N spender’ species); (ii) nutritional imbalances (Michopoulos et al., 2004) and the inability to regulate plant growth in the presence of excess N and water shortage (Padgett and Allen, 1999) and; (iii) NH_4^+ toxicity (when applicable).

There are some examples of these mechanisms within Mediterranean-type ecosystems; e.g., a single application of 50 kg N ha^{-1} (NH_4NO_3) to a semi-arid South African fynbos increased the productivity of herbaceous plants (including restioids, graminoids and annuals) after 2 years, but not of dominant shrubs (e.g., ericoids, proteoids); there was also an increase in shrub litter production and P return in response to N addition

during the peak seasonal litterfall (late-spring to mid-summer) which was interpreted as indicative of increased moisture stress due to enhanced shoot growth (Witkowski, 1989a,b). In a similar manner, one year of increased N availability (40 kg N ha^{-1} either as NH_4NO_3 or NH_4^+ and 80 kg N ha^{-1} as NH_4NO_3) in a Portuguese Mediterranean maquis, dominated by early successional summer semi-deciduous shrubs, altered plant species composition and cover, with ruderals and herbaceous species growing more in N-fertilized than in control plots (Dias et al., in press). By contrast, in a Californian coastal sage scrub (also dominated by summer semi-deciduous shrubs) additions of $50 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ (NH_4NO_3) for five years changed the relative dominance of shrubs but not of herbaceous plant species (Vourlitis and Pasquini, 2009). However, the same N manipulation design in a Californian post-fire chaparral dominated by evergreen sclerophytes did not change the plant community (Vourlitis and Pasquini, 2009). In a combination of gradient and fertilization experiments conducted in Californian coastal sage scrubs with different N deposition backgrounds, N fertilization increased the growth of native and exotic species at the low-N deposition site but not at the high-N deposition site, where only one weed species (*Brassica geniculata* = *Hirschfeldia incana* (L.) Lagr.-Foss.) was benefited (Allen et al., 1998). Finally, Sharma et al. (2010) also tested the hypothesis that an increase in N would increase biomass of an alien annual grass (*A. fatua*) but not of various plant functional groups in Western Cape renosterveld shrublands, concluding that N enrichment threatened the sustainability of remnant renosterveld fragments.

In a common garden experiment, seedlings of *Protea repens* (L.) L. (an ‘N saver’ sclerophyllous fynbos shrub) treated with $40\text{--}640 \text{ kg N ha}^{-1}$ (NH_4NO_3) increased their dry mass production, leaf area and P uptake, even though fertilization also enhanced mortality, which was attributed to a soil N to P imbalance (Witkowski, 1989c). By contrast, *P. repens* growing in competition with the alien *Acacia saligna* (Labill.) H.L. Wendel. exhibited reduced growth at high-N levels (Witkowski, 1991), concurring with its poor nutrient tolerance strategy (Stock and Lewis, 1984). Under elevated N deposition, Padgett and Allen (1999) have also demonstrated that native shrubs are unable to regulate their growth, with earlier senescence as an underlying reason for their poor survival, and are thus replaced by exotic annuals which have more flexible growth strategies (Allen et al., 1998; Padgett and Allen, 1999).

Reduced N has often been found to be more toxic than oxidized N for plants, the effects of which tend to be more associated with changes in competition for resources (Sheppard et al., 2008; Dias et al., in press). For example, the growth of ericaceous and legume shrubs and also of grasses was not stimulated in plots receiving $40 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ as NH_4Cl in a Portuguese maquis, whereas the same amount of N as NH_4NO_3 stimulated the growth of the same plant species (Dias et al., in press), which may be related to plant sensitivity to NH_4^+ (Britto and Kronzucker, 2002; Kronzucker et al., 2003; Cruz et al., 2003).

In addition to shifts in plant communities, N deposition is predicted to alter N and C storage of Mediterranean ecosystems in living and dead biomass (Vourlitis et al., 2007a, 2009) and, because water is another main limiting factor for plants in Mediterranean ecosystems, growth vs. storage strategy of evergreen and deciduous shrub species suffering chronic N deposition is also predicted to be modulated by water availability (Sanz-Pérez et al., 2007). The available literature suggests species-specific strategies of Mediterranean plants when dealing with co-occurring limiting factors such as water and N (competitive species favoring growth over storage at increased both N and water), most likely as a consequence of adaptation to particular habitats with contrasting climate, drought severity, and fertility conditions (Correia and Martins-Loução, 1997; Sanz-Pérez et al., 2007).

As already mentioned, ecosystem response to N deposition in terms of productivity and N storage could also be limited by other nutrients such as P, the plant biodiversity of Mediterranean ecosystems being also frequently controlled by soil N:P ratios (Hobbs and Richardson, 1995; Fanelli et al., 2008). Under field conditions, Sardans et al. (2006) studied the independent effects of N (0, 250 and 500 kg N ha⁻¹ as NH₄NO₃) and P fertilization (0, 125 and 250 kg P ha⁻¹ as Ca₃(PO₄)₂) on two Mediterranean tree species (*Pinus halepensis* Miller and *Quercus ilex* L. subsp. *ballota* (Desf.) Samp.) common in the Iberian Peninsula. Whereas N fertilization did not increase nutrient accumulation capacity through growth or concentration, P fertilization greatly increased the concentration of P and other nutrients (Sardans et al., 2006). This corroborated the importance of P over N at certain Mediterranean sites, particularly those suffering chronic N deposition and where N is no longer limiting.

Leaf N and P concentration and ratios are also likely to be altered by N deposition (Vourlitis et al., 2007a), resorption efficiency frequently decreasing with higher N and P green leaf concentration (Kobe et al., 2005). Therefore, increased litter amount and quality, as consequence of increased atmospheric N inputs into Mediterranean ecosystems (e.g., higher N, lower C:N, lower lignin content, etc. – Witkowski, 1989b; O'Connell and Grove, 1993; Vourlitis et al., 2009), may accelerate decomposition if provided labile C availability is not limiting decomposers (Fig. 2; Sirulnik et al., 2007). This would have direct implications for the C cycle and thus on climate change.

In a Californian coastal sage scrub, once dominated by summer semi-deciduous native species, effects of elevated N deposition on decomposition were monitored using ¹⁵N-labeled litter derived from the widespread exotic annual grass *Bromus diandrus* Roth. (Sirulnik et al., 2007). Litter with different N contents was placed on high or low-N-fertilized plots in a factorial experiment. They demonstrated that elevated soil inorganic N and the ratio of NH₄⁺ to NO₃⁻ at the end of the summer came from both decomposition/mineralization and N deposition, concluding that decomposition was influenced by both litter quality and soil N. Differential accumulation of mineral N in soil mediated by effects of N deposition on litter quality and rates of decomposition and mineralization, can also potentially alter natural plant community composition (Dias et al., unpublished data; Ochoa-Hueso and Manrique, unpublished data).

Plant response to increased N availability also depends on how the additional N reaches the plant (Sparks, 2009). Compared to soil-deposited N, direct foliar N uptake usually has a greater influence on plants (Sheppard et al., 2008; Sparks, 2009). However, in Mediterranean ecosystems the dry N deposition peak coincides with the water-stress period, which is characterized by stomatal closure and low biological activities, so foliar N uptake should be minimal when dry N deposition inputs are at a seasonal maximum (Vourlitis et al., 2007a). However, and to our knowledge, studies on the implications of this temporal mismatch and on physiological or ecological effects of direct N foliar uptake in Mediterranean ecosystems are still lacking.

Additionally, many ecosystems are spatially and temporally heterogeneous and Mediterranean ecosystems are no exception (Gallardo et al., 2000; Cruz et al., 2008). Acknowledgement of this heterogeneity is crucial when analyzing effects of manipulation experiments on plants (Ettema and Wardle, 2002). For example, N fertilization effects on plant biomass in Witkowski (1989a) were initially masked by environmental heterogeneity but covariance analysis, using initial plant cover, significantly clarified the effects of increased N availability on plant productivity. Similarly, Ochoa-Hueso and Manrique (unpublished manuscripts) found that significant impacts of 2–3 years addition of 10, 20 and 50 kg

N ha⁻¹ yr⁻¹ on the annual plant productivity of a semi-arid kermes oak thicket were only evident when between-plot NO₃⁻ differences were taken into account as covariate.

6.3. Nitrogen deposition effects on mycorrhizae and microbial soil communities

Mycorrhizal colonization and soil microbial activity are amongst the most widely used biological indicators of N enrichment, which due to their rapid response can provide early warning of potential 'problems' (Chung et al., 2007). By contrast plants usually experience a lag-phase in their response to N deposition (Egerton-Warburton and Allen, 2000). Extracellular enzymes related to the N, C and P cycles can also provide early indications of N effects. These have been measured in plant roots (Morecroft et al., 1994; Phoenix et al., 2003) and lichen and moss tissue (Hogan et al., 2010; Arróniz-Crespo et al., 2008) but rarely in species from Mediterranean ecosystems (but see Krywult et al., 1996, where nitrate reductase activity of roots of ponderosa pines from Californian forests increased with NO₃⁻ deposition). Based on resource allocation models, mycorrhizal colonization rates and enzymatic activities should be the direct expression of the metabolic requirements of plants and soil communities, respectively, in relation to the available nutrients and thus can be either increased or decreased by N deposition depending on local conditions (Fig. 2). Some of the most widely studied soil enzymes are urease and nitrogenase (for the N cycle), phosphatase (for the P cycle), and β-glucosidase (for the C cycle).

Semi-arid ecosystems have been described as a mosaic of islands and mantles of fertility functionally integrated by exchanges of C and N through a symbiotic fungal network (Green et al., 2008). Mycorrhizal networks also play an important role in plant communities by facilitating and influencing seedling establishment, by altering plant–plant interactions and by supplying and recycling nutrients (Van der Heijden and Horton, 2009). Nitrogen deposition impacts on mycorrhizal communities could therefore have serious implications for the below-ground structure and functioning of arid and semi-arid Mediterranean ecosystems. For example, it has been demonstrated that in Californian coastal sage scrubs a microbially-mediated negative feedback causes poor seedling growth and establishment of the native shrub *Artemisia californica* Less. in sites invaded by *Bromus matritensis* L. and where N deposition is high (Sigüenza et al., 2006a). Along an urban-to-rural N deposition gradient in California colonization of *A. californica* by arbuscular mycorrhizal fungi was highest in low-N soils whereas the colonization of annual exotic grasses by a fine endophyte was unresponsive to soil N level (Sigüenza et al., 2006b). Similarly, N enrichment can reduce the number of large-spored mycorrhizal species and also species richness, diversity and abundance of mycorrhizal species with a parallel proliferation of small-spored *Glomus* species in sites receiving 11–20 kg N ha⁻¹ yr⁻¹ (Egerton-Warburton and Allen, 2000). Furthermore, Yoshida and Allen (2001) have suggested that mycorrhizae are more important in controlling plant growth in native un-eutrophied coastal sage scrub soils dominated by NH₄⁺ rather than by NO₃⁻. The importance of NH₄⁺ mediating responses of mycorrhizae to N pollution has also been supported by Ochoa-Hueso and Manrique, in semi-arid central Spain (unpublished manuscript). They found that mycorrhizal colonization of roots of a short-lived annual species was increased by N fertilization once between-plot differences in soil NH₄⁺ had been accounted for.

Evaluation of soil processes as indicators of N pollution impacts on Mediterranean ecosystems is rare among the specialized literature but, for instance, increases in soil mineral N should reduce the likelihood of N fixation (either via symbiosis or free-living

organisms) because N fixation is a very energetic process. Thus we would infer a potential decline in N fixers (including legumes, cyanolichens, cyanobacteria, etc.) under increasing N deposition scenarios (Vitousek and Field, 1999; Ochoa-Hueso et al., unpublished data). Soil microbial biomass and soil respiration are also frequently reported as negatively affected by N deposition (Treseder, 2008), but again published papers analyzing effects of N pollution on soil microbial communities of Mediterranean ecosystems are still lacking.

6.4. Nitrogen deposition effects on fauna

Not much is known about the main N deposition impacts either on animals or about the potential effects of N deposition on the interaction between animals and plants (Throop and Lerdau, 2004), which should reflect the alteration of either habitat quality or food supply (or both). These interactions are particularly important in the case of Mediterranean-type ecosystems, where faunas are rich and a tight coupling between plant and animal phenology is imposed by the pronounced seasonality.

In coastal Central California N deposition allows non-native annual grasses to vigorously invade serpentine grasslands and displace native herbs, including the larval host plant, *Plantago erecta* E. Morris, and numerous adult nectar sources of the threatened bay checkerspot butterfly, *Euphydryas editha bayensis* (Weiss, 1999). When N is removed from the grasslands by cattle grazing or mowing the native herbs and the checkerspot butterfly recover (Weiss, 1999). The critical load for total N deposition for such effects, based on a roadside gradient experiment, has been estimated at 6 kg N ha⁻¹ yr⁻¹ (Fenn et al., 2010). Other impacts of N deposition mediated by invasive grasses could be related to altered abundance of different arthropod functional groups, mostly increasing generalist-feeding species at all trophic levels, as result of increased levels of detritus derived from plant litter (Wolkovich et al., 2009).

In areas where invasive plants are not the main problem for animals, N deposition-related food web repercussions should be linked to alterations in quality and availability of food-plant tissue, fruit yield, nectar, etc. (Throop and Lerdau, 2004). Changes in mycorrhizal fungi are also important for insect fitness as they can directly influence plant tissue chemistry and assimilate partitioning (Goverde et al., 2000).

Other reported effects of N deposition associated with animals are related to increasing susceptibility to pests e.g., mortality of ponderosa pines in Southern California from bark beetle attack (Grulke et al., 2009; Jones et al., 2004). Nitrogen driven changes in epiphytic oligotrophic lichen communities in the Sierra Nevada of California, which are an integral part of food webs and also used as nesting material by insects, mollusks, and birds may also be relevant (McCune et al., 2007; Fenn et al., 2008). The critical load for this latter effect has been estimated in ~5 kg N ha⁻¹ yr⁻¹, which is the throughfall N deposition load reported to reduce the relative abundance of these acidophytic lichens (the dominant epiphytic lichen group in unpolluted regions) by 50% (Fenn et al., 2008, 2010).

6.5. Critical loads based on experimental evidence

Critical loads for Mediterranean ecosystems appear to be usually less than 10 kg N ha⁻¹ yr⁻¹ (Fenn et al., 2010); this threshold is, however, only based on information from Californian ecosystems and thus generalizations are not possible. In addition, the levels of N fertilization applied in most of the studies reported are too high to be useful for determining critical loads and, therefore, for drawing comparisons with those reported for other ecosystems

(e.g., boreal ecosystems ~5 kg N ha⁻¹ yr⁻¹; temperate ecosystems ~10 kg N ha⁻¹ yr⁻¹; semi-desert and desert ~5 kg N ha⁻¹ yr⁻¹ Bobbink et al., 2010). However, under Mediterranean climates (and particularly under semi-arid conditions) N accumulates in the soil, so that small annual N inputs may increase soil mineral N to levels as high as those used in these short-term, high N-input experiments (Padgett et al., 1999), with potential for long-term effects on vegetation (Clark and Tilman, 2008) and other components of natural and semi-natural Mediterranean ecosystems. Nevertheless, experimental studies using lower levels of N fertilization are still required in Mediterranean ecosystems either within the currently most frequent reported N deposition loads or within the range of predicted N deposition scenarios by 2050, i.e., ~2 kg N ha⁻¹ yr⁻¹ in Southwest Australia, ~7 kg N ha⁻¹ yr⁻¹ in California, ~10 kg N ha⁻¹ yr⁻¹ in Chile, ~15 kg N ha⁻¹ yr⁻¹ in the Cape floristic region, and ~24 kg N ha⁻¹ yr⁻¹ in the Mediterranean Basin (Phoenix et al., 2006), to determine critical loads specific for each region and vegetation type.

7. Likely interactions of N deposition with other global change drivers

Natural systems are suffering unprecedented rates of anthropogenic environmental change (Brooker, 2006). It has been suggested that Mediterranean regions are transitional zones where climatic changes may have the greatest effects (Lavorel et al., 1998) and where particularly intense feedbacks from the land to the atmosphere should be expected (Seufert et al., 1995; Scarascia-Mugnozza et al., 2000). Decades of research on Mediterranean ecosystems have highlighted the importance of plant–plant interactions and environmental heterogeneity (Valladares and Gianoli, 2007), both potentially altered by exogenous N inputs. It has been repeatedly shown that gradients of increased competition occur when the environmental abiotic stress is ameliorated (as stated by the stress gradient hypothesis), although competition can also be important at the most stressed end of the environmental gradients (Maestre and Cortina, 2004). In this sense, competition could play a central role in mediating the impacts of N deposition, climate change, and invasive exotic species (Brooker, 2006) in Mediterranean ecosystems. Further, the refined stress gradient hypothesis (Maestre et al., 2009; Smit et al., 2009) establishes that different combinations of life histories and stresses (abiotic and biotic) are likely to yield different competition outcomes and, given the plethora of environmental stresses, including N pollution or climate change, affecting Mediterranean-type ecosystems, these net outcomes from plant–plant interactions are not easy to predict in such a complex landscape.

In this context of complexity, it is noteworthy that some studies dealing with more than one global change factor at the same time in Mediterranean-type ecosystems have found additive rather than interactive effects (Zavaleta et al., 2003; Matesanz et al., 2008; Ochoa-Hueso and Manrique, 2010a), with similar responses found in other water-limited areas (Niu et al., 2009). For instance, climate change (elevated CO₂, warming and altered precipitation) and N deposition can rapidly reduce biological diversity in Mediterranean-type Californian grasslands, with effects being additive combinations of single-factors (Zavaleta et al., 2003), suggesting that responses of Mediterranean grasslands to N deposition will be strongly dependent on future precipitation patterns (Harpole et al., 2007). Similarly, Ochoa-Hueso and Manrique (2010a) have shown equivalent critical thresholds for biomass production after N fertilization in two different water regimes; in both studies responses were mostly confined to native forbs rather than to native grasses, which were unaffected.

By contrast, it has also been shown that the interactions among elements of global change can be as important as single-factors effects in influencing plant litter chemistry, with N having the greatest influence on decomposition over the short-term (Henry et al., 2005). In addition to these multifactor approaches, it is important to consider that temporal variation in resource availability can be as important as the total annual N dose or water supply for plant performance and that responses to temporal dynamics can also vary between species, which might have implications for community-level processes, competitive hierarchies also switching depending on resource dynamics, including those related with N deposition (Sher et al., 2004).

Ozone (O_3) can be another important driver of change in Mediterranean ecosystems. For example, in mixed conifer forests in the San Bernardino Mountains in southern California the biomass of fine and medium roots and also mycorrhizae of ponderosa pines are drastically reduced at sites with co-occurring high levels of O_3 exposure and N deposition (Fenn et al., 2008; Grulke et al., 1998; Sirajuddin, 2009). In this situation, bark beetle attack usually increases (Grulke et al., 2009; Jones et al., 2004). However, considering the common co-occurrence of O_3 and elevated N deposition in polluted Mediterranean regions, it is sometimes unclear under field conditions whether the effects are due to O_3 , increased N availability or both. More studies looking at the combined effects of N and O_3 are required especially with respect to below-ground changes.

8. Mitigation strategies

Management strategies to mitigate the negative impacts of excessive N should be based on reducing N emissions and the amount of accumulated N, the N capital (Fenn et al., 2010). Within the second approach, the most widely reported practices are biomass removal, prescribed fire and control of N-loving invasive species by mowing, herbicides or animal grazing (Fenn et al., 2010). For example, in N-saturated catchments post-fire N losses may be considered beneficial to mitigate the effects of excess N from atmospheric deposition, although organic N pools in mineral soil horizons are usually only minimally reduced by fire (Johnson et al., 2009; Rundel and Parsons, 1980; Wan et al., 2001). However, in ponderosa pine forests in the SW United States, frequent prescribed fires increase N availability but do not seem able to reduce total site N (Covington and Sackett, 1986). Fire can also increase soil hydrophobicity, a negative consequence that exacerbates erosion losses from catchments (DeBano et al., 1998; Ferreira et al., 2009). Finally, Keeley et al. (2005) do not support the widely held view that prescription burning is a viable management practice for controlling alien species in semi-arid Mediterranean ecosystems, since canopy closure is the main factor controlling alien invasion after fire, not N deposition. But, long-term fire suppression can be problematic in areas adapted to fire because increases in stand density or excessive growth of the understory, which are frequently favored by N deposition, can contribute to multiple stress conditions, situations where drought stress and susceptibility to biotic pests increase.

9. Future work and conclusions

Ecosystems are made up of many different organisms, all with varying sensitivities to N. If we protect the most N sensitive species from the detrimental effects of enhanced N deposition we protect the function and sustainability of the whole ecosystem. For Mediterranean ecosystems we need to identify the most sensitive compartments responding to altered-N cycles and establish appropriate critical loads and legislative limits for N deposition that

provide their long-term protection. As mentioned above, responses of soil microorganisms could be used as an early-warning signal for global change, as they change rapidly, while plants usually experience a lag-phase in response to N deposition (Egerton-Warburton and Allen, 2000). Protists and micro-arthropods are also common in Mediterranean soils and their permeable and thin cuticles should make them reliable indicators of soil N toxicity (Mitchell and Gilbert, 2004). Epiphytic lichens are also highly sensitive indicators of N effects in terrestrial ecosystems, including forests and woodlands in Mediterranean regions (Fenn et al., 2008, 2010; Pinho et al., 2008, 2009).

Concluding, the experimental evidence reviewed here suggests that:

1. Mediterranean-type ecosystems, usually regarded as hot-spots of biodiversity, are highly vulnerable to increased anthropogenic N inputs and not only generalities (high spatial and temporal environmental heterogeneity, fires, drought-tolerant strategies, dry N inputs, etc.) but also specifics (different fertility, etc.) for each Mediterranean region should be taken into account in order to predict potential impacts.
2. As a consequence of their higher human population and of their high reliance on industry, private automobiles, agriculture, etc., the Mediterranean Basin and California are expected to suffer the most negative consequences of N pollution (and other global change drivers) amongst the Mediterranean regions (Table 1). The potential impacts of N deposition are predicted to be intermediate in South Africa and least in Australia and Chile, although there can be local exceptions, as in areas close to major cities or to large agricultural operations (Table 1).
3. Impacts derived from N amendments or real N deposition gradients in Mediterranean regions are often comparatively subtle and lie near the boundaries of statistical and methodological resolution, suggesting the great importance of multivariate and covariance analyses and also seasonal evaluations (Witkowski, 1989a,b,c; Ochoa-Hueso and Manrique, 2010b). However, these apparently subtle impacts can have great implications for functioning and C dynamics at the ecosystem scale (Gallo et al., 2004), making this topic of great concern and suggesting the potential importance of considering different components of global change, such as N deposition and climate change, at the same time to predict responses of semi-arid Mediterranean ecosystems in future scenarios (Barnard et al., 2006; Ochoa-Hueso and Manrique, 2010b).
4. Setting critical loads for N effects should combine studies on N deposition (where N applications should mimic the frequency and temporal nature of the dry and wet deposition at levels low enough to include the range of known N deposition) with observations along representative anthropogenic N deposition gradients (e.g., Bobbink et al., 2010; Fenn et al., 2010). Obviously, more of these kinds of studies are urgently needed in Mediterranean-type climates to assess ecosystem impacts of elevated N.

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