EDITORIAL OPINION

How Much Ecology Do We Need to Know to Restore Mediterranean Ecosystems?

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Abstract

Despite important advances in ecological knowledge of Mediterranean-type ecosystems, advances in restoration ecology have not seen a parallel increase in these systems. Although some concepts such as positive plant–plant interaction (facilitation) have received attention in the restoration ecology community, others such as phenotypic plasticity have not. Some concepts (e.g., environmental heterogeneity) are mature enough for a wide use in restoration, whereas available knowledge on others (e.g., facilitation, plasticity) is less conclusive. However, the scientific knowledge is in general enough to significantly improve the guidelines for restoration of Mediterranean ecosystems. Our review suggests that (1) the extent of facilitation in dry ecosystems is partially understood, with supporting, but somewhat contradictory empirical evidence for its potential use in restoration; (2) the influence of habitat heterogeneity on plant performance and plasticity is only beginning to be understood, with a strong bias toward patterns of structural heterogeneity and negligible information on functional heterogeneity; and (3) sound evaluations of phenotypic plasticity might be useful to increase the success of restoration practices in patchy Mediterranean environments. Future global change scenarios involving temperature rise, reduced precipitation, increased frequency of extreme climatic events, and important land use changes and fragmentation must be particularly considered when restoring Mediterranean ecosystems. Further research on how to incorporate results on facilitation, environmental heterogeneity, and plasticity within a global change framework is clearly needed.

Key words: **abiotic stress, aridity, environmental heterogeneity, extreme climatic events, facilitation, global change, herbivory, local scale, nurse-plants, phenotypic plasticity, positive plant–plant interaction, reaction norm.**

Introduction

Advances in restoration ecology are intrinsically linked to advances in the ecological understanding of the ecosystems to be restored (Temperton et al. 2004). Because ecological research in Mediterranean ecosystems has experienced a steady increase over the past few decades (Thompson 2005 and references therein), restoration ecology can be expected to have experienced an analogous progress in these ecosystems. However, this progress has been slowed by the inherent difficulties of restoring degraded areas in dry regions in general, the scarcity of well-established ways to quickly transfer ecological knowledge to institutions devoted to restoration, and the ecological and logistic complexities that are drawn from the intense and usually prolonged human intervention in many Mediterranean ecosystems (Vallejo et al. 2005; Maestre et al. 2006*a*). Our objective here was to explore whether the ecological knowledge accumulated over the past few decades is ripe to be used in practice to restore degraded Mediterranean ecosystems. To tackle this general objective, we selected the following three specific topics of potential interest in restoration ecology from those that have received increasing attention in Mediterranean ecosystems: (1) the predominance of positive plant–plant interactions (facilitation) under stressful conditions; (2) the consideration of environmental heterogeneity and the local scale when studying ecological processes; and (3) the importance of phenotypic plasticity in heterogeneous environments. We addressed these three topics taking into account the most likely global change scenarios for Mediterranean ecosystems, which include increasing aridity, changes in land use, and fragmentation.

Nurse-Plants and the Generality of Positive Interactions among Plants under Stress

Nurse-plants are those that enhance the establishment of juvenile plants, a phenomenon that has been observed in a variety of communities and ecosystems (Callaway &

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Pugnaire 1999). Nurse-plants have been found to facilitate germination, establishment, growth, and reproduction, and their positive effects have been attributed to protection from herbivory and to amelioration of abiotic stress (Callaway & Pugnaire 1999; Shumway 2000; Gómez-Aparicio et al. 2004). Some of the best examples of nurse-plants occur in the deserts, where shrubs increase survival of juveniles of cacti (Franco & Nobel 1989). In general, the plant acting as a "nurse" is a mature plant of a different species than the juvenile, and this whole concept is attractive in restoration because it can be used to promote the establishment of target species that do not perform well in early stages or suffer a strong herbivory pressure (Gómez-Aparicio et al. 2004; Padilla & Pugnaire 2006). However, in many cases, the protégée, that is, the cactus in deserts or the late successional woody plant in temperate ecosystems, eventually suppresses and may kill the nurse-plant as a result of competition for light, water, or both. Compared with surrounding areas, nutrients and soil moisture below nurse-plants are often high, but light levels are reduced, sometimes to very low levels (Pages et al. 2003). Soil moisture below nurse-plants can even be lower than in the open in particularly adverse years (Valladares & Pearcy 2002). Thus, there are many situations where competition between the nurse-plant and the protégé can override the positive effects of the former on the latter. For example, Sternberg et al. (2004) found no facilitation effect of shrubs on annuals in a Mediterranean dune system in Israel. Besides, nurse-plants can have a number of indirect negative effects on protégées, for instance by sheltering small herbivores (Bartholomew 1970) or making protégées more vulnerable to herbivory (Baraza et al. 2004).

Bertness and Callaway (1994) presented a conceptual model suggesting that facilitation among plants increases at high levels of either stress or herbivory. However, and despite the importance of plant–plant interactions in ecosystem functioning and structure, there is contrasting evidence regarding the relationship between facilitation and abiotic stress. A quantitative meta-analysis of field and common garden studies recently evaluated the effect of abiotic stress on the net outcome of plant–plant interactions in arid and semiarid environments (Maestre et al. 2005). It revealed that the magnitude of the net effect provided by neighbors, either positive or negative, is not significantly greater under high abiotic stress conditions (Maestre et al. 2005). Thus, facilitation would not necessarily increase in importance with abiotic stress. Moreover, competition can predominate at both extremes of such a gradient, as found by Maestre & Cortina (2004). These results imply that current theoretical models predicting the relationship between the net outcome of plant–plant interactions and the abiotic stress are not generally applicable in arid and semiarid environments. Although there is some criticism to the conclusions of the meta-analysis by Maestre and coworkers (Lortie & Callaway 2006), there seems to be consensus in that empirical evidence is providing only partial support for the model (Maestre et al. 2005, 2006*b*; Lortie & Callaway 2006). Nevertheless, part of the controversy might be simply due to different experimental settings and, as suggested by the results of Miriti (2006), also to a shift from facilitation to competition as the protégée grows. The whole issue of facilitation in arid ecosystems clearly requires further research.

Results from studies conducted in Mediterranean ecosystems indicate that although facilitation tends to be common in patchy vegetation made up of shrubs (e.g., Gómez-Aparicio et al. 2004), competition for water tends to render an adverse combination of shade and drought for understory plants in forests (e.g., Valladares & Pearcy 2002). In summary, the generality of facilitation in arid ecosystems is uncertain. Thus, its use in the restoration of degraded Mediterranean ecosystems can be recommended only if the particular characteristics of each site are considered and the sign and magnitude of plant–plant interactions are followed up because they may change with ontogeny and environmental adversity, among other spatial and temporal features (Pugnaire & Luque 2001; Maestre et al. 2003). In our opinion, these uncertainties are particularly high in a global change scenario despite the suggestions of Brooker (2006) that facilitation should become more important as aridity increases with climate change.

Environmental Heterogeneity and Spatial Scales

Ecosystems are intrinsically heterogeneous, being in many cases, both a cause and a consequence of a discontinuous plant cover. This spatial heterogeneity (it must be noted though that most of the following applies equally well to temporal heterogeneity) has an important bearing on the success of most ecological restoration activities, but it is seldom considered in an explicit way (Bakler 2000; Maestre et al. 2006*a*). For instance, important efforts are devoted to maximize plant quality in reforestation and afforestation projects, choosing the right species and from the right provenance, but almost no consideration of local heterogeneity is taken, which leads to high overall mortality and a patchy distribution of surviving individuals (F. Valladares et al. unpublished data; Vallejo et al. 2005).

It is well known that the pattern of environmental heterogeneity can shape the selective pressures that determine the distribution and abundance of organisms (Levins 1968). Thus, the scale to which individuals are responsive is a critical aspect to take into account when designing reforestation experiments (McKay et al. 2005). Population differentiation in plants can occur in a spatial scale of less than 1 km (Linhart & Grant 1996) and particular genotype × environment interactions on plant fitness have been detected at a scale of meters (Antonovics et al. 1987; Stratton 1994). There is evidence of microhabitat differentiation of both mean values and plasticity of functional and life history plant traits (Galloway 1995;

Balaguer et al. 2001; Gianoli 2004). Climatic and microclimatic factors may interact and hence result in unexpected patterns in plant phenotype and performance in Mediterranean ecosystems (Jaksic & Montenegro 1979).

In arid ecosystems, part of the spatial heterogeneity of abiotic factors is generated by shrubs and established vegetation, which have been shown to facilitate the establishment of other plants, frequently tree species. But this facilitation is affected by the spatial scale. The effects of the abiotic heterogeneity generated by shrubs are not consistent across a range of spatial scales, leading to a very complex regeneration niche of target species (e.g., trees) at fine spatial scales (Gómez-Aparicio et al. 2005). In fact, abiotic heterogeneity seems to fit the spatial patterns of seedling establishment only when microsite "noise" is averaged out at greater scales (Gómez-Aparicio et al. 2005). The understanding of the influence of spatial heterogeneity on the performance of target plants is further complicated by the fact that not all scales of environmental heterogeneity are significant. As shown by Gómez et al. (2004), functional heterogeneity (variability of a system property affecting ecological processes) is only a fraction of the available structural heterogeneity (variability of a property measured without reference to ecological effects). The heterogeneity relevant for plant recruitment in patchy Mediterranean ecosystems is not necessarily that of the landscape as a whole (Gómez et al. 2004).

Important efforts in reforestation and afforestation projects that are centered on plant quality, species, and provenance, but with no concern for local heterogeneity, may give poor results. Moreover, simplistic approaches to the categorization of genotypes and microenvironments in rankings of vigor and stressfulness, respectively, may be shortsighted because of the pervasive nature of genotype × environment interactions. The use of broadly adapted genetic mixtures that contain genetic variation necessary for further adaptive differentiation (Lesica & Allendorf 1999) and the matching between collection and restoration sites has been suggested to enhance the feasibility of genetic restoration (McKay et al. 2005).

Phenotypic Plasticity

Basic science has contributed to the improvement of biodiversity conservation and ecological restoration initiatives often and in various ways. For instance, population viability analysis (e.g., Fritts & Carbyn 1995) and the focus on genetic variation within species rather than on mere population sizes (O'Brien et al. 1985; Sanjayan et al. 1996) are valuable tools for biological conservation. It is now widely accepted that understanding patterns of genetic variation within and among populations is essential for defining appropriate units for in situ conservation (Newton et al. 1999), and that the genetic variability of source material is a key issue for the development of restoration strategies (Procaccini & Piazzi 2001). However, availability of genetic variability, and consequent adaptation via either ecotypic differentiation or genetic polymorphism, is not the only strategy that natural populations may show to deal with heterogeneous or challenging environments (Schlichting & Pigliucci 1998). This specialization strategy should be advantageous under extreme abiotic conditions, but a flexible, generalist strategy should prevail in changing or spatially patchy environments (Bradshaw & Hardwick 1989).

Phenotypic plasticity is the ability of an organism to modify its phenotype in response to environmental variation, and it is visualized using reaction norms: the plot of phenotypic trait expression against environmental conditions (Valladares et al. 2006). In the past few decades, phenotypic plasticity has become a central issue of ecological and evolutionary research. It is now clear that phenotypic plasticity may be adaptive, that it can be genetically based, and that individual plastic responses may affect not only population parameters but also community-level interactions and ecological breadth (Pigliucci 1996, 2001; Schlichting & Pigliucci 1998; González and Gianoli 2004; Miner et al. 2005; Saldaña et al. 2005; Richards et al. 2006). The occurrence of phenotypic plasticity might be essential for natural populations to cope with environmental heterogeneity (Bradshaw & Hardwick 1989). Consequently, the reintroduction of individuals into degraded ecosystems should include previous evaluations of plasticity to the prevailing and/or more stressful ecological factors. Surprisingly, the concept of phenotypic plasticity has not been incorporated into the realm of restoration ecology. Thus, literature searches in the Web of Science (time span 1988–2007) with the keywords "phenotypic plasticity" and "reaction norm" rendered only one record and none, respectively, in the main journals of the discipline (*Restoration Ecology* and *Ecological Restoration*). The sole study found (Brewer 2005) addressed habitat restoration for an endangered pitcher plant and evaluated whether plant fitness increased after experimental neighbor reduction in the field.

The adoption of plasticity estimates may be useful in the development of restoration initiatives, particularly in the case of Mediterranean ecosystems, which exhibit substantial environmental heterogeneity at temporal and spatial scales (Lavorel et al. 1994; Valladares et al. 2002; Gianoli & González-Teuber 2005). The fact that different populations of Mediterranean species such as the evergreen oaks *Quercus coccifera* and *Q. ilex* exhibit different levels of phenotypic plasticity (Balaguer et al. 2001; Gratani et al. 2003) reveals a potentially important evolutionary role of plasticity in these ecosystems. However, there are studies showing both that Mediterranean woody plants exhibit a tendency for a reduced plasticity as part of a conservative resource use strategy (Valladares et al. 2002) and that woody plants co-occurring in Mediterranean ecosystems exhibit different degrees of plastic adjustments to different environments (Valladares et al.

2005). This leads to a widening of our approach to phenotypic plasticity, whose maximization is not necessarily adaptive for all plants dwelling in Mediterranean ecosystems (Valladares et al. 2005), and to consider the complexity of the phenotypic responses of organisms to multiple ecological factors. For instance, shade and drought may interact in a nonintuitive fashion when affecting plant performance (Valladares & Pearcy 2002; Valladares et al. 2005), high overall plasticity levels may be negatively associated with tolerance to extreme abiotic stress (Sánchez-Gómez et al. 2006), and both herbivory (Quezada & Gianoli 2006; Gianoli et al. 2007) and correlated traits (Gianoli 2001, 2003) may constrain plant reaction norms to abiotic factors.

In summary, experimental evaluations of the reaction norm of source material to water availability, irradiance, temperature, herbivory, or the interaction between these factors, which should be determined depending on the particular ecological setting of the ecosystem to be restored, may significantly increase the success of reintroductions.

Restoring Mediterranean Ecosystems under Global Change Scenarios

Global change has the potential to affect the practice and outcomes of ecological restoration because of the modified environmental conditions that will be found in the future. In contrast to this view, there is a general emphasis on the historical conditions either as the basis for explicit objectives or to reset ecological processes to predisturbance conditions (Harris et al. 2006). Restoration must involve a proper balance between rebuilding past systems and attempting to build resilient systems for the future.

A number of ecophysiological features enhancing performance under drought and heat, two conditions to be exacerbated by climate change, are frequently looked for in plants to be used in restoration of Mediterranean ecosystems (Vallejo et al. 2005). However, different functional traits and life cycle strategies co-occur in plants presumably adapted to these stress factors, and evidence for which ones could be advantageous in the new climatic scenarios is scant and often speculative. For instance, an experimental study suggested that high drought tolerance coupled with a conservative water use (a strategy observed in some *Quercus* spp. saplings) seems to render good results under current climatic conditions, where chronic drought alternates with seasonal rainfall, whereas the opposite more opportunistic syndrome (observed in *Pistacia* spp. saplings) could enhance performance under future scenarios characterized by extreme aridity and more unpredictable rainfalls (Valladares et al. 2005). But these predictions are hard to test under realistic conditions.

Interestingly, a somewhat complementary approach to that focused on global warming and increased aridity has been recently put forward: the extreme increases in water availability typical of "El Niño" events in some Mediterranean ecosystems may be used as "windows of opportunity" for reforestation practices, as far as the likely associated herbivore population outbreaks can be controlled (Holmgren et al. 2006).

Global change in Mediterranean ecosystems involves not only increased aridity but also significant changes in land use and fragmentation (Valladares 2004). Fragmentation may favor increased phenotypic plasticity over local adaptation, provided some migration and dispersal among patches, as shown in modeling exercises (Sultan & Spencer 2002). But whether this potentially increased plasticity will enhance plant performance in a climate change scenario or will make plants more vulnerable to unpredictable environmental fluctuations remains uncertain. Global change is not only having an effect on the performance of individual plants but also on the interactions among plants (Brooker 2006), the sign and intensity of which could be drastically affected by increased aridity (Maestre & Cortina 2004; Maestre et al. 2005). However, and despite all these uncertainties, current and future levels of abiotic stress and habitat fragmentation must be taken into account when planning the restoration of a Mediterranean ecosystem.

Conclusions

A complete understanding of the functioning of Mediterranean ecosystems is a far-reaching objective, if reachable at all. Besides, this eventual understanding will require constant updates as global change is invariably bringing new environmental conditions. Therefore, we cannot wait to have such an encyclopedic and fully updated knowledge to transfer ecological results to restoration projects. However, we should identify the most urgent research lines with this aim in mind. Here, we have seen that (1) the extent of facilitation in dry ecosystems is partially understood, with supporting, but somewhat contradictory empirical evidence for its potential use in restoration; (2) available ecological information has a strong bias toward patterns of structural heterogeneity, with negligible information on functional heterogeneity and its effects; (3) the potential influence of habitat heterogeneity on plant performance and plasticity is only beginning to be understood; and (4) sound and realistic evaluations of phenotypic plasticity might be useful to increase the success of restoration practices for some Mediterranean plants. Thus, the answer to the question "How much ecology do we need to know to restore Mediterranean ecosystems?" seems to be "We know enough ecology to significantly improve current restoration practices, but we still have fundamental gaps in specific and critical issues, such as those discussed here, which should guide the research on restoration ecology of these ecosystems."

Implications for Practice

- The use of nurse-plants to facilitate the establishment of target plant species is a promising practice. However, facilitation in arid environments is less general than commonly assumed, and it has been shown to be context dependent. For instance, competition (for water) and not facilitation have been found in the understory of dense forests, whereas facilitation tends to be more common under the canopy of sparse shrubs.
- The remarkably high environmental heterogeneity of Mediterranean ecosystems should be explicitly and a priori considered in restoration activities such as reforestation and afforestation. For instance, extensive planting with a given species or seeding with a fixed density and mixture of species usually leads to poor and patchy results because this heterogeneity is overlooked.
- A high level of phenotypic plasticity is in general a good a priori feature of candidate plants for restoration because plasticity enhances the capacity to cope with heterogeneous environments. However, it must be checked (1) whether the particular environmental grain would select a specialization strategy (ecotypic differentiation) over a flexible strategy, that is, high plasticity levels might be negatively associated with tolerance to extreme levels of stress and (2) whether the other ecological factors and the plant responses to them influence the expression and adaptive value of the focus traits.
- Future global change scenarios must be taken into account when planning restoration projects. Temperature rise, reduced precipitation, increased frequency of extreme climatic events, and important land use changes involving fragmentation must be particularly considered in restoring Mediterranean ecosystems. More research on how to incorporate results on facilitation, environmental heterogeneity, and plasticity within a global change framework is clearly needed.

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