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Key issues in Northwestern Mediterranean dry grassland restoration

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Dry grasslands of the Northwestern Mediterranean Basin are seminatural species-rich ecosystems, composed of many annual species and some structuring perennial species. As these grasslands have been used as rangelands for centuries, human management (grazing; fire regimes) is one of their main ecological and evolutionary drivers, along with the Mediterranean climate. Despite EU conservation policy, damage to such grasslands still occurs and efficient ecological restoration is needed. This article reviews restoration constraints, effective techniques, and research perspectives for restoring them in the light of their ecological characteristics. Major restoration constraints specifically include (1) a poor contribution of the internal (seed bank) and external (seed rain) species pools, and (2) low establishment of some perennial species. The latter may be the result of the low seed quantity or quality of perennial species, stochastic or extended droughts, high soil nutrient content that may lead to competition (e.g. between weed and target species), inappropriate grazing management or fire regimes leading to shrub encroachment, or the death of target species seedlings in early stages of restoration. Successful restoration techniques include seeding, transplanting, hay transfer, and timely soil transfer, all of which have to be adapted to regional plant phenology and to local Mediterranean climate. They must be combined with appropriate grazing or fire management. Their success may depend on years with particular rainfall amounts or patterns or on particular target plant species. We discuss research perspectives contributing to a better understanding of seed dispersal, seedling recruitment, and soil processes and suggest the benefits of using ecosystem engineer species.

Key words: drought, grazing and fire management, local adaptation, Natura 2000 habitat #6220, rangeland, seed bank, seedling recruitment, species pool

Implications for Practice

- Constraints for the restoration of dry grasslands of the Northwestern Mediterranean Basin include poor dispersal, low establishment of perennial species, poor quality of the long-term seed bank, and competition between weeds and target species.
- Successful restoration techniques include soil and hay transfer, seeding, and transplanting before autumn rains, applied along with appropriate management (winter–spring grazing and summer fires).
- Restoration success is highly dependent on interannual climatic variability which creates contingency in restoration outcomes, which are generally better in wetter years.
- More research is needed to improve the restoration of dry grasslands of the Northwestern Mediterranean Basin, particularly in the areas of seed dispersal, population biology of key species, soils, ecosystem engineers, fire regimes, and plant-arthropod relationships.

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Introduction

Mediterranean grasslands are characterized by warm, dry summers and cool, wet winters. Grasslands of the Mediterranean Basin are seminatural ecosystems and one of many "Mediterranean cultural landscapes" (Grove & Rackham 2001). They are largely maintained by human land management, such as grazing and pastoral fires (San Miguel 2008). Their long historical use as rangelands has played an important role in determining their recent ecological and evolutionary dynamics, and has resulted in their relatively high tolerance to grazing (Perevolotsky & Seligman 1998). Because they are often species-rich and support wildlife as well as extensive grazing, and therefore sustainable human livelihoods, seminatural Mediterranean grasslands are protected under the EU habitat directive (San Miguel 2008). For ecological restoration purposes, these ecosystems are considered as appropriate references (Gann et al. 2019).

Because conservation and restoration practices in the Mediterranean Basin vary with latitude and longitude (Nunes et al. 2016), we focus here on Northwestern (European Union) Mediterranean-type ecosystems. Despite EU conservation policy, ecological restoration is still needed for some of these grasslands. They are still sometimes subjected to degradation and even well-managed rangelands may support fewer species than they once did, or could if restored. This article reviews and discusses the restoration constraints and techniques of dry grasslands of the Northwestern Mediterranean Basin (NwMedB hereafter), in the light of their ecological characteristics. Among these grasslands, this article emphasizes species-rich dry grasslands, "Pseudo-steppe with grasses and annuals (Thero-Brachypodietea)," most of which are in Spain, Italy, Portugal, and France and cover over 26,000 km^2 in these countries (Table S1, Supporting Information; EUNIS 2020). These Mediterranean dry grasslands are found in plains, hills, and plateaus, and this article thus excludes watered meadows and alpine grasslands. We here give a general summary of multiple aspects of the restoration of these communities, which may also apply to the restoration of other ecosystems (e.g. similar grasslands or the same grassland type in Eastern Europe; Fig. S1, Table S1). This article is not a comprehensive literature survey or meta-analysis, but instead draws upon experts in various aspects of Mediterranean grassland restoration. Mediterranean grasslands share many restoration challenges with other ecosystems, but also show specific constraints, in particular the strong summer drought and the unique land-use issues of this region. This article aims to highlight some of these differences, while still being useful for ecosystems with similar challenges.

Major Constraints for the Restoration of Northwestern Mediterranean Grassland Plant Communities

Limited Spatial Seed Dispersal

Plant recruitment via seed rain in degraded grasslands is generally described as low, including in NwMedB grasslands (Gomez & Espadaler 1994; Buisson & Dutoit 2004; Buisson et al. 2006; although see the section below on Using Animals to Restore Plant Communities). This may be because small-seeded species without specialized dispersal structures are over-represented in these grasslands (Azcárate et al. 2002). Small seeds without specialized dispersal appendices are mainly barochorous (gravity-dispersed) and do not disperse very far. They penetrate the soil more easily where they escape secondary dispersal (Peco et al. 2003). They therefore do not easily reach degraded areas. Longer seeds or dispersal units with specific structures are preferentially preyed upon and potentially dispersed by ants (Azcárate et al. 2005).

Although seeds of NwMedB herbaceous species can be dispersed by ants, rabbits, deer, and livestock, dispersal distances have rarely been evaluated. Assessing the contribution of local versus distant diaspore sources is difficult, which may explain why estimating seed dispersal distance has generally been overlooked in seed rain studies in grasslands (Arruda et al. 2018). Moreover, dispersal by livestock is reduced compared to temperate grasslands because grazing rarely occurs at the time of seed dispersal (summer, when forage quantity and quality are low) (Joffre et al. 1988; Buisson et al. 2006).

Life History Traits and Regeneration

Plants of NwMedB grasslands are adapted to summer drought, unpredictable rainfall events, grazing, and fire (Blondel et al. 2010). Some species, such as *Dactylis glomerata* and *Brachypodium retusum*, undergo vegetative summer dormancy, resulting in a reduction of growth sometimes combined with the senescence of aboveground parts (e.g. Volaire & Norton 2006). Many perennial plants can survive and resprout from a belowground bud bank (rhizomes; roots) after such stresses and disturbances (De Luis et al. 2004; Grigulis et al. 2005; Nedjimi 2016). Such plants are vulnerable to intense soil disturbance that destroys the bud bank and underground organs (Fernández Ales et al. 1993). Additionally, decades of cultivation also can greatly reduce native seed banks (Römermann et al. 2005; Fig. 1).

Annual plants are common in the Mediterranean Basin (Blondel et al. 2010), especially in areas with strong summer droughts (Clary 2008). They survive the unfavorable dry season (summer) as seeds. They can produce a small amount of large seeds, which may better survive ruminant ingestion (Peco et al. 2006a). However, they are predominantly represented by species that produce large number of small seeds that may live longer and have a better chance to be found in the persistent seed bank (Peco et al. 2003; Blondel et al. 2010). Delayed germination (via hardseededness or other mechanisms) is a characteristic of some Mediterranean annual forbs, particularly Fabaceae (Azcárate et al. 2002; Peco et al. 2003). However, many species and seeds germinate with autumn rain to benefit from bare ground left after summer drought. As an adaptation to their variable environment, some of these species form a small persistent seed bank allowing them to germinate in later years to cope with the unpredictability of rainfall (Ortega et al. 1997). All together, few seeds join the long-term seed bank (Ortega et al. 1997; Römermann et al. 2005; Buisson et al. 2006, 2018; Fig. 1), which therefore stays relatively poor in species and seeds.

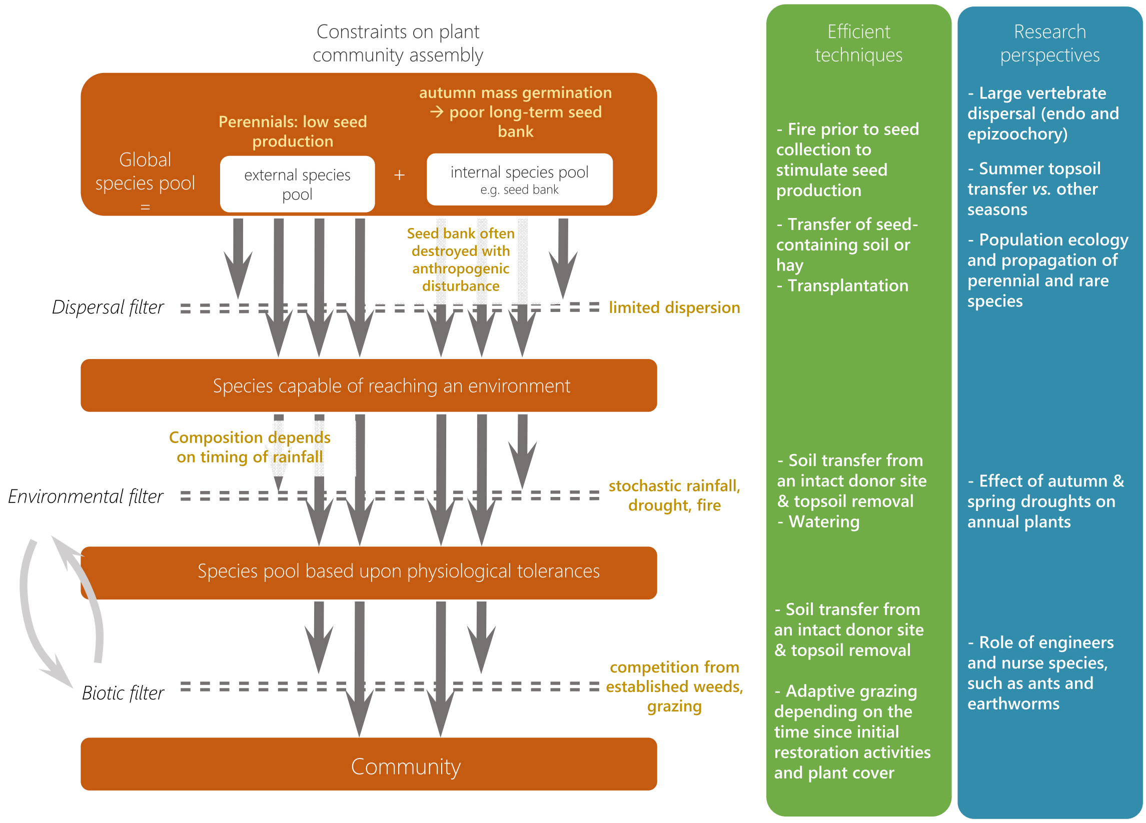

Figure 1. The main processes or filters structuring a plant community are represented on the left side of the figure (in orange), modified from Lortie et al. (2004). Each process/filter is represented by a double horizontal line and the corresponding description is in italics on their left. Community assembly constraints in Northwestern Mediterranean Basin dry grasslands are written in pale orange on the right of the double horizontal lines. Dark gray arrows depict the movement of species through the filters. Light gray arrows represent the feedback loop between the abiotic environment and the biota. To the right of the figure, in a green column the successful techniques for the restoration of Northwestern Mediterranean Basin dry grasslands, and in a blue column the research perspectives.

Seedling Recruitment and Establishment

Mediterranean grassland species mainly germinate with autumn or winter rains. The optimal conditions for germination (temperatures and rainfall timing) strongly vary across plant species (Espigares & Peco 1993). For example, some species of the genera *Lotus*, *Melilotus*, *Medicago*, and *Trifolium* acquire increased germination efficiency with cold stratification or fluctuating temperatures (Assche et al. 2003). The timing of the rainy season, and the associated temperatures, and rainfall patterns may thus change plant species composition from one year to another (Fig. 1). Such annual climatic variability may produce strong contingency in restoration outcomes (Stuble et al. 2017).

Typical Mediterranean perennial grassland species often show a relatively low seedling recruitment (e.g. *B. retusum*, *Asphodelus* sp.), which may be due to (1) low seed production or quality (Coiffait-Gombault et al. 2012; Vidaller et al. 2019a), (2) on-site competition with established plants (Buisson et al. 2015), or (3) drought stress (Bochet et al. 2007; Vidaller et al. 2019a). Sporadic spring droughts, such as in 2003, may also lead to high mortality of well-established adult perennial plants (Buisson et al. 2015). Other perennial species, particularly found in Spain and Italy, show high allocation to sexual reproduction (*Stipa tenacissima*, *Ampelodesmos mauritanicus*), ability to form soil seed banks (*S. tenacissima*), and high resistance to drought stress (*Lygeum spartum*, *S. tenacissima*) (Grigulis et al. 2005; Cortina et al. 2009; Nedjimi 2016). They are therefore particularly promising for the restoration of degraded areas where they would naturally occur (Mariotti & Zotti 2010).

Most NwMedB grasslands grow on soils with low nutrient content, which, depending on species characteristics, may reduce competitive interactions allowing higher species richness (Maestre et al. 2009). If the degradation is due to intensive agriculture, persisting fertilizer residues (Standish et al. 2006) may favor weeds in competition with target species (Zefferman et al. 2015) and jeopardize the recovery of species-rich plant communities (Fig. 1), even if target propagule dispersal is artificially increased (Jaunatre et al. 2014a).

Inadequate Grazing Management

Grazing is one of the main drivers of plant diversity in Mediterranean grasslands (Peco et al. 1983; Carmona et al. 2015), and domestic grazing is recognized as a major factor in the maintenance of many Mediterranean open habitats (Noy-Meir et al. 1989; Perevolotsky & Seligman 1998; Fig. 1). Because of a history of livestock grazing, Mediterranean herbaceous communities are considered highly resilient to stocking rate variability (Sternberg et al. 2000) although overgrazing can lead to soil degradation and desertification (Sales-Baptista et al. 2016). Grazing abandonment may cause major shifts in plant and invertebrate communities and to shrub encroachment (Saatkamp et al. 2010).

Techniques to Overcome Constraints for the Restoration of Northwestern Mediterranean Grassland Plant Communities

Opportunities and Limits of Soil Transfer

After major soil disturbance (e.g. road construction, quarries, pipeline laying), Mediterranean grassland recovery may be very slow (Römermann et al. 2005; Pueyo et al. 2009; Coiffait-Gombault et al. 2011; Helm et al. 2019). While finding commercial seed sources of local Mediterranean species is still a challenge, soil transfer, as loose soil or as turf, has already produced encouraging results, at least over shorttime periods, as compared to other ecological restoration techniques (e.g. hay transfer; Jaunatre et al. 2014a). Soil transfer is defined as the translocation of soil material and its native biota. It involves the transfer of the soil substrate and its assemblage of species from an intact donor site to an area requiring restoration (Pywell et al. 1995). This may not only overcome dispersal limitation, but also some other biotic and abiotic filters that constrain the establishment and development of plant communities (Lortie et al. 2004; Fig. 1). The transfer of a soil from a donor to a restoration site provides physico-chemical elements, soil organic matter, and a part of the pedofauna, flora, and microbial biomass (bacterial, algal, and fungal; Wubs et al. 2016). Soil transfer has proven useful for the recovery of species-rich Mediterranean grasslands on typical Mediterranean soils (e.g. Haplic Cambisol), in various situations: (1) restoration of abandoned intensive orchards (Jaunatre et al. 2014a), (2) after a pipeline leak (Bulot et al. 2014b; Bulot et al. 2017), or even (3) long-term restoration of abandoned dry quarries (Chenot et al. 2017).

Stockpiling of soil may lead to the colonization by weeds (i.e. undesirable native ruderals or invasives) often promoted (1) directly, by piles collecting seed rain, and (2) indirectly, by the release of nitrate due to accelerated decomposition of organic matter (Bruelheide & Flintrop 2000) during stockpiling. Translocated soil, even without stockpiling, may also carry a higher nutrient content due to the disturbance of soil structure (Bruelheide & Flintrop 2000), and compaction that may occur during transfer by construction machineries (Trueman et al. 2007). Direct or timely transfers may minimize the loss of propagule viability, soil structure, or microbial biomass (Anderson et al. 2008).

Despite these advantages, soil transfer should be applied with caution, because soil formation is a long-term process and soils are not a renewable resource. Mediterranean soils often develop over thousands of years (Molliex et al. 2013), and destruction may be effectively irreversible. Soil transfer should be limited to cases in which the destruction of the soil of the donor site is preplanned or has already occurred independently of the restoration project (Bulot et al. 2014b). Moreover, all transfers of large quantities of soil require the use of unsustainable civil engineering methods (i.e. hydrocarbon consumption, pollutant emissions, soil alteration, and compaction).

To limit the environmental impact, soil should be transferred without the delays associated with stocking (Bulot et al. 2014b; Bulot et al. 2017; Buisson et al. 2018). Dilution of loose soil reduces the volume of soil removed or restores larger areas (Jaunatre et al. 2014a; Dutoit et al. 2019a). Transferring scattered turfs that would allow perennial plants to survive transfers and act as nuclei for plant recolonization has provided inconsistent results (Dutoit et al. 2019b).

Establishment of Key Species

Low seedling recruitment in Mediterranean grasslands may result from a low number of available seeds and/or drought-mediated low germination and establishment. To optimize restoration strategies, knowledge of these underlying mechanisms is required. For example, if recruitment is seed-limited, seed addition is the best strategy, but if the density of viable seeds is sufficient, priority should be given to an improvement of environmental conditions, or timing of seeding. In the following sections, we explore the use of population biology and population genetic methods in ecological restoration and explain their particular importance in Mediterranean systems using *Brachypodium retusum* as a model species. In NwMedB grasslands, *B. retusum* is the dominant species showing numerous interactions with other typical species (Saiz & Alados 2011). Its establishment and performance are important indicators of restoration success.

Population Genetics and Seed Provenance

Hay transfer using local species-rich source communities may be a cost-efficient restoration technique. Its success depends on hay seed density (number of seeds/m^2) and competition at the restoration site (whether sown on bare ground or within settled vegetation) (Coiffait-Gombault et al. 2011; Jaunatre et al. 2014b; Fig. 1). The effectiveness of hay transfer in different seasons has not been studied, but most likely the transfer or sowing of seeds just before the first autumn rains is adequate to maximize germination while minimizing seed loss by ants or wind. Appropriate source communities are not always available or may not contain enough viable seeds of the desired species (Kiehl et al. 2010; Coiffait-Gombault et al. 2011). Active restoration by sowing or planting often requires the purchase of plant commercial material, usually as seed (Vander Mijnsbrugge et al. 2010). This plant material is often not strictly local since seed production is usually based on relatively few populations, raising the question of how local the seed material used in ecological restoration needs to be (McKay et al. 2005).

Vidaller et al. (2018) demonstrated that adaptive population differentiation in germination and early growth of *B. retusum* contributes to different colonization patterns, and that the provenance needs to be carefully considered in restoration planning. Summer drought, stone cover, and grazing intensity are major drivers of adaptation in this species (Vidaller et al. 2018). Thus, populations originating from sites with higher summer rainfall or lower grazing pressure may not establish as well on restoration sites with strong summer drought or high grazing pressure. However, locally adapted does not necessarily mean geographically close. Distant populations growing in similar environments may be more appropriate for sowing at a given restoration site (Bischoff 2014). Additionally, even local seed sources may be inappropriate if inbred and genetically impoverished (Broadhurst et al. 2008), or if changing climate has changed (or will change) the local climatic envelope (Durka et al. 2017).

Conditions of Establishment and Their Manipulation to Improve Restoration Success

In NwMedB grasslands, soil stability, water availability, and grazing regimes are known to be limiting factors for plant species establishment (Cortina et al. 2009; Pueyo et al. 2009; Vidaller et al. 2019a, 2019b; Fig. 1). An increase in soil water availability generally favors seedling recruitment (Bochet et al. 2007; Pueyo et al. 2009), but germination is not necessarily moisture-limited if seeds are sown in autumn (Vidaller et al. 2019a). A higher soil moisture may also increase competition by ruderal species outcompeting desirable dry grassland species (Masson et al. 2015). Traditional grazing in winter and spring is essential to maintain NwMedB grasslands but can cause considerable damage by increasing plant mortality and decreasing plant performance in the early stages of restoration (Buisson et al. 2015; Vidaller et al. 2019a). Initial watering has a positive effect on *B. retusum* performance in grazed but not in ungrazed plots, suggesting that watering may compensate for grazing stress. Grazing can reduce seedling survival and performance over at least 2 years (Vidaller et al. 2019a). Bunchgrasses, such as *Lygeum spartum*, can be successfully reintroduced to degraded grasslands if environmental conditions are improved (e.g. decreasing water runoff and increasing water availability; Pueyo et al. 2009). *Lygeum spartum* and *Stipa tenacissima* have the potential to reduce soil erosion and improve their nearby environment and thus facilitate the establishment of other species (Cortina et al. 2009; Nedjimi 2016).

The role of fire is less clear than that of grazing but several studies have shown that typical Mediterranean grassland species benefit from occasional fire (Naveh 1975; Grigulis et al. 2005; Vidaller et al. 2019a), especially from summer fire mimicking natural fires (Vidaller et al. 2019b), suggesting that a trade-off similar to grazing may be assumed for fire. High fire frequency may reduce performance and survival but occasional fires may help to preserve grasslands, in particular if sites are under-grazed or if grazing has been abandoned (Vidaller et al. 2019b). Fire strongly increases seed production of *B. retusum* and *Ampelodesmos mauritanica* (Grigulis et al. 2005; Vidaller et al. 2019b) and has a positive effect on community diversity (Incerti et al. 2013; Vidaller et al. 2019b). This suggests that an adequate fire regime, in particular summer fire, is a key factor in preserving and restoring steppe ecosystems (Fig. 1). Moreover, fire may replace grazing as a conservation measure since the species composition of abandoned grasslands showed a post-fire community shift toward typical steppe communities (Vidaller et al. 2019b). Managing strategies, including type, intensity, and timing of grazing, prescribed burning or watering, need to be based on reliable information on the specific influence of these factors on plant populations.

On soils with high nutrient content, competition by nontarget species but also competition with over-abundant target species (e.g. with *Anisantha* spp.) may decrease perennial species establishment and growth (Buisson et al. 2015) as well as annual species establishment (Jaunatre et al. 2014a). Topsoil removal (or other soil impoverishment techniques) decreases soil nutrient content and arable weed seed bank, and may improve target species establishment (Jaunatre et al. 2014b).

Using Animals to Restore Plant Communities

Constraints in the restoration of Mediterranean grasslands may be overcome by the promotion or reintroduction of animals considered ecological engineers. These organisms directly or indirectly modulate the availability of resources to other species by causing physical state changes in biotic and abiotic materials (Jones et al. 1994), and they can contribute to the resilience of ecosystems after disturbances (Peterson et al. 1998). Although few studies have experimentally tested the use of ecological engineers to restore Mediterranean grasslands (e.g. Bulot et al. 2014a; De Almeida et al. 2020), we suggest several promising lines of research in the following sections.

Seed Dispersal

Seed dispersal is a central plant–animal mutualism influencing seedling recruitment, population dynamics, species distributions, plant-community composition, and gene flow (Nathan & Muller-Landau 2000). Seed dispersal can also reduce competition with the parent plant, and losses to seed predators and pathogens (Howe & Smallwood 1982).

Arthropods are ubiquitous, and one of the most important animal groups involved in seed dispersal and establishment (Lengyel et al. 2009). Among arthropods, ants are the primary seed dispersers in terrestrial ecosystems (Wills & Landis 2018) including Mediterranean grasslands. In these grasslands, species from the genus *Messor* are the most abundant granivorous ants (Cerdá & Retana 1994; Gomez & Espadaler 1994; Azcárate & Peco 2007). Depending on the plant species, 46–100% of the newly produced seeds can be removed by these harvester ants (Westerman et al. 2012). Only a small percentage of these is dropped on the way and dispersed, but an ant colony can transport up to 50,000 seeds a day and the average number of nests per hectare can reach 200 (Detrain & Tasse 2000; Arnan et al. 2010). In the Mediterranean region, foraging tracks of more than 80 m have been observed for the ant species *Messor barbarus* (Detrain et al. 1996), which may increase the potential of plant recovery from the nearby reference site. Within this context, where *M. barbarus* cannot naturally colonize, its reintroduction using mated queens already tested by Bulot et al. (2014a) may be a valuable tool to restore its populations (De Almeida et al. 2020).

Seedling Recruitment

Seed dispersal, especially by ants, benefits plants not only by reducing competition and predation, or minimizing the effects of fire through burial, but also by depositing seeds in more productive sites (Ness & Bronstein 2004). Granivorous ants are ecologically important because of their strong effects on plant communities, including nutrient cycling and microclimate modification. Although they do directly prey upon seeds (Schöning et al. 2004), they play a key dispersal role when they accidentally drop seeds, during the transport, in microsites with suitable conditions for germination (Detrain & Tasse 2000) or in refuse piles, increasing seedling recruitment (Retana et al. 2004; Azcárate & Peco 2007; Bulot et al. 2016).

Bulot et al. (2014a) experimentally reintroduced *M. barbarus* to later test their potential as ecosystem engineers. This ant species was chosen based on its key functions (see section above) in Mediterranean grasslands (Azcárate & Peco 2007). Seven years after the establishment of the first colonies, ants increased soil nutrients. They accelerated the ecological recovery of Mediterranean dry grassland plants by directly and indirectly facilitating their reestablishment (De Almeida et al. 2020). This innovative experiment provides a promising option in using invertebrates to overcome seedling limitation in Mediterranean grassland restoration.

Grazing Management

In cases of long-term high and destructive livestock pressure, grassland restoration may require the temporary exclusion of grazing. However, while grazing exclusion has initial positive effects including the recovery of the herbaceous cover and an increase in species richness, it can also lead to a decrease in plant species richness and to shrub encroachment (Golodets et al. 2010; Saatkamp et al. 2010). Grazing abandonment may lead to a reduction in the number and cover of small, early flowering and annual species and to their replacement by perennials, in particular graminoids (Noy-Meir et al. 1989; Peco et al. 2006b; Peco et al. 2012; Mesléard et al. 2017; Saatkamp et al. 2018). It may further decrease soil multifunctionality (Peco et al. 2017). Grazing exclusion also affects arthropod communities by (1) increasing ant and beetle species richness (Blight et al. 2011; Azcárate & Peco 2012), (2) shifting beetle composition toward assemblages less typical of NwMedB grasslands (Fadda et al. 2008; García-Tejero et al. 2013), or (3) decreasing Orthoptera abundance (Fonderflick et al. 2014). The decrease in livestock is now considered a major cause of changes in Mediterranean landscapes (Perevolotsky & Seligman 1998) and livestock has been reintroduced to preserve or restore open habitats in protected areas and in many rangelands where it had disappeared or declined. Traditional grazing is used in NwMedB grasslands to control colonization by woody species and to enhance species richness, in particular that of annual or subordinate species (Bernués et al. 2005; Mesléard et al. 2017; Koerner et al. 2018) as well as for the conservation of threatened species (Bröder et al. 2019).

Grazing can therefore be a major restoration tool and must be carefully considered in restoration planning, as its outcome may depend on productivity (de Bello et al. 2007). It should be adapted to fluctuating environmental conditions linked to the Mediterranean climate, particularly stochastic rainfall events, and to climate change which increases the frequency of such events (Carmona et al. 2012). Drought may reduce the number of species by limiting germination and survival or, in contrast, favor the coexistence of species by the reduction of dominant plant cover (Espigares & Peco 1995; Pérez-Camacho et al. 2012). To avoid soil degradation, desertification or shrub encroachment, grazing intensity should be reduced in dry years and, at the opposite, increased when a lot of fodder is available.

Conclusion and Research Perspectives

Much research is still needed to maximize NwMedB grassland restoration success (Fig. 1):

Dispersal

Both wild and domestic vertebrates are seed dispersers in dry grasslands (Benthien et al. 2016) because they facilitate seed dispersal in two ways: ingestion of seeds or transport of seeds attached to their fur. Studies on dispersal by mammals remain scarce in NwMedB grasslands (Malo & Suárez 1995, 1996), and dispersal distances are rarely evaluated although most grasslands are grazed. Further research should focus on evaluating the fate of seeds transported by both vertebrate and invertebrate animals, on its contribution to restoration, and on the spatial implementation of grazing in order to optimize seed dispersal.

Plant Material

Ecological restoration projects in the Mediterranean Basin still lack wider use of native species of local provenance (Nunes et al. 2016). Research is needed on the population biology and propagation of keystone species. Incentives for the use of local populations in restoration projects (e.g. the French label "*végétal local*"; Malaval et al. 2015) should continue to be supported. Combining studies of neutral markers (not selected by environmental conditions: amplified fragment length polymorphism, microsatellites) and adaptive quantitative traits (under selection by environmental conditions) for NwMedB grassland plants will help improve our understanding of the relative importance of drift and adaptive processes to the overall genetic differentiation among populations (Vidaller et al. 2020).

Soil Transfer and the Soil Black Box

Because many annual species germinate with autumn rains, it is likely that topsoil transfer carried out at the end of summer, right before the first rains, would maximize recovery from the seed bank. While spring and autumn soil transfers have been implemented and compared in the same area (Buisson et al. 2018), late summer transfer remains to be tested using an experimental design that allows a comparison of transfers in different seasons.

Soil inversion (burial of the topsoil under a layer of subsoil) has been used in temperate grassland restoration to decrease soil nutrients and reduce the seed bank of undesirable species (Glen et al. 2017). Various versions of this (compaction, soil inversion, topsoil removal) should be tested on the same Mediterranean ecosystem-type using similar protocols.

Establishment

Other less-studied organisms can play a role in seedling recruitment, such as nurse plant species (Cortina et al. 2009; Incerti et al. 2013) or earthworms. The latter have been used in mesic grassland restoration (Butt 2008) to improve soil structure and physico-chemistry and to ingest seeds that are later deposited in their casts (Forey et al. 2011). These seeds show higher establishment in this nutrient-rich biostructure than those of the surrounding soil seed bank (Lavelle et al. 2006). Although no similar studies have been carried out in Mediterranean grasslands, we might expect a similar influence of earthworms on their plant communities.

Also, further research of safe sites to improve germination and seedling establishment should be conducted. Their positive role (e.g. modifying microclimate) in the revegetation process, in interaction with grazing, has been shown in stressful environments (Buisson et al. 2015).

Occasional spring droughts may lead to high mortality of perennial species (Buisson et al. 2015) but the effects of such droughts on reproductive success of annual species and on the community composition of the following year still has to be evaluated, taking into account the phenological stage at which such events occur.

Fire is already used as a grassland management or restoration tool under various climates (Bond & Keeley 2005; Pyke et al. 2010). These studies have shown that fire-prone ecosystem restoration requires appropriate fire regimes for species establishment and survival. Such knowledge is not available for Mediterranean grasslands because the use of fire has been abandoned for more than a century and is now controversial. Detailed studies on the effect of various fire regimes are needed to best inform restoration and conservation (Vidaller et al. 2019b).

Grassland Invertebrates

In the Mediterranean Basin, arthropods, such as spiders (García et al. 2009), beetles (Alignan et al. 2018b), and Orthoptera (Alignan et al. 2014, 2018a) are used as bioindicators of restoration success because of their high sensitivity to changes in vegetation structure (height and density) or composition. Continuing to explore plant-arthropod relationships and ecosystem engineers, such as ants and earthworms, will contribute to a more integrative response for overcoming key constraints in NwMedB grassland restoration.

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Supporting Information

The following information may be found in the online version of this article:

Figure S1. Natura 2000 sites containing habitat #6220 are represented as green dots on a map of all Natura 2000 areas.

Table S1. Type of grasslands covered by the paper and for which the paper may be relevant.

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