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# Assessing the impact of land abandonment, nitrogen enrichment and fairy-ring fungi on plant diversity of Mediterranean grasslands

Giuliano Bonanomi · Guido Incerti · Marina Allegrezza

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**Abstract** Semi-natural calcareous grasslands are of great conservation interest because of their high species richness, but they are threatened by land abandonment and nitrogen eutrophication. These plant communities evolved as a result of a long history of human activity, which generated and maintained these habitats by extensive grazing and mowing. Calcareous grasslands are listed as a priority for conservation in the EC Habitats Directive. However, the effects of different management regimes, nitrogen enrichment, and soil-borne pathogens on plant species diversity are less clear for grasslands of the Mediterranean Basin, compared to meadows in Northern and Central Europe. In this study, we assessed the impact of land abandonment, nitrogen enrichment, and fairy-ring fungi on species diversity in semi-natural grasslands found in the Mediterranean Basin by comparing the available literature with findings from recent studies carried out in Central Italy. In a series of field experiments, the cutting of abandoned grassland consistently reduced the living biomass of the dominant perennial grasses, such as *Brachypodium rupestre* and *Bromus erectus*, and promoted a rapid increase in species richness and diversity by allowing the establishment of rare species. There was a similar, but less effective, restoration of species diversity and composition in mowed grassland after litter removal. We also show that nitrogen enrichment at levels comparable to atmospheric deposition depresses species diversity, which also hampers the positive effects of litter removal. Our findings are consistent with previous results achieved in Northern and Central Europe, which however, mainly focused on grasslands with intermediate to high primary productivity levels. The limited availability of data from low-productivity, drought-prone Mediterranean grasslands requires further studies to assess the impact of land abandonment and nitrogen eutrophication in such ecosystems. Finally, we discuss the role of fairy-ring fungi in the maintenance of plant diversity in species-rich grassland. We show that fairy-ring

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fungi (e.g. *Agaricus campestris*) critically affect the spatial distribution and diversity of coexisting plant species. By killing the dominant perennial herbs, these radially growing plant pathogens produce empty niches for rare, short-lived species, thus affecting the vegetation pattern. Overall, our results are of interest for environmental managers, as they provide guidelines for the restoration of abandoned areas and the conservation of these species-rich habitats.

**Keywords** Biodiversity conservation · Semi-natural grassland · Soil-borne pathogen · Species coexistence · Species diversity · Vegetation pattern

## Introduction

Calcareous grasslands are considered to be among the most species-rich ecosystems at the small scale (Kull and Zobel 1991; Wilson et al. 2012), and a significant part of this biodiversity is concentrated in semi-natural, managed stands. Since the Neolithic Era, these plant communities have been generated and maintained as a result of land use related to husbandry and farming, including the extensive use of fire, grazing, and mowing (Poschold and WallisDeVries 2002). However, nowadays, calcareous grasslands are threatened by land abandonment (Cramer et al. 2007) and nitrogen (N) eutrophication (Bobbink et al. 2010), as well as by climatic changes (WallisDeVries et al. 2002; Grime et al. 2008).

Understanding the mechanisms that regulate the coexistence and relative abundance of plant species is crucial for a successful management of natural resources. Indeed, grasslands represent a broad spectrum of species richness values, which can range from monospecific or species-poor stands, to highly diverse communities, as in the case of dry grasslands over calcareous substrates. Such large variability, which can often occur on small spatial scales (van der Maarel and Sykes 1993), has fascinated, and at the same time frustrated, plant ecologists who have tried to explain the ecological processes underlying species coexistence (Huston 1994). A plethora of different hypotheses have been proposed (Palmer 1994), including mechanisms that produce equilibrium through niche partitioning (Tilman 1994), non-equilibrium coexistence dynamics (Huston 1994) related to disturbance (Connell 1978), plant interactions with soil microbes and pathogens (Kulmatisky et al. 2008), and fluctuations in the environmental conditions (Chesson 2000). At present, there is little consensus on the relative importance of such processes in different plant communities. In the framework of plant diversity in grasslands, many experimental studies have been aimed at conservation applications, with investigations into the impact on grassland diversity of different types of disturbance, such as fire (Uys et al. 2004), grazing (Farris et al. 2010), and mowing (Antonsen and Olsson 2005), as well as their interactions (Harrison et al. 2003). In this regard, management practices that lead to litter accumulation and N eutrophication can have negative effects on grassland species richness, as has been consistently demonstrated in the Midwest of the USA (Foster and Gross 1998) and in Northern and Central Europe (Bobbink and Willems 1991; Enyedi et al. 2008). In contrast, there have been few studies that have addressed these issues in Mediterranean grasslands (e.g. Catorci et al. 2011).

In this review, we focus on three main issues that affect species diversity in species-rich plant communities in semi-natural grasslands occurring in the Mediterranean Basin: (i) the impact of land abandonment; (ii) the effect of N eutrophication; and (iii) the role of the so-

called ‘fairy-ring’ fungi. Land abandonment and N eutrophication have been included here because they represent two well recognized threats for species-rich grasslands. The issue of fairy-ring fungi has also been included because, despite the availability of some breakthrough empirical studies (Klironomos 2002; van der Putten et al. 2013), soil-borne fungal pathogens are still under-appreciated as ecological factors that could help to maintain plant species coexistence and relative abundance in grasslands. Here, we summarise how these three important controlling factors can contribute to the regulation of grassland diversity, while also providing management and restoration guidelines for the conservation of these highly biodiverse Mediterranean ecosystems.

### Effects of land abandonment on grassland diversity

It is well known that the vegetation of the Mediterranean region has been shaped by human activities for millennia. Grasslands have been created, extended, and maintained by human-induced activities, such as fire, extensive grazing, and mowing (Bugalho et al. 2011). However, traditional agro-pastoral practices have been subject to rapid changes during the last half century (Mazzoleni et al. 2004). In Southern Europe, the active rural human population, i.e. the number of people actively involved in agro-pastoral activities, has dramatically decreased over the last 30 years, from more than 24 million people to less than 9 million people (FAOSTAT 2012). As a consequence of these socio-economic changes, grasslands are losing their traditional economic functions, and thus they have considerably decreased all over Europe (Poschlod and WallisDeVries 2002; Vassilev et al. 2011).

Remarkably, land abandonment has primarily affected the less productive areas, such as semi-natural grasslands, that are often the most species-rich and can harbour many rare and endemic species. Land abandonment of managed grassland leads to alterations in the plant communities, because as anthropogenic activities cease, natural secondary successions start (Galvánek and Lepš 2012). In Western Europe, several studies have reported a progressive increase in the dominance of a few competitive, tall-grass species (Bobbink and Willems 1987; Muller 2002) that are suppressing small and short-lived plants. As a consequence, species diversity, richness, and evenness is decreasing.

In addition to competition, the accumulation of litter after land abandonment has a crucial role in the effects on plant-species richness. A dense litter layer can inhibit seedling establishment through a variety of mechanisms, which include the release of phytotoxic compounds during decomposition (Bonanomi et al. 2011), physical obstruction (Wedin and Tilman 1993), and the reduction and alteration of the amount and quality of light available at ground level (Facelli and Pickett 1991), which affects both productivity and soil temperature regimes. A meta-analysis based on 35 studies, which included several ecosystem types reported a negative effect of litter accumulation on species diversity, and an increase of this effect with productivity (Xiong and Nilsson 1999). The impact of litter is believed to increase progressively with time, as it becomes relevant only a few years after the land abandonment, when a significant amount of above-ground litter has accumulated (Bonanomi et al. 2009).

Such negative effects of litter accumulation on species richness at community level, and especially on forb establishment, have been reported by a number of studies that have manipulated litter in a variety of grassland ecosystems (Table 1). However, in a few cases, litter occurrence has shown positive effects on seedling recruitment and establishment (Eckstein et al. 2012). This was mainly observed in semi-arid and arid grasslands, where

the litter usually does not exceed  $200 \text{ g m}^{-2}$  (Xiong and Nilsson 1999). Under such conditions, a thin litter layer due to moderate litter deposition can insulate the soil from incident solar radiation, thus protecting it from extreme temperatures, and thereby reduce evaporation, and maintain soil moisture higher than under the equivalent bare-soil conditions.

Such positive effects of plant litter are likely also to be observed in Mediterranean grasslands, as these are subject to prolonged dry periods during the summer months. However, the evidence of positive buffering effects of plant litter has been limited to extremely dry ecosystems (Xiong and Nilsson 1999), and to some mesic grasslands (Donath et al. 2006; Eckstein et al. 2012). This is not surprising, considering that there have been no manipulative field experiments that have assessed the effects of litter on plant diversity in Mediterranean Basin grasslands (Table 1).

To fill this gap, we recently carried out a study in two sub-Mediterranean grasslands of the Apennine Peninsula (EC Habitat Directive code, 6210) located in the Apennines (Central Italy) and included in the ‘Sites of Community Importance’ (SCIs) of the Natura 2000 network. According to a bioclimatic classification (Rivas-Martínez 2004), the two study sites belong to the sub-mediterranean variant of the temperate macrobioclimate, oceanic bioclimate. Study site 1 was located within the area of Valle Vite-Valle dell’Acquarella (SCI code: IT5320012) at an altitude of 350 m a.s.l. ( $43^{\circ}20'N$ ,  $13^{\circ}00'E$ ). The grasslands here were abandoned 15 to 20 years ago and are now dominated by the perennial grass *Brachypodium rupestre*. The vegetation can be attributed to the phytosociological *Festuco-Brometea* class, *Brometalia erecti* order and *Bromion erecti* alliance (Biondi et al. 2005). Study site 2 is in the Puro-Rogedano-Valleremita Mountains area (SCI code: IT5320011), at an altitude of 870 m a.s.l. ( $43^{\circ}17'18"N$ ,  $12^{\circ}51'16"E$ ). The vegetation belongs to the *Phleo ambigu-Bromion erecti* alliance, *Brometalia erecti* order and *Festuco-Brometea* class (Rodwell et al. 2002; Biondi et al. 2005). The study site includes two almost adjacent areas, which are characterised by the same underlying soil, but which have different management histories. The first area within study site 2 had been mowed annually over the previous 50 years, while in the second area mowing had been stopped 20 years ago. On a small scale, the species richness of vascular plants was higher in the mowed area as compared to the abandoned area, with mean species richness of  $9.8 \pm 1.2$  vs.  $4.7 \pm 0.8$ , respectively, for plots of  $400 \text{ cm}^2$ , and of  $24.6 \pm 3.5$  vs.  $18.9 \pm 2.6$ , respectively, for plots of  $4 \text{ m}^2$  (Bonanomi et al. 2009).

For both study sites, we carried out a three-year interventional experiment to determine the effects of plant litter removal and artificial cutting, coupled with N fertilisation on the vascular plant species diversity. Both the abandoned grasslands and the adjacent mowed areas were treated, to evaluate their restoration potential and the impact of management abandonment. In the mowed areas, cessation of cutting depressed the species diversity by promoting an increase in the cover of perennial grasses (predominantly *B. rupestre* and *Bromus erectus* at study sites 1 and 2, respectively), while progressively reducing the abundance of several rare forbs. At both study sites, cutting significantly increased species richness and Shannon diversity in the abandoned areas, by positively affecting the biomass of almost all of the annual and biennial species, and reducing the dominance of the perennial grasses. In general terms, the living biomass of all plants, as well as that of grasses, was negatively correlated with species richness and Shannon diversity (Table 2). Consistent with the well-known humped-back relationship between net primary productivity and species richness (Fridley et al. 2012), there was a steep decrease in species richness and diversity when the amount of living biomass plus the above-ground litter exceeded  $550\text{--}600 \text{ g m}^{-2}$ . In the data from Bonanomi et al. (2006, 2009), species richness

**Table 1** Summary of manipulative field experiments assessing litter effects on plant diversity in grasslands

Ecosystems & Country	Experimental treatment	Effect of litter manipulation	References
Annual Mediterranean grassland (California, USA)	Litter removal and addition (1 year)	Litter removal increased species richness by favoring forbs and annual grasses with small seeds	Amatangelo et al. (2009)
Semi-natural, species poor Mediterranean grassland (Italy)	Litter removal in combination with cutting (3 years)	Litter removal increased species diversity but less than mowing	Bonanomi et al. (2006)
Semi-natural, species rich calcareous Mediterranean grassland (Italy)	Litter removal in combination with cutting (3 years)	Litter removal increased species diversity but less than mowing	Bonanomi et al. (2009)
Old field (USA)	Litter removal and addition (2 years)	Litter removal increases species richness, in contrast, litter addition reduced species richness	Carson and Peterson (1990)
Flood plain grassland	Litter addition (2 years)	Contrasting effect of litter addition with positive effect on some species and negative for others	Donath et al. (2006)
Semi-natural grassland (Germany)	Litter removal and addition (1 year)	Litter addition favor seedling emergence and establishment by improving water availability	Eckstein et al. (2012)
Successional grassland (USA)	Litter removal and addition (2 years)	Litter addition decreased species diversity by inhibiting forbs establishment	Foster and Gross (1998)
Semi-natural grassland (USA)	Litter removal (1 year)	Litter removal increase forbs establishment	Goldberg and Werner (1983)
Annual Mediterranean grassland (California, USA)	Litter removal and addition (4 years)	Litter removal favored forbs compared to some annual grasses	Heady (1956)
Fen grassland (Germany)	Litter removal in combination with cutting (1 year)	Litter removal favor forbs seedling establishment	Rasran et al. (2007)
Steppe grassland (Romania)	Litter removal in combination with cutting (2 years)	Litter removal alone, or in combination with cutting, increases species diversity	Ruprecht et al. (2010)
Oligotrophic wet meadow (Czech Republic)	Litter removal (4 years)	Litter removal favor forbs seedling establishment	Špačková and Lepš (2004)
Fen, prairie and barrens grasslands (USA)	Litter removal (1 year)	Litter removal facilitate seedling emergence	Suding and Goldberg (1999)
Steppe (Mongolia)	Litter removal and addition (3 years)	Litter removal had no effect on species richness. Species richness was reduced by spring litter addition but enhanced when applied in autumn	Wang et al. (2011)
Semi-natural grassland (USA)	Litter removal	Litter accumulation dramatically decreased species richness	Weaver and Rowland (1952)

**Table 1** continued

Ecosystems & Country	Experimental treatment	Effect of litter manipulation	References
Semi-natural grassland (Canada)	Litter removal (3 years)	Litter removal favored forbs productivity and reduced grasses relative abundance	Willms et al. (1986)

Bibliographic search was carried out in all indexed international ecological journals by online access to Biological Abstract, Science Citation Index, ISI Web of Knowledge, Science Direct, Scopus and JSTOR (accessed up to 15 April 2013). Used key words were “Mediterranean”, “grasslands”, “litter”, “manipulation”, “removal”, “addition”, “species richness”. The reported references are a subset of our search hits, relevant to the present review. For the studies carried out in Europe, grasslands belong to the classes *Festuco-Brometea* and *Molinio-Arrhenatheretea* (Rodwell et al. 2002)

and Shannon diversity were negatively correlated with above-ground litter (Fig. 1). The above-ground litter in abandoned areas was about 13-fold and 15-fold greater than that in mowed fields at study sites 1 and 2, respectively, and it was mainly composed of grass remains. Above-ground litter and the living biomass of perennial grasses progressively increased after land abandonment, which corresponded to a decrease in the forb living biomass. This resulted in a sharp decrease in species diversity and relative abundance of the forbs (Bonanomi et al. 2006, 2009). Similarly, a strong negative correlation between litter and plant species richness was recently also reported by Deak et al. (2011) in highly productive (up to 1,480 g m<sup>-2</sup>) grasslands in Hungary.

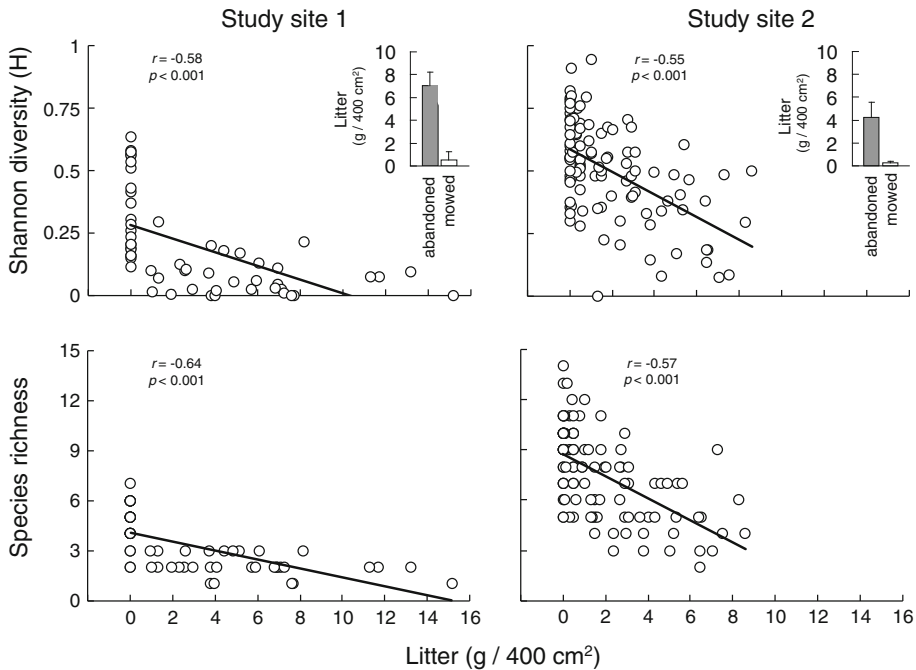
Considering the levels of primary productivity and the amounts of litter at the study sites (Fig. 1; Table 1), the inhibitory effects of plant litter on species diversity was consistent with findings reported for other ecosystems (Xiong and Nilsson 1999; Table 2). Our results indicate that at least for Mediterranean grasslands with intermediate productivity

**Table 2** Correlation (Pearson’s *r* coefficient, and associated statistical significance) between productivity parameters and two parameters of plant diversity (Shannon diversity and species richness) at the two study sites (plots size = 0.20 m × 0.20 m, *n* = 56 and 105 for study sites 1 and 2, respectively)

Productivity parameters (g m <sup>-2</sup> )	Study site 1		Study site 2	
	Shannon diversity	Species richness	Shannon diversity	Species richness
Living biomass of all plants	-0.42; <i>p</i> = 0.001	-0.46; <i>p</i> < 0.001	-0.39; <i>p</i> < 0.001	-0.41; <i>p</i> < 0.001
Living biomass of grasses	-0.54; <i>p</i> < 0.001	-0.55; <i>p</i> < 0.001	-0.66; <i>p</i> < 0.001	-0.67; <i>p</i> < 0.001
Biomass of most common grass <sup>†</sup>	-0.92; <i>p</i> < 0.001	-0.60; <i>p</i> < 0.001	-0.68; <i>p</i> < 0.001	-0.57; <i>p</i> < 0.001
Litter	-0.58; <i>p</i> < 0.001	-0.64; <i>p</i> < 0.001	-0.55; <i>p</i> < 0.001	-0.57; <i>p</i> < 0.001
Total living biomass and litter	-0.55; <i>p</i> < 0.001	-0.60; <i>p</i> < 0.001	-0.52; <i>p</i> < 0.001	-0.51; <i>p</i> < 0.001

Mean values and range of variation (in brackets) of plant above-ground living biomass at site 1 and site 2 were 382 (range 63–1,047) and 284 (range 62–682) g m<sup>-2</sup>, respectively; for standing litter 79 (range 0–378) and 47 (range 0–215) g m<sup>-2</sup>, respectively. Data from Bonanomi et al. (2006, 2009)

<sup>†</sup> The most common grasses at study sites 1 and 2 were *Brachypodium rupestre* and *Bromus erectus*, respectively



**Fig. 1** Correlation (Pearson's  $r$  coefficient and associated  $p$  value) between litter and two parameters of plant diversity (Shannon diversity and species richness) for the two study sites. For each site, the *inset* in the *top panel* shows the amount (mean + SD) of litter in the plots (size 0.20 m × 0.20 m;  $n = 56$  and 105 for study sites 1 and 2, respectively) that were either annually mowed or abandoned. Data from Bonanomi et al. (2006, 2009)

levels, litter accumulation negatively affects grassland species richness and Shannon diversity. However, a recent meta-analysis based on 42 studies carried out in natural and semi-natural grasslands (Loydi et al. 2013), showed that the litter layer can positively affect seedling emergence and survival, which becomes progressively more beneficial with decreasing water availability, and mostly when the litter levels is below 500 g m<sup>-2</sup>. Based on this recent evidence, further studies are urgently required to assess the sign and magnitude of the effects of litter accumulation on species diversity in the more drought-prone, low-productivity, Mediterranean grasslands.

These findings provide useful insight into our understanding of the ecological mechanisms underlying the reduction of species diversity following land abandonment. A dual effect has been suggested, which relates both to resource competition and to progressive accumulation of plant litter. Cutting acts as a periodical disturbance and it reduces the above-ground competition (Tilman 1988), thus delaying the competitive exclusion of forbs by highly competitive perennial grasses. The reduced dominance of perennial grasses after cutting might be due to a reduction in their energy reserves in the form of non-structural carbohydrates in the rhizomes, which might reduce the vigour of the new shoots in the seasons that follow (Bobbink and Willems 1991). At both study sites, the litter removal effects were similar to those of cutting, although litter removal produced lower increases in species diversity (Bonanomi et al. 2006, 2009). In general terms, plant diversity was depressed by both the competition from living plant biomass and the accumulation of litter in abandoned areas, through the prevention of the recruitment of annual and biennial forbs.



The relative importance of resource competition and inhibition by litter accumulation, as well as magnitude and kinds of interactions have not been clarified yet. Indeed, further studies are required to determine the joint roles of competition and litter accumulation in Mediterranean grasslands that encompass a wide range of primary productivity levels.

### Nitrogen eutrophication as a threat to grassland diversity

In addition to land abandonment, plant diversity in grasslands is threatened by N eutrophication, partly due to application of N fertilisers, but especially through atmospheric deposition (Stevens et al. 2004). The potential ecological effects of N eutrophication on plant diversity have been investigated in several ecosystems, including arctic and alpine areas (e.g. Körner 2003), and boreal (e.g. Nordin et al. 2006), temperate (e.g. Gilliam 2006) and tropical forests (e.g. Tanner et al. 1998), heathlands (e.g. Berendse 1990), as well as temperate grasslands (e.g. Bobbink 2004). In contrast, only a few studies have been carried out in Mediterranean ecosystems, with most of these referring to California, USA, while the other Mediterranean areas (Mediterranean Basin, South Africa, Chile and Australia) remain understudied (Ochoa-Hueso et al. 2011).

For grasslands, several studies have reported that N enrichment in Dutch grasslands drives a rapid change from species-rich calcareous grasslands into tall-sward, species-poor communities that are dominated by a few highly productive perennial grasses, such as *Brachypodium pinnatum* and *Bromus erectus* (Bobbink and Willems 1991; Willems 2001). By contrast, in calcareous grasslands of the UK N enrichment did not reduce species richness, probably because there primary productivity is co-limited by N and phosphorous (P) availability (Wilson et al. 1995). Mediterranean grassland productivity is often limited by N availability in spring and autumn, and by water availability in summer. This co-limitation of primary productivity by N and water suggests that the response of this ecosystem to N enrichment would be less rapid and dramatic compared to non-water-stressed systems, such as in the case of Dutch grasslands (Bobbink et al. 2010).

However, the few studies that have been carried out in Mediterranean grasslands, which have all been performed in California, have consistently indicated that N enrichment depresses species richness (Table 3). This usually occurs because N fertilisation drives the dominance of the grasses, which in several cases are non-native species, which thus reduce the abundance of forbs, and especially of N-fixing species that belong to the Fabaceae family (Table 3). Atmospheric N depositions in Central Italy are still quite low ( $1.5 \text{ g N m}^{-2} \text{ year}^{-1}$ ) compared to those reported for Northern, and in particular, Western Europe. To understand the impact of N pollution on grassland diversity, we applied a rate of  $3.5 \text{ g N m}^{-2} \text{ year}^{-1}$ , which simulates a doubling of the N deposition through air pollution. N enrichment was combined with cutting and litter removal for three consecutive years at study sites 1 and 2. After N enrichment, there was a marked increase of living biomass, as well as a decrease in species diversity of vascular plants (Bonanomi et al. 2006, 2009). However, the magnitude of these effects was dependent on the type of sward management (Fig. 2). In more detail, species diversity was negligibly affected in abandoned areas. On the contrary, N application counterbalanced, or at most limited, the positive effects of litter removal on rare species, thus reducing the overall species diversity.

Given the general positive effects of N enrichment on living biomass, it appears likely that by increasing the intensity of above-ground competition, N application might negatively affect grassland diversity. Our data indicated that the responses to N enrichment of

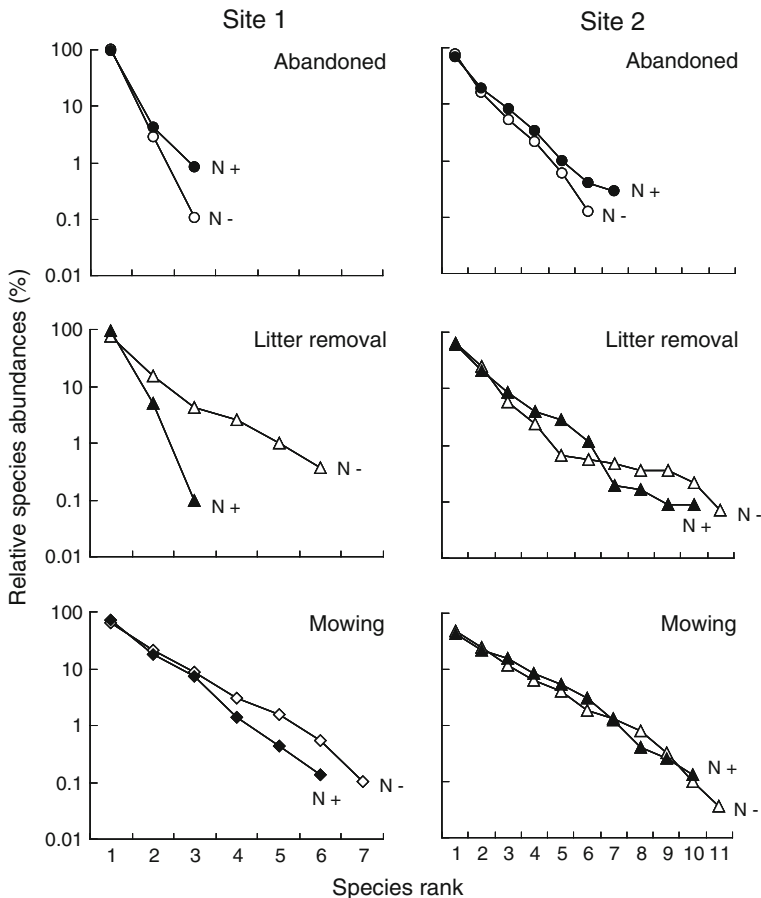
**Table 3** Summary of experimental studies addressing N addition effects on plant diversity in Mediterranean grasslands

Ecosystem and country	Experimental treatment (kg N ha <sup>-1</sup> year <sup>-1</sup> )	Effect of N enrichment	References
Semi-natural, species poor grassland (Mediterranean Basin, Italy)	35 (3 years)	Nitrogen increased aboveground biomass. Species diversity remained low when cutting or litter removal were combined with N addition	Bonanomi et al. (2006)
Semi-natural, species rich calcareous grassland (Mediterranean Basin, Italy)	35 (3 years)	Nitrogen increased aboveground biomass and reduced species diversity	Bonanomi et al. (2009)
Grassland (California, USA)	70 (5 years)	Nitrogen suppressing forbs and enhanced annual grasses	Henry et al. (2006)
Serpentine grassland (California, USA)	100 (2 years)	Nitrogen addition reduced species diversity by favors invasion of exotic annual grasses that replace forbs	Huenneke et al. (1990)
Serpentine grassland (California, USA)	100 (1 year)	Nitrogen increased aboveground biomass and reduced forbs relative abundance	Koide et al. (1988)
Serpentine grassland (California, USA)	40 (2 years)	Nitrogen addition foster invasion of annual non-native species	Seabloom et al. (2003)
Serpentine grassland (California, USA)	188 (1 year)	Nitrogen increased aboveground biomass favoring annual grasses	Turitzen (1982)
Serpentine grassland (California, USA)	4–15 (10 years)	Nitrogen addition reduced species diversity by favors invasion of exotic annual grasses that replace forbs	Weiss (1999)
Grassland (California, USA)	70 (3 years)	Nitrogen decreased species diversity by suppressing forbs, especially N-fixing species, but enhancing grasses	Zavaleta et al. (2003)

Bibliographic search was carried out in all indexed international ecological journals by online access to Biological Abstract, Science Citation Index, ISI Web of Knowledge, Science Direct, Scopus and JSTOR (accessed up to 15 April 2013). Used key words were “Mediterranean”, “grasslands”, “nitrogen”, “fertilization”, “eutrophication”, “species richness”. The reported references are a subset of our search hits, relevant to the present review. For the studies carried out in Europe, grasslands belong to the classes *Festuco-Brometea* and *Molinio-Arrhenatheretea* (Rodwell et al. 2002)

the grasslands of the Mediterranean Basin are consistent with the findings reported for Californian grasslands (Table 3).

In conclusion, our data suggest that an increase in N pollution from atmospheric deposition, which at present still remains under critical values in the mountains of Central Italy, can drive further reductions in grassland species diversity if coupled with persistent land abandonment. However, it should be noted that only a few studies have addressed the impact of N enrichment on the structure and diversity of Mediterranean grasslands (Table 3). In this context, the large number of agronomic studies that have been carried out on Mediterranean grasslands have little relevance, due to treatments with excessive doses of NPK fertilisers (e.g. Basso et al. 1992). Moreover, our studies were carried out in mountain grasslands, where the summer drought is less marked compared to



**Fig. 2** Species rank-abundance relationships at the two study sites in plots (size 0.20 m  $\times$  0.20 m;  $n = 56$  and 105 for study sites 1 and 2, respectively) without and with N fertilization (*open and closed symbols*, respectively), according to different management practices: land abandonment (*top*), litter removal (*centre*) and mowing (*bottom*). Data from Bonanomi et al. (2006, 2009)

Mediterranean coasts. As a consequence of the small amounts of experimental data, indications of critical load for N in Mediterranean grasslands are still difficult to define.

Finally, it should be noted that several studies that were carried out in Californian grasslands reported N enrichment as a factor that greatly enhances the invasion of non-native European annual grasses (Table 3). Unfortunately, no studies have addressed this issue in grasslands of the Mediterranean Basin, thus highlighting the urgent need for future studies in this geographical area.

### Are ‘fairy-ring’ fungi a keystone species of calcareous grassland?

Circles of mushrooms coupled with regular rings or arcs of greener plants are commonly observed in grasslands (Fox 2006). This pattern is often referred to as ‘fairy rings’, and it has been described for several natural plant communities, including sand dunes (Abesha

et al. 2003), grasslands in the USA (Clements 1916), Europe (Edwards 1984), and Japan (Terashima et al. 2004), and the undergrowth of temperate forests (Peter 2006). These regular vegetation patterns are produced by a network of fungal mycelia that grow radially below ground, to produce these fairy rings (Dowson et al. 1989). Over 50 basidiomycete species are known to be able to produce such an interesting shape, with *Agaricus*, *Amanita*, *Clitocybe*, *Lepista*, *Marasmius*, *Tricholoma* being the most represented genera (Ogawa 1985). However, fairy rings caused by soil-borne fungi can be confused with those formed by insects (Juergens 2013), as well as by clonal plants (Watt 1947). The latter, during their ontogenetic cycles, can produce clones of a circular shape, which progressively degenerate in the older inner area, thus producing a weaker or dieback central zone (Carteni et al. 2012).

In Table 4, we provide a summary of studies that have addressed the impact of fairy-ring fungi in natural and managed ecosystems. The majority of the available studies investigated the development of fairy rings, often addressing their effects on soil quality and microbial communities (Table 4). Although the occurrence of fairy rings in natural grasslands was initially reported many years ago (Clements 1916; Shantz and Piemeisel 1917; Bayliss-Elliott 1926), these intriguing plant–microbe interactions have been mainly studied in managed turfs, as in the case of golf greens, where they are recognized as a widespread phytopathological problem (Smith et al. 1989). Indeed, fairy-ring fungi can interact with plants in different ways. First, these fungi can affect plants directly, with plant roots being damaged by mycelium penetration into the living tissues (Terashima et al. 2004), or by the release of phytotoxins, such as hydrogen cyanide (Blenis et al. 2004). In addition to the direct effects on plants, fairy-ring fungi can greatly modify the soil quality, thus indirectly affecting plant growth. Indeed, the passage of the mycelia during this radial below-ground expansion reduces the soil organic C in the inner ring zones, as well as the stocks of K, P and Ca, compared to the external grassland (Fisher 1977; Edwards 1984; Bonanomi et al. 2012). This is a consequence of the special trophic strategy evolved by these fungi, which tend to accumulate large mycelial nutrient stocks, as they are periodically required to produce huge quantities of sporophores (Edwards 1988). Accordingly, fairy-ring fungi colonise the soil by killing the established plants, and at the same time, they can enhance organic matter mineralisation, and also affect the further soil properties, such as pH and salinity, and they can induce remarkable soil hydrophobicity (Fidanza et al. 2007; Bonanomi et al. 2012).

In spite of the growing knowledge of their impact on soil quality, the effects of fairy-ring fungi on plant species diversity have been largely ignored (Table 4). In a recent study (Bonanomi et al. 2012), we investigated if and how the fairy-ring fungus *Agaricus campestris* affects vascular plant diversity in a species-rich calcareous grassland. Fairy rings are relatively common in mountain calcareous grasslands in Central Italy (Fig. 3). Although the ecological factors that control the distribution of fairy-ring fungi are still unknown, we noted that these patterns are more common in grasslands that are regularly managed with summer mowing (personal observation G.B.). The cryptic below-ground activity of fairy-ring fungi can become evident above ground because of clear-cut effects on vegetation, which show regular rings or arcs of greener plants that often grow luxuriantly (Figs. 3, 4). These greener areas are often surrounded by an external zone of either dormant or dead vegetation (Figs. 3, 4).

We selected a study site (Monte Rogedano, 43°17'18" N, 12°51'16" E; 913 m a.s.l.; central Italy) where fairy rings of *A. campestris* are widespread and exceptionally well developed (Figs. 3, 4). The grassland studied lies over a shallow sandy soil that is rich in organic matter, N and K, and it is managed with regular summer mowing (Bonanomi et al.

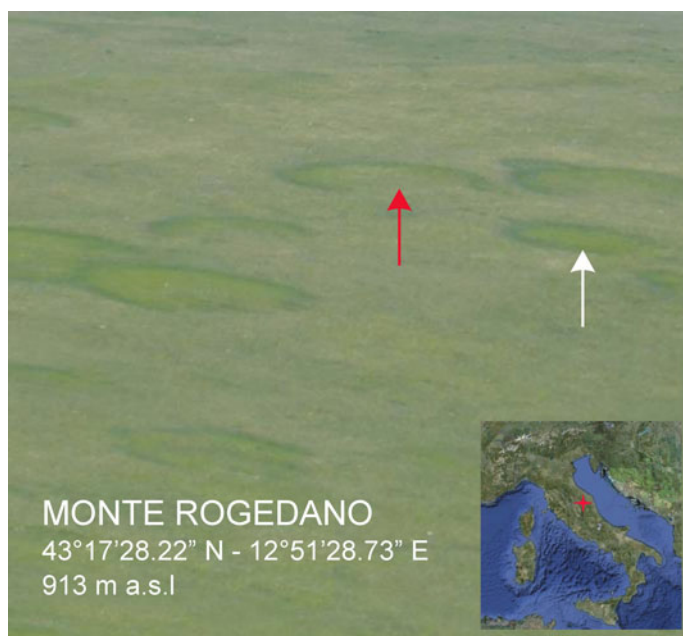
**Table 4** Summary of experimental studies on fairy ring fungi in different ecosystems

Fungal species	Ecosystem and country	Study objectives	References
<i>Agaricus campestris</i>	Mediterranean, semi-natural grassland (Italy)	Effect of fairy ring on grassland plant diversity, soil microbes and soil quality	Bonanomi et al. (2012)
<i>Agaricus campestris</i>	Semi-natural grassland (UK)	Effect of fairy ring on plant growth and soil quality	Edwards (1984)
<i>Agaricus campestris</i>	Semi-natural grassland (UK)	Effect of fairy ring on plant growth and soil quality	Edwards (1988)
<i>Agaricus campestris</i>	Turf grass (USA)	Effect of fairy ring on soil quality	Fidanza et al. (2007)
<i>Armillaria luteo-virens</i>	Grassland (China)	Effect of fairy ring on plant growth, soil microbes and soil quality	Wang et al. (2011)
<i>Bovista dermoxantha</i>	Turf grass (Japan)	Effect of fairy ring on plant growth	Terashima et al. (2004)
<i>Clitocybe nebularis</i>	Deciduous woodland (UK)	Fairy ring spatial and temporal dynamics	Dowson et al. (1989)
<i>Marasmius oreades</i>	Sand dune (Norway)	Fairy ring spatial and temporal dynamics	Abesha et al. (2003)
<i>Marasmius oreades</i>	Semi-natural pasture (UK)	Effect of fairy ring on plant growth	Bayliss-Elliott (1926)
<i>Marasmius oreades</i>	Semi-natural grassland (Canada)	Effect of fairy ring on plant and fungal growth	Blenis et al. (2004)
<i>Marasmius oreades</i>	Turf grass (Germany)	Effect of fairy ring on soil quality	Djajakirana and Joergensen (1996)
<i>Marasmius oreades</i>	Laboratory study	Parasitic activity of a fairy ring fungus	Filer (1965)
<i>Marasmius oreades</i>	Semi-natural grassland (Canada)	Effect of fairy ring on soil quality	Fisher (1977)
<i>Marasmius oreades</i>	Semi-natural pasture (Germany)	Effect of fairy ring on soil microbes and soil quality	Gramss et al. (2005)
<i>Marasmius oreades</i>	Turf grass (Canada)	Parasitic activity of a fairy ring fungus	Lebeau and Hawn (1963)
<i>Marasmius oreades</i>	Laboratory study	Effect of fairy ring on organic matter decomposition	Mathur (1970)
<i>Marasmius oreades</i>	Turf grass (USA)	Effect of fairy ring on soil quality	Norstadt et al. (1973)
<i>Marasmius oreades</i>	Turf grass (Canada)	Evaluation of different methods to control fairy ring in man managed turf grass	Smith (1980)
<i>Marasmius oreades</i>	Turf grass (Canada)	Effect of fairy ring on soil microbes	Smith and Rupps (1978)
<i>Marasmius oreades</i>	Turf grass (UK)	Effect of fairy ring on soil quality	York and Canaway (2000)
Several species	Natural grassland (UK)	General description of the phenomenon	Clements (1916)
Species not identified	Semi natural grassland	Effect of fairy ring on soil quality	Dekker and Ritsema (1996)
<i>Tricholoma matsutake</i>	Coniferous forest (Japan)	Fairy ring spatial and temporal dynamics	Lian et al. (2006)

**Table 4** continued

Fungal species	Ecosystem and country	Study objectives	References
<i>Tricholoma matsutake</i>	Coniferous forest (Japan)	Effect of fairy ring on soil microbes	Ohara and Hamada (1967)
<i>Tricholoma matsutake</i>	Mixed forest stand (Finland)	Effect of fairy ring on soil microbes and soil quality	Vaario et al. (2011)
<i>Tricholoma mongolium</i>	Herbaceous steppe (Mongolia)	Effect of fairy ring on grassland plant diversity, soil microbes and soil quality	Zhao et al. (2003)
<i>Vascellum curtisii</i>	Turf grass (Japan)	Effect of fairy ring on plant growth	Terashima et al. (2004)

Note that only one study investigated fairy ring effects on plant diversity in Mediterranean grassland (Bonanomi et al. 2012). Bibliographic search was carried out in all indexed international ecological journals by online access to Biological Abstract, Science Citation Index, ISI Web of Knowledge, Science Direct, Scopus and JSTOR (up to 15 April 2013). Used key words were “fairy ring”, “grasslands”, “soil-borne pathogens”

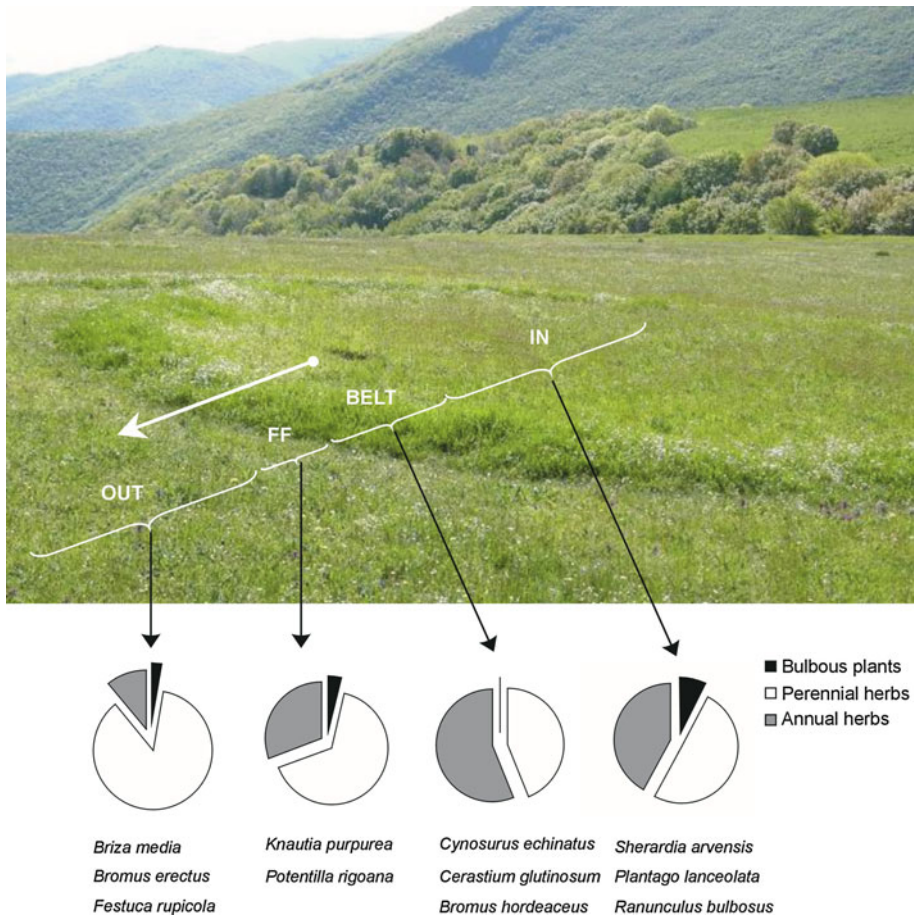


**Fig. 3** Photograph of Monte Rogedano (taken by G. Bonanomi) at the beginning of the growing season, showing several fairy rings formed by the fungus *Agaricus campestris*. White and black arrows indicate fairy rings with circular and arc shapes, respectively. Inset shows location of the study site in Central Italy

2012). From a phytosociological point of view, the grassland belongs to the *Phleo ambigu-Bromion erecti* alliance, *Brometalia erecti* order and *Festuco-Brometea* class (Biondi et al. 2005). Our study objectives were to address the following questions: Do *A. campestris* fairy rings affect the spatial distribution of coexisting plant species? Is the ring development related to changes in the soil physical, chemical, and/or microbiological properties?

Fairy rings were monitored for plant biomass and species richness and composition by sampling linear transects that orthogonally crossed the ring circumference (Fig. 4). Moreover, to determine the effects of *A. campestris* on soil quality, the fairy rings were





**Fig. 4** Schematic representation of the four sampling zones used to investigate the effects of fairy rings on grassland vegetation and soil quality. *OUT* external area outside the ring, *FF* fungal front with large amount of white mycelia in the topsoil, *BELT* internal ring margins with flourishing vegetation, *IN* inner ring area. *White arrows* direction of fungal spread, which occurred at a rate of about 25 cm year<sup>-1</sup>. The passage of fungal mycelium produces dramatic changes in the biological forms (*pie-charts* relative frequency of different growth forms in each area. Herbs include both forbs and grasses) and plant species composition (for details see main text and Bonanomi et al. 2012)

sampled through selecting four discrete areas, each defined as follows: the external grassland, outside the ring (*OUT*), the fungal front, where an abundant mat of white mycelia was evident in the top soil (*FF*), the greenest belt area, with flourishing vegetation (*BELT*), and the inner area (*IN*) (Fig. 4). Seventeen soil parameters were analysed, including the physico-chemical variables (water holding capacity, pH, electrical conductivity, organic C, P, total N,  $\text{NH}_4^+$ ,  $\text{NO}_3^-$ , hydrophobicity, cyanide concentration) and microbiological properties (enzymatic activity by hydrolysis of fluorescein diacetate, a community-level physiological profile using BIOLOG EcoPlates<sup>TM</sup>, microbial biomass, fungal mycelia, culturable actinomycetes, bacteria, fungi).

Plant biomass and species richness were highest in the *OUT* and *IN* areas, and lowest in the *FF* samples where the mycelia were abundant. The plant species composition also

dramatically changed in response to the fairy-ring development, and with the disappearance of the grassland species from the most external belts. In more detail, the commonest guild in the OUT area were perennial grasses (e.g. *Briza media*, *B. erectus*, *Festuca rupicola*), and after the passage of the fungal front, these were largely replaced by annual grasses and forbs (e.g. *Bromus hordeaceus*, *Cerastium glutinosum*, *Cynosurus echinatus*) (Fig. 4). Consequently, the species composition was profoundly different in the four sampled areas. Interestingly, the effects of the passage of the fairy ring were generally limited to a belt 160–180 cm wide from the FF zone. Indeed, in the IN zone of the fairy rings, the perennial species that dominate the OUT zone appeared to recover from the biotic disturbance, considering both forbs (e.g. *Ranunculus bulbosus*, *Centaurea ambigua*, *Plantago lancaeolata*) and grass (e.g. *B. erectus*) species (Bonanomi et al. 2012).

Dramatic changes in the floristic composition were observed across the fairy-ring zones, with corresponding abrupt changes in soil quality. The soil properties were found to change after the passage of the fungus, with a consistent reduction in the C and N stocks, and an increase in the soil enzymatic activity (fluorescein diacetate) and microbial functional diversity. Soil from the fungal zone showed remarkable increases in mineral N forms, which indicate consistent organic matter mineralization, as well as an increase in electrical conductivity. Similar results have been reported in semi-natural grasslands in the UK, where the passage of *A. campestris* through the soil drove a sharp decline in organic matter content and nutrient stocks (Edwards 1984). Finally, a dramatic increase in the hydrophobicity was recorded corresponding to the fungal mycelia (the FF zone), while there was no cyanide detected. The increase in the water repellency of the soil, which corresponds to the fungal mycelia, appears to be a general feature of fairy rings (Dekker and Ritsema 1996; York and Canaway 2000; Fidanza et al. 2007; Bonanomi et al. 2012). However, the causal mechanisms and the ecological relevance of such processes in the inhibition of plant growth under field conditions remain to be clarified. Our data provided robust evidence that by killing established perennial plants and promoting soil heterogeneity at a very local scale, fungal fairy rings are a pivotal factor to allow species coexistence and to enhance plant diversity at the community scale. Future studies will deal with the mechanisms through which these fairy-ring fungi can kill the established perennial grasses.

### Concluding remarks and recommendations for management of Mediterranean grasslands

Periodic, anthropogenic actions of disturbance over the long term have moulded the present-day form of grasslands found in the Mediterranean Basin, and maintained their species richness, coexistence, and relative abundance. Among these, in systems with intermediate levels of primary productivity, the cessation of regular mowing can rapidly lead to the formation of high-biomass but low-diversity communities that are dominated by a few perennial grasses. This process is mediated by a reduction in the light availability at ground level, due to both the uncut living biomass and the progressive accumulation of a persistent layer of grass litter. Both factors strongly suppress annual and small-sized perennial forbs, thus reducing the species richness of these communities.

Our findings are consistent with the available literature, and they provide useful indications for correct management and possible ways for restoring abandoned grasslands, oriented towards biodiversity conservation. Regular cutting appears to be by far the most effective practice for restoring species richness and diversity, because it both mitigates the dominance of prevailing grasses, and promotes the establishment of rare species. In this



respect, litter removal is only partially effective, because it can favour the spread of rare species, but it does not limit the locally dominant perennial grasses. Moreover, compared to cutting, litter removal is a more expensive and laborious management practice.

In terms of management strategies, annual cutting does not appear to be necessary for the conservation of species-rich grasslands, but cutting applied every 2 or 3 years would probably be sufficient (Bonanomi et al. 2009). In any case, periodical disturbance is required for the maintenance of highly diverse, semi-natural grasslands. In this regard, it is worth noting the similar effects of mowing and fairy-ring fungi on grassland diversity, with the locally dominant perennial grasses limited either by cutting or by fungal passage, and co-occurring with, or being replaced by, annual, biennial, and small-sized perennial forbs (Bonanomi et al. 2012). It follows that fairy-ring fungi can be considered to act as a local biotic disturbance, which by affecting the established vegetation, provides free empty space for the development of new and additional pioneer species. In addition, such soil-borne pathogens significantly affect most of the soil quality parameters, to produce a remarkable environmental heterogeneity at a very small spatial scale, which suggests a key role of these fungi in shaping the spatial arrangement of species-rich grasslands. Unfortunately, very few studies have investigated the impact of fairy-ring fungi in semi-natural grasslands. As a consequence, the knowledge of their general ecological response to different management practices, and in particular to the impact of land abandonment and N pollution, is still very limited. Therefore, further studies should specifically investigate these issues, to provide useful information for the design of the appropriated management strategies for these Mediterranean grasslands.

N deposition still remains under the critical values in the mountains of central Italy. In this context, in line with data from other Mediterranean regions, the results of experimental studies suggest that an increase in N pollution from atmospheric deposition might exacerbate the reduction in the grassland species diversity, particularly when coupled with land abandonment. Indeed, land abandonment and N eutrophication can interact synergistically, to accelerate the reduction in the grassland species diversity, by providing an increased competitive advantage for perennial grasses over annuals and perennial forbs. However, further studies are required to quantify the magnitude of these interactive effects, particularly in the low-productivity, drought-prone grasslands of the Mediterranean Basin.

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