

More Ecology is Needed to Restore Mediterranean Ecosystems: A Reply to Valladares and Gianoli

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Abstract

Valladares and Gianoli (2007) tried to answer a key question, “how much ecology do we need to know to restore Mediterranean ecosystems?” by focusing on (1) plant–plant interactions; (2) environmental heterogeneity and the potential adaptation of transplanted plants; and (3) phenotypic plasticity of the planted species. We consider their choice of topics incomplete and potentially misleading because (1) it is clearly biased toward a narrow set of research topics (phenotypic plasticity, facilitation, and climate change); (2) it assumes that active restoration, and specifically revegetation, is needed; and (3) it conveys a false perception that other basic ecological aspects of Mediterranean ecosystems are sufficiently known. Instead, we review the current knowledge on seed dispersal, succession, and ecosystem functioning for Mediterranean ecosystems. We argue that decades of research on these topics have yielded few practical guidelines for restoration, something that needs to be urgently corrected. First,

the current “establishment limitation paradigm” for plant recruitment does not acknowledge the role of dispersal limitation at large spatial scales. More attention should be paid to nucleation processes and directed seed dispersal mediated by animals. Second, studies of vegetation dynamics and succession in the Mediterranean have led to an overly simplistic view of successional dynamics. How fast and deterministic succession is remains mostly unexplored; long-term monitoring of successional dynamics at different spatial scales is urgently needed. Third, information on the functional status of Mediterranean ecosystems is required to identify processes hindering natural recovery after disturbances and to set priorities on the areas and ecosystem components to be restored.

Key words: degradation thresholds, disperser-mediated facilitation, ecosystem functioning, landscape ecology, nucleation, restorability, seed dispersal, stable alternative states, succession.

In a recent opinion article, Valladares and Gianoli (2007; V&G hereafter) pose an interesting question, “how much ecology do we need to know to restore Mediterranean ecosystems?,” a question that every practitioner should ask him- or herself before starting any restoration project. They address the following three main topics: (1) the use of plant–plant interactions in restoration; (2) environmental heterogeneity and the potential adaptation of transplanted plants used in restoration projects; and (3) phenotypic plasticity, again related to the potential success of transplanted plants. Their discussion of these topics is tied up with a consideration of future climate scenarios, which could affect the ecological processes behind the three topics discussed, particularly in the Mediterranean.

We recognize the relevance of the topics addressed by V&G but at the same time would like to point out that they are clearly biased toward a relatively narrow set of

research topics, namely, phenotypic plasticity, facilitation, and climate change. Other practitioners could have picked different aspects of ecological theory as important as these to guide restoration efforts in Mediterranean ecosystems. In this essay, we seek to widen the list of topics proposed by V&G by revisiting key ecological concepts such as seed dispersal, succession, and ecosystem functional status. The topics chosen by V&G assume that something has to be done when dealing with degraded ecosystems and, more specifically, that these actions necessarily imply revegetation. Instead, the topics addressed in our list are mainly related to passive restoration, that is, they mainly try to assess which basic ecological properties of Mediterranean ecosystems can be used to save effort in restoration and how key ecological processes and attributes can be effectively used as a restoration aid. We begin by dissecting the major question of this article in three more specific and mechanistic questions: (1) How important is seed dispersal at different spatial and temporal scales in Mediterranean ecosystems? (2) How fast and deterministic is succession in Mediterranean ecosystems? and (3) How much do we know about the functionality of Mediterranean ecosystems? We believe that answering these questions will lead to a more comprehensive—and easier to transfer—interpretation of some of the topics selected by V&G (e.g., plant–plant facilitation). More importantly, it will

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shed light on additional topics as relevant as those selected by V&G on an objective basis, as reflected by previous reviews of the ecological basis of restoration practice (Holmes & Richardson 1999; Falk et al. 2006; Walker et al. 2007). Our aim was also to show that there are further gaps in our knowledge of Mediterranean ecosystems that need to be filled if we want to provide guidelines to restore them that are both ecologically sound and effective.

The Role of Seed Dispersal in Restoration

Propagule input plays a pivotal role in the restoration of degraded habitats and impoverished plant communities (Honnay et al. 2002). Mediterranean-based ecologists have greatly contributed to the study of seed dispersal, especially by animals (e.g., Herrera 1995 and references therein), but, paradoxically, and contrary to what happened in other bioregions such as the tropics (e.g., Holl et al. 2000; Martínez-Garza & Howe 2003), little of this knowledge has been effectively transferred to conservation and restoration practices in these environments (but see Tellería et al. 2005). Early studies pointed to a supposed role of seed disperser animals as “habitat shapers” in Mediterranean systems (Herrera 1985), resulting from their ability to generate nonrandom distributions of plant propagules within the landscape. However, this idea was subsequently called into question by the development of the “establishment limitation paradigm,” that is, the common assumption that plant recruitment in Mediterranean habitats, contrary to temperate and tropical ones, is more limited by the availability of microsites for establishment than by the availability of seeds. In other words, typically Mediterranean postdispersal factors, such as summer drought, act as strong establishment bottlenecks overshadowing the effects of seed dispersal, and determining ultimately that the sites receiving more seeds are not necessarily those promoting effective recruitment (e.g., Herrera et al. 1994; Rey & Alcántara 2000; García 2001). In this context, our aim here was to identify a (nonexhaustive) list of key concepts addressing why seed dispersal matters for restoration in Mediterranean ecosystems. At the same time, we seek to highlight how the establishment limitation paradigm weakens when considering the mechanistic role of seed dispersal over large-scales, such as the temporal extent of ecological succession and the spatial extent of the landscape.

First, we must consider that seed dispersal by animals is probably the main mechanism behind the *nucleation processes* occurring in natural succession in degraded lands, such as abandoned old-fields. By nucleation, we mean the spontaneous occurrence of vegetation clumps or “recruitment foci” spatially associated to preexisting structures, such as crop trees in abandoned orchards (e.g., olive and carob trees; Debussche & Isenmann 1994; Verdú & García-Fayos 1996; Pausas et al. 2006). Nucleation results first from a “perch effect,” that is, the quantitative effect

of the disproportionate deposition of seeds under a preexisting structure that is used by seed dispersers (mostly frugivorous birds) as a perch for resting or feeding (Debussche & Isenmann 1994; Pausas et al. 2006). Second, nucleation emerges from the improvement of environmental conditions for seedling establishment under the perch, that is, from a facilitation process driven by the preexisting structure acting as a nurse-plant (e.g., by enhancing soil humidity and nutrients or by providing protection against herbivores; Verdú & García-Fayos 1996; Maestre et al. 2003; Pausas et al. 2006). The consequence of this process of *disperser-mediated facilitation*, which leads to the aggregation of seedlings and juveniles of woody plants on nucleation foci, is an accelerated succession, as it mostly drives to the early appearance of late-successional species (e.g., *Rhamnus lycioides* and *Pistacia lentiscus* in abandoned carob orchards; Verdú & García-Fayos 1996; Pausas et al. 2006). The consideration of plant–plant facilitation as a process frequently linked to nonrandom seed dispersal by animals offers a tool for restoration more robust than the classical facilitation concept because it identifies the perch effect as a first determinant, and natural driver, of propagule input toward nurse-plants. Moreover, the concept and their derived restoration tools are probably wide enough to be applied to a large range of purposes, from vegetation recovery on abandoned lands to the regeneration of endangered species in unaltered habitats (e.g., the relict tree *Taxus baccata*; García et al. 2000).

A wider consideration of *directed dispersal* (i.e., the disproportionate deposition of seeds in those sites most favorable for seedling establishment; Wenny 2001) may also be worthy to discern how seed dispersers do the restorer’s job in Mediterranean ecosystems. Besides the abovementioned deposition under potential nurse-plants, we must consider here the frequent dispersal by caching, scatter-hoarding animals of some Mediterranean late-successional trees (such as the European jay [*Garrulus glandarius*] dispersing oak and beech acorns; e.g., Gómez 2003; Pons & Pausas 2007). In that case, the “favorable microsite” is the soil cache in which animals bury the seeds and that provides protection from drought, freezing, and postdispersal seed predation (Gómez 2004). Moreover, this process of directed dispersal may be scaled up from the microsite to the landscape extent because jays are able to move acorns over long distances toward selected habitat patches that result the most suitable for long-term regeneration of oaks (such as afforestations or abandoned lands; Gómez 2003; Pons & Pausas 2007). As a result, greater tree regeneration is found in those landscape patches receiving more dispersed seeds, despite that, within the patch, the small-scale demographic effects of seed dispersal may be still screened-off by establishment limitations (Kunstler et al. 2007). Thus, discerning the extent of this sort of *landscape-level dispersal limitation* among different plant life forms is crucial for understanding the contribution of dispersal to the restoration of degraded patches in the highly fragmented and variegated

landscapes of the Mediterranean regions. Moreover, disentangling the mechanisms behind the hierarchical response of seed dispersers to the multiscaled spatial heterogeneity of Mediterranean environments will allow us to identify which combinations of disperser assemblages and landscape scenarios are the best for effective plant regeneration.

Using Succession Vegetation Models in Restoration

It is widely accepted that a profound knowledge on vegetation dynamics is strictly necessary to be mimicked in restoration projects and land management (Bradshaw 1983; Wiebleg & Felinks 2001). As a corollary, it is desirable to develop a theory of vegetation dynamics at every spatial and temporal scale (van der Maarel 2005) to be subsequently translated into adequate restoration designs.

In this sense, the status quo in the Mediterranean Basin seems favorable for designing good restoration projects because, probably, the vegetation of this region is one of the best known at a global scale. This is due to the exhaustive work and local abundance of botanists and phytosociologists, who have accumulated a valuable and useful knowledge of the flora and vegetation of most regions. In addition, a complex classification of vegetation types and deterministic dynamic models with an evident Clementsian influence have been proposed. They are based on the existence of the so-called “climax” vegetation and relatively simple degradation–succession pathways. These models have been organized in a complicated taxonomy of vegetation series (i.e., *sigmetum*) and, in certain cases, in graph networks where the change between conspicuous vegetation states is causally linked one to one by specific factors (i.e., grazing or wildfire). This effort has culminated in some encyclopedic works such as the map of the potential natural vegetation of the Iberian Peninsula (Rivas Martínez 1987; see also Bredenkamp et al. 1998, for a review of different possibilities to deal with potential vegetation).

However, the usefulness of this knowledge to restoration purposes is limited. First, the utility of detailed floristic description beyond providing a list of candidate plants for revegetation is not clear. Second, some ecologists consider that phytosociology conveys a too rigid view of successional processes in the Mediterranean (e.g., Mazzoleni et al. 2004) and, consequently, extremely difficult to translate into appropriate restoration protocols at adequate spatial scales. It is undeniable that phytosociologists have tremendous difficulties in adequately incorporating recent ecological developments such as inhibitory or parallel succession, alternative stable states, small-scale patch dynamics, or degradation thresholds in their models of vegetation dynamics. Basic questions that should be urgently answered, such as how fast and deterministic succession is in Mediterranean ecosystems, remain scarcely explored. Phytosociologists should inte-

grate current ecological knowledge in their dynamic models (Cortina et al. 2006). More specifically, vegetation models should consider that dynamics is governed by three general processes: differential site availability, species availability, and species performance (see details in Pickett & Cadenasso 2005). These three processes interact and reflect the type of disturbance and the neighborhood of the site where succession occurs at several spatial scales. Site availability is mainly the result of disturbance, species availability is related to dispersal and seed bank dynamics, and differential species performance is based on life history peculiarities. If these processes are incorporated into vegetation models, it is difficult to imagine deterministic and unambiguous succession trajectories.

In addition, some well-established and accepted ecological concepts are being revised. For instance, the concept of direct regeneration or autosuccession in Mediterranean ecosystems, especially after wildfires, has become a paradigm for many Mediterranean community ecologists (e.g., Hanes 1971; Lloret et al. 2002; Buhk et al. 2007). However, recent studies (Rodrigo et al. 2004; Baeza et al. 2007) have found that direct regeneration is not the unique response after severe perturbations, at least for some Mediterranean pine woodlands. Consequently, the idea that autosuccession in these Mediterranean ecosystems was a feedback mechanism promoting persistence in a scenario of continuous and historical human pressure should not be taken as a dogma.

Patch dynamics at small spatial scales seems the usual successional driver in most stressful Mediterranean habitats such as saxicolous communities (Escudero 1996), salt marsh communities (Castellanos et al. 1994), and semiarid shrublands (Pugnaire et al. 1996). Factors at hierarchic scales may control the vegetation dynamics of some Mediterranean habitats; for instance, at a large-scale, both individual and plant community patterns on gypsum hills are related to some soils' properties linked to topography (Rubio & Escudero 2000) or some biotic allelopathic constraints (Escudero et al. 2000a), but at smaller scales, the establishment of gypsophytes is closely linked to the physical characteristics of the biological soil crust (Escudero et al. 2000b, 2007; Romao & Escudero 2005). Furthermore, small variations in substrate conditions at very small scale may cause profound changes in the vegetation dynamics (Pueyo & Alados 2007).

We need studies of primary and secondary succession on human-made Mediterranean habitats (Marrs & Bradshaw 1993; Bonet 2004; Dana & Mota 2006), which will improve our still relatively scarce knowledge on the dynamics of Mediterranean vegetation. Unfortunately, there are very few studies that have been carried out over chronosequences (Bonet & Pausas 2004; Mazzoleni et al. 2004), and limited information from permanent plots or long-term studies is available. There is a long tradition from permanent plot studies in central Europe (Bakker et al. 1996), but there is not this type of

infrastructure in the Mediterranean Basin. This should be a priority for the Mediterranean scientific community.

Current vegetation knowledge may be useful for broad and landscape-scale planning, but most restoration projects need an improvement of our scarce knowledge of small-scale spatial vegetation dynamics. With such a type of information, we will greatly advance in the establishment of sound restoration measures. Mediterranean phytosociologists and community ecologists should integrate their complementary knowledge to build new vegetation dynamics models (Carmel & Kadmon 2000), which could be used to improve our restoration designs.

Ecosystem Functioning and Restoration

A major challenge facing today's ecologists is to determine the links and relative importance of abiotic and biotic factors as drivers of *ecosystem functioning* (Loreau et al. 2001). Such knowledge is relevant for restoration ecologists and practitioners for two primary reasons. First, because restoration actions ultimately aim to recover those ecosystem attributes and functional processes that have been lost or reduced with degradation, such as carbon fixation, soil stability—particularly important in many desertification-prone Mediterranean areas—infiltration, run-off control, and nutrient cycling (Whisenant 1999; Maestre & Cortina 2004a). Second, because incorporating information on the ecosystem's functional status and its drivers may help save resources for restoration by improving the criteria to select the areas to be acted upon, and the ecosystem components or functions that should be restored first (Tongway & Hindley 2000; Maestre & Cortina 2004b).

Many theories predicting how ecosystem composition, structure, and functioning are linked along degradation/restoration trajectories have been developed during recent decades (e.g., Bradshaw 1984; Aronson et al. 1993; Hobbs & Norton 1996; Suding & Gross 2006). Many of the conceptual models developed often imply that the lack of certain ecosystem components and/or functions may limit restoration efforts (Whisenant 1999). Some of them, such as the highly influential model proposed by Bradshaw (1984) for the reclamation of derelict land, assume that increases in structure (any description of community composition, and the way organisms are organized; Bradshaw 1984) parallel the recovery of ecosystem functioning in a linear way. This notion of a direct and simple relationship between ecosystem structure and functioning has largely influenced ecologists and restorers in the Mediterranean (Maestre & Cortina 2004a), who have often assumed an oversimplified theoretical framework assuming a single equilibrium end point (*sensu* Suding & Gross 2006). Most restoration actions in these areas have aimed to the direct recovery of ecosystem structure through the planting of seedlings of pioneer trees (mostly *Pinus* sp.) using highly mechanized procedures (Pausas et al. 2004; Amir & Rechtman 2006) and have assumed that this step

would accelerate natural succession and the recovery of ecosystem functioning under most circumstances (Ruiz de la Torre 1973; Rojo et al. 2002). Although a growing number of studies are showing that this action does not always recover either ecosystem structure or functioning, particularly under semiarid climates (e.g., Andrés & Ojeda 2002; Maestre & Cortina 2004a; Chirino et al. 2006; Goberna et al. 2007), afforestations are still being recommended and executed in the same way as has been carried out during the past decades (Rojo et al. 2002).

Despite the wide, and renewed, interest on the topic created by the rise of the biodiversity–ecosystem functioning perspective (Naeem 2006), the relationships between ecosystem structure, functioning, and *restorability* (i.e., the difficulty to bring a degraded ecosystem to a desired target state, or the effort needed to do so; Cortina et al. 2006) have been seldom assessed in Mediterranean environments. In one of such studies, Baeza et al. (2007) evaluated the relationships between ecosystem structure and functioning in shrublands and forests along a 30-year fire chronosequence in eastern Spain (see also Cortina et al. 2006). They found metastable states, hysteresis, and thresholds in the successional trajectory of vegetation, as well as a negative relationship between species richness and productivity. In other study, Maestre et al. (2006) explored the relationship between ecosystem functioning and restorability in *Stipa tenacissima* steppes from southeast Spain. They found that the survival of seedlings of the late-successional shrub *Pis. lentiscus*—their measure of restorability—was mainly controlled by abiotic conditions and showed a negative relationship with surrogates of ecosystem functioning such as the infiltration capacity of the soil.

Results such as these indicate that relationships between ecosystem structure and functioning in Mediterranean environments are complex and that the functional status of the ecosystem may not necessarily determine the outcome of restoration processes. They also highlight some of the limitations of the predominant conceptual paradigms and set the case for an invigorated research effort in the field. As a previous, but necessary, step to fully incorporate ecosystem functioning into ecological restoration, we advocate the development of a research agenda aiming to explore the relationships between ecosystem composition/structure and its functioning along landscape or degradation gradients comprising ecosystems targeted for conservation or management. Such information would be an invaluable tool to improve current restoration protocols and procedures and would also serve as a test of theories and models currently employed by restoration ecologists (see Falk et al. 2006, for a recent review).

An example of the utility of this approach is provided by recent studies carried out along degradation gradients in semiarid *S. tenacissima* steppes from southeast Spain (Maestre 2004; Maestre & Cortina 2004b; Maestre & Cortina 2005). They have found that basic attributes of patches (landscape units that collect water, sediments, and nutrients coming from run-off), such as their density and

the distance between them, and the cover of late-successional sprouting shrubs were major drivers of species diversity and richness and of soil stability, infiltration, and nutrient cycling in these steppes. Using this information, a two-stage restoration procedure for these steppes can be established. When they are highly degraded, restoration efforts should focus on the recovery of ecosystem structure by increasing the number of patches. This can be easily done by inserting brush piles parallel to land contours, a technique successfully employed in semiarid regions of Australia (Ludwig & Tongway 1996; Tongway & Ludwig 1996). Such artificially created patches would act as sinks of resources (soil, water, and nutrients) and seeds, providing favorable microenvironments for the recovery of vascular plants and biological soil crusts (Aguiar & Sala 1999; Bowker 2007). Once this intervention has reduced degradation processes, the next step to restore these systems should be the introduction of seedlings of native sprouting shrubs. This introduction would foster the recovery of nutrient cycling in the long term, increase ecosystem resilience, and provide suitable habitats for further spontaneous plant and wild animal colonization (Trabaud 1991; Verdú & García-Fayos 1996; López & Moro 1997).

Given the inherent difficulties associated to assessing whether a particular landscape is in need of restoration (Hobbs 2002), and what components/functions should be restored first, an in-depth consideration of the functional status of ecosystems, its drivers, and dynamics should prominently figure among the research agendas of restoration ecologists. Although challenging, any advance in the field will undoubtedly represent a step forward to develop a specific technology to establish ecologically sound restoration practices in Mediterranean ecosystems.

Concluding Remarks

The relevance of ecological theory for restoration practice has been a controversial topic since the birth of ecological restoration in the 1980s. A dominant view has considered restoration practice as an applied spin-off of ecological theory. According to this view, ecological theory provides basic conceptual tools to restoration practitioners (Halle 2007), and restoration practice becomes a test of the soundness of ecological concepts (Bradshaw 1987). This feedback has been opposed by critics arguing against the convincingness of such a link between restoration practice and ecological theory (Halle 2007) or that restoration practice does not actually derive any beneficial input from theory (Cabin 2007). Probably, truth lies somewhere in the middle between practice based on intuition and skillfulness and that based in sound knowledge of ecological principles of ecosystem functioning. In any case, we believe that an open debate around the question “how much ecology do we need to know to restore specific—Mediterranean or other—ecosystems?” will help find that middle ground. We encourage the editors and readers of *Restoration Ecology* to pursue such debate.

Implications for Practice

- Restoration ecologists should always consider which ecosystem features facilitate or hinder restoration. In Mediterranean ecosystems, seed dispersal, speed and determinism of succession, and ecosystem function are key topics. Paradoxically, decades of research on these topics have yielded few practical guidelines for restoration.
- Seed dispersers can save lot of work to restorationists. The establishment limitation paradigm does not acknowledge the role of dispersal limitation at large spatial scales. Nucleation processes, frugivore-mediated facilitation, and directed dispersal can be determinant at larger spatial scales even if at small scales microsite availability limits plant recruitment.
- The enormous typification work carried out by Mediterranean phytosociologists has led to an overly simplistic view of successional dynamics. How fast and deterministic succession is remains mostly unexplored. The possibility of parallel successional trajectories, stable alternative states, small-scale patch dynamics, and degradation thresholds need to be taken into account, and long-term monitoring of successional dynamics is urgently needed.
- The relationship between ecosystem structure and functioning in Mediterranean environments is complex. Information on the functional status of ecosystems is helpful to identify processes hindering natural recovery after disturbances and to set priorities on the areas and ecosystem components to be restored.

Acknowledgments

F.T.M. was supported by a Ramón y Cajal contract from the Spanish Ministerio de Educación y Ciencia (MEC). This review was made possible thanks to the REMEDINAL (S-0505/AMB/0335), CGL2006-09431, CGL2006-27872-E, and INTERCAMBIO (BIOCON06_039) projects, funded by Comunidad de Madrid, MEC, and Fundación BBVA, respectively.

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