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REVIEW PAPER

A review of the development of Mediterranean pine–oak ecosystems after land abandonment and afforestation: are they novel ecosystems?

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Abstract
• ***Context*** Mediterranean landscapes are composed of different interacting vegetation patches. Pine and oak ecosystems form contiguous patches within these landscapes, in pure stands, or as mixed pine–oak ecosystems. During the nineteenth century, pine forest distribution in the Mediterranean Basin increased dramatically as a result of large-scale re-forestation and spontaneous forest regeneration. At the same time, secondary succession of abandoned agricultural land allowed development of pine and oak ecosystems. Consequently, a pine–oak mosaic has developed, which created opportunities for cross-colonization, i.e. species colonization from one ecosystem in the reciprocal system. Pines shed their wind-dispersed seeds and colonize Mediterranean oak vegetation. Oaks regenerate in different ecosystems, including pine forest understories.
• ***Research question*** This paper reviews fire-free landscape-scale dynamics of pine–oak Mediterranean mosaics and analyze how landscape-scale interactions are leading to pine–oak ecosystems by different processes.
• ***Results*** Published information from the Mediterranean Basin illustrates pathways of pine–oak ecosystems formation. Using Mediterranean literature, I try to elucidate the factors that (1) control colonization potential and (2) modulate the resistance to colonization, in different habitats, land uses, and landscape settings.
• ***Conclusion*** Management implications for these mixed pine–oak ecosystems are suggested. The question of whether they are novel ecosystems is discussed.

Keywords Mediterranean · *Pinus* · *Quercus* · Colonization · Novel ecosystems · Emerging ecosystems · Landscape · Land-use change · Forest regeneration · Plantations · Succession

1 Introduction

Mediterranean regions are home to a tremendous diversity of habitats and species. Mediterranean landscapes typically form a patch mosaic where different vegetation types are intermingled in complex patterns created by the variation in physical, biological, and anthropogenic landscape conditions. Vegetation types can range from forests to woodlands, savannas, shrublands, and grasslands. Furthermore, Mediterranean landscape mosaics are a heterogeneous combination of both "natural" (although adapted to thousands of years of human impact) and man-made patches interleaved with one another in complex patterns that result from different edaphic conditions, topography, exposure to wind and sun, fire and other disturbances, and land-use histories (Blondel and Aronson 1999).

In this review I focus on the spatial landscape-scale fire-free dynamics of pine–oak Mediterranean mosaics and how landscape-scale interactions are leading to the formation of pine–oak ecosystems through different processes and pathways. Through this literature review, I aim at characterizing the two cross-colonization processes, i.e., pine colonizing oak ecosystems and oaks developing in pine understories, and try to unravel the factors that control colonization potential and factors that control successful establishment

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(resistance or facilitation) in these case studies. This review is confined to the Mediterranean Basin although similar processes may apply to other Mediterranean ecosystems (MTEs) as well as to other biomes.

2 Pines and oaks in the Mediterranean Basin

Forests of the Mediterranean Basin contain about 100 tree species, of which pines and oaks are the dominant trees in most MTEs (Blondel and Aronson 1999). Pine forests cover about 13 million hectares in the Mediterranean Basin, which constitute ~5% of Mediterranean forested area (Barbéro et al. 1998). Ten species of pines are distributed in these regions. The most common species are *Pinus halepnsis* Mill., common to the western part of the Basin, and replaced in the east by *Pinus brutia* Ten. Other species such as *Pinus pinaster* Ait, *Pinus nigra* Arn., *Pinus sylvestris* L., and *Pinus pinea* L. are found in scattered distributions, three species (*Pinus mugo* Turra, *Pinus heldreichii* Christ., and *Pinus uncinata* Ram.) are typical mountain pines, and *Pinus canariensis* Chr. Sm. is found only in the Canary Islands (Barbéro et al. 1998). Many pines are characterized by traits of pioneer species such as fast growth, early maturity, massive seed production and dispersal, and the ability to establish in harsh environmental conditions (Richardson 1998; Ne'eman and Trabaud 2000). Accordingly, pines dominate in disturbed ecosystems (Barbero et al. 1990; Grotkopp et al. 2002).

Oak species are more diverse than the pines, forming a continuum from summer green to evergreen phenologies. Six main evergreen oaks are widespread dominants throughout the Mediterranean Basin: *Quercus ilex* L. (holm oak) is the most common oak in the west of the Basin and replaced in the east by *Quercus calliprinos* Webb. The rest of the species are *Quercus suber* L., *Quercus coccifera* L., *Quercus alnifolia* Poech, and *Quercus aucheri* Jaub. et Spach. Deciduous oak species are much more diverse taxonomically, encompassing more than 35 species; among these, some common species are *Quercus pubescens* Willd., *Quercus ithaburensis* Decne., *Quercus cerris* L., *Quercus infectoria* Oliv., *Quercus libani* Oliv., *Quercus robur* L., *Quercus faginea* Lam., *Quercus afares* Pomel, *Quercus brantii* Lindl., *Quercus frainetto* Ten., and *Quercus macranthera* Fisch. et Mey. (Blondel and Aronson 1999). Oaks, although they are pioneering species in many ecosystems, in Mediterranean ecosystems are considered late successional species that follow the pioneer pine stage (Barbéro et al. 1998). Sclerophyllous oaks develop shrub or tree formations and are characterized by long life spans, late sexual maturity, moderate seed production, large heavy seeds, low chance of germination, but high persistence of established individuals (Roda et al. 1999). Oaks can be found in shrublands and forests, either as the dominant species, co-occurring with other Mediterranean species, or forming a sub-canopy below pine forests. Late-successional species have been characterized by low growth rate, long lifespan and shade-tolerance compared to early- successional species (Verdu 2000; Ogaya et al. 2003; Zavala et al. 2000, 2011).

Disturbances are very common in Mediterranean ecosystems (Naveh and Dan 1973). Oaks evolved mechanisms of strong and effective vegetative regeneration following disturbances (Margaris 1981; Tsiouvaras et al. 1986; Tsiouvaras 1988; Espelta et al. 1999). In contrast, pines cannot regenerate vegetatively and are obligate seeders, except *P. canariensis* (Ne'eman and Trabaud 2000; Tapias et al. 2004). Seeds of both pines and oaks lose viability quickly after dispersal and do not create a persistent viable soil seedbank. Acorns desiccate within a few days, and their chance of germination decreases drastically (Retana et al. 1999). Pine seeds lose viability during the first year after dispersal, but as obligate seeders, most pine species evolved serotinous cones as a mechanism to generate a canopy seed-bank (Nathan et al. 2001).

Many Mediterranean Basin forests are characterized by specific pine–oak associations. The most common and widely described one is the *P. halepensis* and *Q. ilex* association, but many other combinations occur throughout the Mediterranean Basin (Table 1). Blondel and Aronson (1999) claimed that "the segregation often seen today…whereby pines or evergreen oaks can form nearly pure stands, is almost always a product of human interventions, and does not reflect the natural dynamics of these forests."

3 Evolution of pine and oak ecosystems in the Mediterranean Basin

Pine and oak species first appeared in the Mediterranean Basin 3.5–2.3 million years ago (Ma), changing formation, composition, and distribution according to climatic fluctuations (Blondel and Aronson 1999; Thompson 2005). Deciduous oak forests started to spread in these areas during warm humid interglacials of the Pliocene (5.3–2.5 Ma). Climatic changes lead to the creation of the bi-seasonal pronounced Mediterranean climate, with a mild rainy winter and hot dry summer and, consequently, to the evolution of sclerophyllous life forms and the typical pine–oak ecosystems that are the basis of contemporary Mediterranean maquis. Dramatic climate fluctuations during the Pleistocene (last 2.5 Ma) lead to a variety of vegetation changes and spatial fluctuations: Glacial retreat was followed by the spread of steppe vegetation with pines, maquis and garigue shrublands with oaks, conifer forests with pines, or deciduous oak forests. During drier periods, vegetation shifted toward more Mediterranean type vegetation with evergreen oaks dominance (Thompson 2005).

Table 1 Reported pine–oak associations in the Mediterranean Basin

Pine	Oak	Country	References
P. halepensis	*Q. ilex*	Spain	Espelta et al. 1999; Zavala et al. 2000; Rouget et al. 2001
P. halepensis	*Q. ilex*	France	Davi et al. 2008
P. halepensis	*Q. ilex*	Croatia	Trinajstic 1993
P. halepensis	*Q. ilex*	Algeria	Meddour and Ouzuo 2002
P. halepensis	*Q. ilex*	Tunisia	Touchan et al. 2008
P. halepensis	*Q. ilex*	Morocco	Benslama et al. 2010
P. brutia	*Q. calliprinos*	East Mediterranean	Barbéro et al. 1998
P. pinaster hamiltoni	*Q. suber*		Barbéro et al. 1998
P. sylvestris	*Q. humilis*		Barbéro et al. 1998
P. nigra	*Q. faginea*	Spain	Gracia et al. 2002
P. pinea	*Q. suber*	Portugal	Falcao and Borges 2005
P. pinaster and *P. laricious*	*Q. ilex*	France	Campos et al. 2007
P. brutia and *P. nigra*	*Quercus* spp.	Turkey	Özkan and Gülsoy 2010
P. pinaster	*Q. suber*, *Q. ilex*, and *Q. pubescens*	France	Curt et al. 2009
P. pinaster	*Q. pyrenaica*	Morocco	Ajbilou et al. 2006
P. latifolia	*Q. coccifera*	Morocco (high elevations)	Ajbilou et al. 2006
P. pinaster	*Q. ilex*	Italy	Copenheaver et al. 2010

MTEs of the Mediterranean Basin had been sustainably impacted by humans for at least 50,000 years (Naveh and Dan 1973). Human population growth and intensive exploitation of the land with upland agriculture, animal domestication, and wood consumption sharply increased in the Holocene (last 10,000 years). Large-scale human impacts led to the clearance of much of the vegetation and deforestation (Blondel and Aronson 1999; Etienne et al. 1998; Thompson 2005). Exploitation of pine and oak forests caused their degradation, which today have only partially recovered into relatively degraded formations (maquis or matorrals) and not resumed the original forest structure. The decline of each major civilization in the region was followed by spontaneous forest recovery. Deforestation slowed and the expansion of man-made patches decreased only by the eighteenth century, following demographic and socioeconomic changes, such as the industrial revolution, urbanization, and the shift to fossil fuel. Forest clearance decreased during the nineteenth and towards the twentieth century and allowed slow recovery. Much of the land that used to be exploited, mainly for agriculture, gradually changed. Recovery started with the abandonment of marginal areas. These areas are mostly situated in the mountains, where traditional land uses progressively became economically nonviable (Le Houerou 1992; Lepart and Debussche 1992; Etienne et al. 1998) and slowly expanded towards the lowlands. These trends occurred mainly in the northern parts of the Mediterranean Basin, while in the southern parts forest destruction is still ongoing (Quézel 1980; Barbero et al. 1990; Scarascia-Mugnozza et al. 2000).

4 Land abandonment and secondary succession

Land use and exploitation decreased, mostly at the onset of the nineteenth century, leaving much of the Mediterranean landscapes in an almost barren state, with poor vegetation cover. “Natural” vegetation started to recover spontaneously on abandoned agricultural land by secondary successional processes. In uncultivated landscape patches, but in which the vegetation had been severely degraded by wood-cutting or grazing, succession also commenced following a decrease in land exploitation (Debussche et al. 1999).

In many cases, Mediterranean succession begins with a pioneer stage of *P. halepensis* colonization, whereby in mesic conditions with no further perturbations pine forests are later replaced by oak forests (Zavala et al. 2000; Rouget et al. 2001; Capitanio and Carcaillet 2008). Successional paths, mechanisms, and rates depend initially on species establishment and mainly on propagule input from the surrounding landscape (Platt and Connell 2003). Pines are wind-dispersed species with a high capacity to colonize open spaces (Nathan et al. 2000), whereas late-successional species such as oaks are usually animal-dispersed (mainly birds), and therefore, their colonization is expected to be more gradual in time (Bonet and Pausas 2004). Late-successional sclerophyllous evergreen species are characterized by drought tolerance (Corcuera et al. 2002), relative shade tolerance at least during the establishment stage (Sánchez-Gómez et al. 2006), and a high resprouting capacity (Espelta et al. 1999) that favors persistence under frequent disturbances (Pausas 1999).

Succession starts with the arrival of both oak and pine seeds. Many times oak propagules (nuts) are cached in recently abandoned fields early in their succession (e.g., Pons and Pausas 2007). However, oak dominance depends on the presence of pines, which ameliorate habitat conditions for successful oak establishment and growth (e.g., Santana et al. 2010). The classical pine replacement by oaks is explained by pine modification of shade, moisture, and temperature conditions under their canopy, thus improving oak establishment (Lookingbill and Zavala 2000; Gomez 2004; Pons and Pausas 2006, 2007). Alternative successional scenarios may lead to the development and stable existence of either species separately. Oak maquis can directly establish in some cases without a pioneer pine stage. Such trajectory results from oak resprouting in sites that were previously covered by oak maquis and did not suffer severe damage (e.g., Carmel and Kadmon 1999). A different successional pathway results in the formation of a stable "pine climax", usually in unproductive sites, where mid- and late succession species are not able to dominate (Barbéro et al. 1998).

Disturbances, the most frequent of which in MTEs is fire, can divert secondary succession. For instance, Gracia et al. (2002) showed that, after a fire, the vegetation recovered in an inversed successional sere in which oaks regrew from stools in the first years after a fire and pines established at a later stage. Other post-fire successional scenarios show that even a single fire can change pine forests into alternative stable states, such as *Rosmarinus officinalis* communities, that prevent colonization by later successional stages; high fire recurrence can further change the vegetation into dwarf shrubs and herbs (Santana et al. 2010). Much attention has been devoted to post-fire oak and pine development in Mediterranean ecosystems (e.g., Naveh 1975; Trabaud and Prodon 1993; Bond and van Wilgen 1996; Capitanio and Carcaillet 2008). In this review I concentrate on fire free pine–oak dynamics.

Following the climax view of succession, pine–oak mixed ecosystems could be considered as a transitional phase leading to oak dominated forests. However, both palynological (Carrión et al. 2001) and modeling studies (Zavala and Bravo de la Parra 2005) underline the ability of pine species to persist at least at the landscape level. Pine forests are considered part of the climax community, for example in extensive areas in Algeria, Tunisia, and Greece (Maestre and Cortina 2004). Pollen records from Lake Kinneret in the Mediterranean region of Israel and from the Ghab valley in Syria show the coexistence of low levels of *P. halepensis* pollen when *Q. calliprinos* forest dominated the landscape, reflecting a possible climax of oak–pine forest (Baruch 1986; Yasuda et al. 2000; Jalut et al. 2010). This phenomenon has been explained as a result of a trade-off between the competition and colonization capacities of the two species or between the shade tolerance of oaks vs. drought tolerance of pines, as found in the case of *P. halepensis*–*Q. ilex* ecosystems (Zavala and Zea 2004; Fyllas et al. 2007; Zavala et al. 2011).

5 Active afforestation of degraded landscapes

The regeneration of degraded MTEs and abandoned agricultural landscapes was not always left to rely on passive secondary succession and natural regeneration alone. Starting at the onset of the eighteenth century, many Mediterranean countries undertook large-scale afforestation projects, i.e., the conversion of abandoned cropland and grazing land to tree plantations, sometimes regarded as a unique form of active restoration by some authors (e.g., Vallauri et al. 2002; Pausas et al. 2004; Chadzon 2008). Afforestation aimed at fast revegetation of degraded land and to control soil erosion (Wojterski 1990; Maestre and Cortina 2004; Pausas et al. 2004). Tree plantations focused mostly on pine species (but also other conifers and eucalypt species), using mostly native pine species but not necessarily native genetic sources (Schiller and Waisel 1989; Schiller et al. 1997).

Monospecific afforestation in this region has been studied in many contexts. Pausas et al. (2004) reviewed the use of pine afforestation for restoration of pine and oak landscapes in Mediterranean Spain and compared it to examples of reforestation projects throughout the Mediterranean Basin. They showed that these reforestations include 1–4 million hectares of forests that were planted with conifers (mainly pines) and cover 47–94% of the total area reforested during the last decades in each country. Scarascia-Mugnozza et al. (2000) compared Mediterranean afforestation in Italy with different places in the Mediterranean Basin ranging from 1.2 million hectares in northern Africa to 300,000 ha in Italy. They stressed the need to transform the simplified pioneer forest ecosystems to more durable and diverse forests in order to increase their stability and resilience and claimed that besides revegetation and erosion control "northern Mediterranean forests are expected to provide also significant wood production." Similarly, accounts of such large afforestation campaigns and their consequences can be found in Moreira et al. (2001) for Portugal, Willoughby et al. (2008) and Tonon et al. (2005) for Italy, Vallauri et al. (2002) for France, and Isik and Kara (1997) for Turkey.

In Israel, reforestation started at the beginning of the nineteenth century, prior to the establishment of the country, and continues to be managed to these days by the Israeli Land Development and Forestry Authority (KKL). Plantations of conifers, primarily two Mediterranean pine species (*P. halepensis* and *P. brutia*), were carried out mainly during 1920–1980 and now cover approximately 12% of the Mediterranean landscape in Israel (about 0.85 million hectares, KKL, 2008). Conifer forests dominate in these areas (~75%), and 40% of the afforested area is composed of *P. halepensis* stands (Perevolotsky and Sheffer 2009).

Afforestation dramatically changed Mediterranean landscapes in the last century. Following these massive reforestation projects, Mediterranean forests cover almost 10% of their potential area. Specifically, the current distribution of pine species and pine forests, as an outcome of natural and planted pines, is the most important aspect of these changed landscapes (e.g., Ruiz Benito et al. 2009).

6 Dynamics of pine and oak colonization in human-altered landscapes

As a result of passive and active restoration, most Mediterranean landscapes are now a mosaic of two principal coexisting patch types: (1) pine forests, mainly planted, and (2) different stages of regeneration of the "natural" vegetation. Regeneration stages range from low sparse shrublands, to garrigues, and dense matorrals, with different degrees of woody vegetation cover, densities, and heights.

Spatially contiguous oak and pine patches interact at the landscape scale through flow of material, energy, and information from one patch type to its neighboring patches (Chapin et al. 2002). Species flow, mainly by seed movement, is a prevalent form of landscape interaction. Seeds from a source patch arrive to other distinct patch types in the landscape and lead to colonization of species from the source patch in the sink patch. Successful colonization depends on seed dispersal strategies, landscape physiognomy, colonization potential, and recruitment patterns (Nathan and Muller-Landau 2000). Landscape-scale cross-colonization, i.e., colonization of species from one patch type in another patch type where the species does not occur, is typical in altered, young, or unstable ecosystems, where species distributions are not in steady state. Cross-colonization is mainly studied in the context of introduced species that become invasive, while examples of cross-colonization by natives are rare.

In the Mediterranean Basin, the complex landscape mosaic has created opportunities for cross-colonization of both pines and oaks. Pines from the forests shed their wind dispersed seeds and establish within Mediterranean regenerating oak vegetation. Oaks regenerate either through direct resprouting from their root stocks or germinate from seeds in different vegetation formations. However, it seems that the understories of planted pine forests make an especially suitable habitat for oak regeneration. There are a few fundamental questions regarding the regeneration or transformation of Mediterranean pine or oak ecosystems into more natural and stable, perhaps mixed, ecosystems; the dynamics of spontaneous forest expansion on abandoned farmland, and the management of these stands (Etienne 2001; Scarascia-Mugnozza et al. 2000). In the following parts, I describe landscape-scale interaction within pine–oak Mediterranean mosaics and different processes and pathways by which pine–oak ecosystems are being formed.

7 Factors controlling colonization

Colonization dynamics can be related to two main types of factors: factors that control the potential of colonization and factors that modulate the permeability or resistance to colonization. In the context of invasion biology, these two types of factors have been termed factors that control the "invasiveness" of the species and the "invasibility" of the system (Richardson and Pyšek 2006). The first set of factors is determined by seed dispersal patterns and varies across spatial scales, for example seed availability, the spatial structure of seed sources in the colonized landscape (distances, topography and aspects), and seed dispersal vectors (wind for pines, animals for oaks). Dispersal ability is a major spatial process driving landscape dynamics, and recent studies have increased the understanding of how the spatial pattern of seed sources and colonized sink patches can influence the spatial and temporal course of colonization (Gustafson and Gardner 1996; With and King 1999; Cadenasso and Pickett 2001). Local habitat conditions may facilitate or reduce the chances of successful colonization from incoming seeds. In MTEs, pine and oak recruitment is limited mainly by water availability, edaphic conditions, and disturbance regimes. The conditions for cross-colonization may differ among the two species (Zavala et al. 2000). In the following parts, I review available literature of cross-colonization processes that are leading to the formation of pine–oak ecosystems and the factors that control them.

8 Pine colonization from planted forests

Pines spread, mostly from planted stands, and colonization of non-planted habitats by pines occur throughout the Mediterranean Basin (Etienne 2001). Early successional communities of colonizing pines in abandoned arable land are the most frequent case. The general patterns of pine spread and colonization are related to the local distributions of pine forests from which propagules disperse and the state of neighboring landscape patches amenable to colonization. In most of the Mediterranean Basin, *P. halepensis* and *P. brutia* are the main colonizers, depending on their dominance in the area, whereas in Mediterranean mountains (e.g., Alps, Pyrenees, etc.) mountain species, mainly *P. sylvestris*, demonstrate similar phenomena. Colonization patterns also depend on the local biotic and abiotic attributes of the colonized system and the land-use history. Table 2 summarizes pine colonization studies from Mediterranean countries. According to the presented literature, it seems that pine colonization potential exists in most Mediterranean landscapes that contain pine seed sources. The strongest colonization occurs near the edges of pine stands sharply decreasing with increasing distances (e.g., Osem et al. 2011). Many studies reflect the importance of rock–soil conditions, drought, disturbance (fire, previous land use, and grazing), and competition with other types of vegetation (herbaceous and woody) as the main factors that control establishment (see details and references in Table 2). The general trends indicate that pine colonization increases in less disturbed areas with low to intermediate vegetation cover, depending on the type of habitat. For example, in grasslands, shrubs seem to facilitate pine establishment, whereas in the maquis, the woody vegetation, and specifically the densities of oak and pine seedlings, competes with the colonizing pines. Dry habitats and dense vegetation are more resistant to pine colonization.

After World War II forests underwent a rapid natural expansion in the landscapes of many Mediterranean European countries, following urbanization processes and migratory fluxes of populations from rural marginal areas (e.g., Willoughby et al. 2008). Even in the last 30 years, abandonment of agriculture and sheep-farming have resulted in natural recolonization of several areas, which are now again covered by woods and forests. The forest expansion rate is still high in some places. For example, in Italy, pine forests grew spontaneously at a rate of about 0.3% of the land per year during 1990–2000, compared with an average European rate of about 0.1%. Spontaneous pine forests are still developing, more in the mountain regions than in lowland and productive areas (Willoughby et al. 2008).

When the spreading pine species is not native, the same colonization process is considered an invasion. Invasions were common in Southern France, where exotic planted *P. pinaster* and *P. sylvestris* rapidly colonized abandoned fields and grazing lands (Prevosto et al. 2003). Mediterranean pines are known for their strong invasibility. Mediterranean pine species planted in southern hemisphere MTEs are becoming aggressive invaders of the native vegetation [e.g., in South Africa (Richardson 2000), Australia (Richardson and Higgins 1998), Argentina (Ares and Peinemann 1992), and New Zealand (Richardson and Higgins 1998)].

9 Oak development in the understory of pine forests

The second process of landscape-scale cross-colonization leading to the formation of pine–oak mixed ecosystems is the development of oaks in pine vegetation. Oaks develop either from vegetative regeneration (resprouting) or are established from propagules. Seedling recruitment is difficult in Mediterranean oak species and less frequent compared to resprouting (Broncano et al. 1998). In general, the regeneration niche of the late successional oaks is limited compared to the easier recruitment of pioneer pines (Broncano et al. 1998). Accordingly, and based on the successional scenario of oak replacing pines, one of the motivations for planting pines was the assumption that these plantations would facilitate the reintroduction of late-successional broadleaved species (Barbéro et al. 1998). Etienne (2001) described a general pattern by which fire prevention has been promoting the substitution of pine woodlands by oak forests in the Mediterranean Basin, a process incremented by insect driven early pine mortality.

Oak establishment seem to be facilitated under pine canopies in some habitat conditions. Pine trees may assist oak development by increasing seed input or ameliorating habitat conditions and thus reducing recruitment limitations. The factors that determine oak seed recruitment include seed availability, i.e., the abundance of seed sources in the landscape, and seed dispersal vectors. The main vector of oak seed dispersal is the European jay (*Garrulus glandarius* L., Gomez 2003). The factors controlling successful germination and establishment depend on the conditions in the subcanopy of planted pine stands. Table 3 summarizes examples of oak development in the understory of pine stands throughout the Mediterranean Basin and the factors that promote or inhibit these dynamics.

Animal behavior (mainly Jays) is the main form of long-distance oak seed dispersal. Many of the reviewed studies found that seeds are dispersed at short to intermediate distances (<500 m) from the oak seed sources and a positive effect of increasing oak sources within this distance. Pine forests form a suitable habitat for the nut caching behavior of jays since the jays prefer directing dispersal to open soil or underneath forest cover actively avoiding closed shrublands where they face higher predation risk (Bossema 1979; Frost and Rydin 2000; Gomez 2003). The movement of seeds to forests and away from conspecific oak adults also improves their survival by reducing the high acorn predation risk and competition with adult oak trees.

Pine forests of intermediate tree densities ameliorate the conditions for successful colonization by creating partial shading, reducing solar radiation and improving the water status of oak seedlings. Pine trees are considered as “safe sites” for oak establishment (see Table 3). This finding is in accordance with the general assumption that oak

Table 2 Studies of Mediterranean pine colonization of different habitats and the main factors that determine the spatial colonization pressure and colonization success

Pine source	Colonized ecosystem	Colonization potential	Habitat factors	Region	Reference
P. halepensis and *P. pinaster*	Abandoned agriculture and fallow land	Spontaneous colonization	Wildfire frequency (+)	France—Provence	Barbéro et al. 1998; Debussche et al. 1999; Etienne 2001
P. sylvestris	Abandoned agriculture	Natural reforestation	Cessation of grazing (+) Pastures (+) Ploughed areas (−)	France—Alps Mountains	Etienne 2001
P. pinaster	Abandoned agriculture	Natural regeneration		Portugal	Moreira et al. 2001
P. pinaster and *P. halepensis* with little *P. sylvestris* and *P. nigra*	Abandoned land	Natural regeneration	Decreased grazing (+)	Spain	Willoughby et al. 2008
P. sylvestris scaterred forests	Abandoned agriculture, grassland and cropland	Spontaneous afforestation	Broadleave species (−) Grass cover (−) Cattle grazing (−) Dry habitat conditions (−)	Spain—Pyrenees Mountains	Llorens et al. 1997; Gonzalez-Martinez and Bravo 2001; Poyatos et al. 2003
P. pinea and *P. pinaster*	Agricultural areas			Spain—Center	Romero-Calcerrada and Perry 2004 (transition model)
P. nigra plantations	Abandoned rangelands			Italy	Paci and Romoli 1992
Native *P. sylvestris* L. and introduced *P. nigra*	Grasslands	Controlled by seed supply	Rock-soil substrate (!) Shrubs (+) Drought intensity (−)	France	Boulant et al. 2008
Planted *P. halepensis*	Oak degradation stages			Algiers	Wojterski 1990
Planted *P. halepensis*	Shrublands and regenerating oak maquis	Strongly decreasing from pine forest edge up to 200 m away	Rock-soil substrate (!) Medium vegetation density (+) Cattle grazing (+)	Israel—Mediterranean region	Lavi et al. 2005; Osem et al. 2011; Sheffer et al. unpublished
P. halepensis (and *P. nigra*, *P. pinaster*, *P. pinea*, *P. sylvestris*, and *P. uncinata*)	Maquis, degraded *Q. ilex* forests and mixed degraded *Q. ilex*–*P. halepensis* forests (Forest inventory plots)		Evergreen species cover (−) Other *Pinus* sp. seedlings (−) *Quercus* seedlings (−)	Spain—Catalonia (NE)	Rouget et al. 2001
P. nigra	Regenerating *P. nigra*–*Q. faginea* forest 40 years after fire	Decreased sharply with distance from pine forest edges	Oak development (+)	Spain—Catalonia (NE)	Gracia et al. 2002
Introduced *P. pinaster* forests	*P. nigra* forest	Invasive spread replacing native pine	Acidic soils (+)	France—Montpellier	Debazac 1963; di Castri et al. 1990
P. pinaster plantations	*P. pinea* forest	Replacement		Italy	Gatteschi and Milanese 1988
Planted *P. pinea*	Understory of *Juniperus phoenicea* open woodlands			Spain—La Doñana National Park	Armas C., Personal communication

Factors that control (!), promote (+), and resist (−) successful colonization are indicated in the "Habitat factors" if available

Table 3 Studies of Mediterranean oak colonization in pine forests and factors that determine spatial colonization pressure and colonization success

Oak sp.	Colonized pine	Colonization process	Control factors	Region	Reference
Q. calliprinos	*P. halepensis* planted forests	Oak dominate forest understories Log-Normal jay dispersal	Increasing rainfall >500 mm/yr (+) North facing slope (+) Intermediate pine age and density (+)	Israel	Osem et al. 2009; Reisman-Berman et al. 2010; Sheffer et al. unpublished
Q. pubescens	*P. sylvestris* forests	Clustered spatial pattern of seedlings Animal-dispersal pattern	Pine understories (−)	France—Massif Central	Kunstler et al. 2004
Q. ilex	Pine and oak forests	Heterogeneous seed deposition pattern Animal-dispersal activity (+) by improving seed presence, depth at which seeds were buried and distance from the nearest adult oak	Pine microhabitats (+) Lower irradiance (+ survival, − growth) Moderate shade conditions (!)	Spain—Sierra Nevada National Park (SE)	Puerta-Piñero 2010
Q. ilex	*P. halepensis*, *P. nigra*, *P. sylvestris*, and *P. pinaster* plantations	Distance of 250–500 m from oak source Increasing distance to oak (−)	Pine tree density (+) Shade conditions (+ establishment, − survival)	Spain—Sierra Nevada National Park (SE)	Espelta et al. 1995; Gonzalez-Moreno et al. 2011
Q. ilex	*P. halepensis* planted forests	Spontaneous oak colonization Close to oak seed sources (!)	Favorable environmental conditions (!)	Spain	Pausas et al. 2004
Q. ilex	Pine plantations	Increasing distance to oak source forest (−)	Low- to mid-altitude (+) High altitude (−) Stand densities >1,500 pines/hectare (−) Moderate pine densities (+)	Spain—south	Gomez-Aparicio et al. 2009
Q. ilex and *Q. cerrioides*, occasionally *Q. suber*	Mainly *P. halepensis* and *P. pinea*, also *P. nigra*, and *P. pinaster*	Increasing amount of oak source forest in the 500 m surrounding landscape (+)	Patch historical dynamics	Spain—Catalonia, Valles lowlands (NE)	Guirado et al. 2008
Q. ilex	*P. halepensis*		Elevation (+) Fire (−)	Spain	Zavala 1999 (succession model); Broncano et al. 2005
Q. ilex	*P. halepensis*		Disturbances (−)	Spain—mesic homogeneous forest	Zavala and Zea 2004 (Simulation model)
Q. ilex	*P. halepensis* old plantations	Developing maquis	No fire or other human interference (!) Structurally developed vegetation (!)	Italy—Liguria	Barbero et al. 1992
Q. ilex	*P. halepensis*	Few oak seedlings reached the sapling stage	Pine as safe sites (+) Higher soil moisture (+) by improved water status	Spain—mesic areas	Retana et al. 1999; Lookingbill and Zavala et al. 2000
Q. ilex	*P. halepensis*		Adult pine trees (+)	Spain—Catalonia (NE)	Rouget et al. 2001

Table 3 (continued)

Oak sp.	Colonized pine	Colonization process	Control factors	Region	Reference
Q. ilex and *Q. faginea*	*P. nigra*	Segregation between oak seedlings and adult trees	Seed predation under adult oaks (−) Distance from parent trees (+) Oak canopy microhabitat (−) Adult pines (+) High water availability (+) Pine safe sites (+) by lower predation	Spain—Guadalajara, Alto Tajo Natural Park	Granda et al. 2011
Q. ilex and *Q. pubescens*	*P. halepensis* forest naturally established 40–50 years ago	Experimental sawing and seed from the oak subcanopy	High water availability (+) High light availability (+ survival for *Q. pubescens* + growth both)	France—west of Marseille (S)	Prevosto et al. 2011a,b
Q. ilex and *Q. pubescens*	*P. halepensis* forest 90 year old	Sylvicultural sawing of seeds	Local seedling-scale composition of soil cover (!) Fire treatment (+) by reducing soil seed banks and root systems	France—Marseille (S)	Prevosto et al. 2011a, b
Q. petraea and *Q. pyrenaica*	*P. sylvestris* even-aged stand	Planted 1-year-old seedlings	Moderate pine canopy density (+) Light with low water deficit (+)	Spain—Center	Rodriguez-Calcerrada et al. 2010
Q. suber	*P. pinaster* forests	Similar to the recruitment under *Q. suber* forests	Shrubs (−) *P. pinaster* density (+) *Q. suber* density (+) Bare soil (+) Herb cover (+)	Spain—Valencia	Pausas et al. 2006; Pons and Pausas 2006
Q. suber	Pines species	High recruitment in pine and oak forests Source forest fragmentation affects dispersal Shorter dispersal distances (jay flights)	Seedlings germinate in favorable microsites Dessication risk of seedling bank (−) Shade (+ survival, − growth) Nurse shrubs (+) Shrub cover (−)	Spain—Valencia, heterogeneous landscapes	Pausas et al. 2006; Pons and Pausas 2006
Q. suber, *Q. ilex*, and *Q. pubescens*	*P. pinaster*	Post fire recruitment	Mixed pine forests (+) Mixed oak forests (+) Fire recurrence (−) Stand maturation (+) Pine thinning (+)	France—Maures massif (S)	Curt et al. 2009
Q. pubescens	*P. sylvestris* mixed forest	Partial displacement of pines by oaks	Past forest use practices (−)	Switzerland—Valais, Alpine dry valley	Weber et al. 2008 (Model)
Q. coccifera	*P. halepensis* plantations	Very low oak cover Dominance of early successional shrubs		Algiers	Benabdeli 1998

Table 3 (continued)

Oak sp.	Colonized pine	Colonization process	Control factors	Region	Reference
Native oaks	*P. halepensis* and *P. brutia* planted forests	Sylvicultural management considers these natives as an undesirable component since it competes with pines for soil moisture and nutrients and decreases forest yield		Greece	Willoughby et al. 2008

Factors that control (!), promote (+), and resist (−) successful colonization are indicated in the "Habitat factors" if available

establishment depends more on local conditions of the seed micro-habitat. Nevertheless, many authors noticed a contradiction between these suitable recruitment conditions and appropriate condition for further oak tree growth and development past the seedlings and saplings stages (Mosandl and Kleinert 1998; Montero et al. 1994; Reisman-Berman et al. 2010; Puerta-Piñero et al. 2007).

Facilitation of oak colonization by pines is not observed under all Mediterranean environmental conditions. Maestre and Cortina (2004) reviewed the implications of pine afforestation as a leading technique for the restoration of degraded dry Mediterranean ecosystems in arid condition of southern Spain. They found that, even though *P. halepensis* stands improved soil properties in a few years to decades, plantations usually did not reach the fertility levels of relatively undisturbed broadleaved ecosystems in the same landscape. Pine stands usually decreased soil moisture, which may reduce oak recruitment in their subcanopy. Low solar radiation levels or competition for water with pines may reduce oak colonization in dense forests with poor environmental condition. Some studies suggest that semi-arid pine plantations decrease overall plant cover and species richness and do not facilitate the establishment of oaks (Maestre et al. 2003; Bellot et al. 2004; Maestre and Cortina 2004). Disturbances, fire, and past land use also reduce oak colonization.

The difference between pine forests that develop oak understories and those in which oak regeneration is inhibited seems to be primarily related to the habitat conditions in these forests. Habitat conditions below the canopies of managed forests can be manipulated with proper management such as forest thinning. Oak colonization transforms pure pine stands into a mixed ecosystem with a tall pine canopy and a dense oak subcanopy. Changes in the structure and composition of these systems are bound to affect ecosystem processes [water dynamics and nutrient cycling (Royo and Carson 2006)], which in turn may alter future colonization dynamics.

10 Discussion and summary

Landscape-scale colonization of pines within "natural" oak Mediterranean ecosystems and the reciprocal process of oak regeneration within pine stands are now leading to the formation of pine–oak ecosystems. Examples of pine–oak cross-colonization are found in many Mediterranean countries and are strongly associated with the patterns of pine plantations in each region. Both processes occur at significant rates. Oak development is a steady and slow process, leading to the formation of oak maquis. These maquis are usually simply structured dense woodlands with oak as the dominant species. Pine colonization of open ecosystems is strong in some places, although not in all afforested landscapes, and seems to decrease were oaks form dense and developed covers.

Scarce published data on reciprocal pine and oak colonization processes suggest that the recruitment rate of both species at present is relatively low. However, in some ecosystems, colonization has already formed or is starting to develop mixed systems. Further research of the controls and consequences of reciprocal colonization is necessary, especially in order to understand whether these changes will cause positive feedback and lead to further colonization, or arrest at some relatively stable state through negative feedbacks.

Several issues remain open in the context of pine and oak cross-colonization dynamics. First is the discrepancy between low oak recruitment in both pine and oak ecosystems, reciprocal colonization dynamics of pines, and the classical succession from pine to oak climax (Crow 1988; Urbieta et al. 2011). Oaks, as the late successional species, are strong colonizers of disturbed areas (both abandoned land and planted forest stands), but their further regeneration in their own ecosystems is very slow. On the other hand, pine stands are better habitats for oak establishment compared to oak forests. These dynamics suggest a paradox between the dominance of late successional species in the landscape and their regeneration niche. Furthermore, given increasing pine distribution in the landscape, pine propagule pressure and pine colonization are becoming stronger compared to the first half of the nineteenth century, when afforestation was young. Consequently, oak ecosystems are being colonized by pines, perhaps even more than oak regeneration in their own ecosystems. Thus, one proposed scenario could be a cyclic replacement of mature oak ecosystems by an intermediate stage with pines. Such scenario would be even more probable with increasing disturbance frequencies, especially fires. Wildfire is the most common form of disturbance in MTEs and increases with increasing aridity. Therefore, one can expect an increase in pine colonization rate of oak systems if fire frequency will increase. We still do not understand these dynamics enough as to predict whether pine–oak systems will persist without disturbance? Or will these landscapes develop into mature oak forests while old pine stands collapse or remain only in poor habitat conditions (e.g., Zavala et al. 2000).

The second issue concerning the future development of colonized systems is the apparent "seed-seedling conflict", which argues that beneficial conditions for seed germination and early seedling survival later become insufficient and may constrain further growth (Retana et al. 1999). A mismatch between suitable recruitment conditions and further survival and growth had been found in pines (Zavala et al. 2011) but mainly in studies of oak colonization [e.g., Perez-Ramos et al. (2011), although not in all cases, e.g., Broncano et al. (1998)]. Thinning of pine forests, either naturally or by sylvicultural management, could help the development of recruited oak seedlings into saplings and mature trees. The formation of pine–oak systems strongly depends on further development of the seedling and sapling stages of co-existing pines and oaks and not only the establishment of new seedlings, but research of these life stages is scarce. Zavala et al. (2011) explained the formation of mixed and pure pine and oak ecosystems as an interaction between recruitment patterns and interspecific differences at the sapling stage. They claim that in the xeric end of Mediterranean conditions, oaks are missing due to low recruitment, whereas in the mesic end of the Mediterranean, mortality of pine saplings explains the formation of pure oak ecosystems. Furthermore, the combination of environmental conditions and neighborhood competition creates differences in pine and oak growth in the mixed ecosystems. Pines are highly sensitive to interspecific competition from the oaks, which strongly reduced their growth potential, whereas oaks are most resistant to competition (Gómez-Aparicio et al. 2011).

A third issue relates to the question of whether pine–oak cross-colonization is leading to the emergence of novel ecosystems. Emerging ecosystems were defined as "ecosystems where species occur in combinations and relative abundances that have not occurred previously within a given biome and that are the result of deliberate or inadvertent human action" (Hobbs et al. 2006). In the context of pine–oak ecosystems in the Mediterranean Basin, the assumptions that such species composition has not "occurred previously," and the effect of human action should be examined. Mixed pine–oak ecosystems are known from historical records of Mediterranean vegetation as well as from different places in the Basin today (Table 1). Hobbs et al. (2009) distinguished between three ecosystem states: the historical system that is found within its historical range of variation (*sensu* Landres et al. 1999); a hybrid system, i.e., a biotic or abiotic alteration of the historical system; and a novel ecosystem, which is formed by large modifications, many times irreversible. Thus, pine–oak colonization does not seem to form a completely novel ecosystem but rather a historical or a hybrid ecosystem (Seastedt et al. 2008), depending on local historical contexts and the degree of system alteration following the change in species composition. The threshold between hybrid and novel ecosystems is related to how much of the ecosystem traits (structure, composition, and functioning) have changed. Biotic changes, in this case shifts in the range of native pine and oak to colonize where they did not previously exist, may result in the mere alteration of species composition. The novelty of naturally developing and changing pine–oak ecosystems should be investigated based on their structure and function compared to other mixed ecosystems or to the pure pine or oak systems. A novel ecosystem will significantly differ from the historical one in ecosystem features (structure) and functions (processes and dynamics). An emerging novel ecosystem should be sustainable and maintain ecosystem productivity, diversity, resistance, resilience, and soil fertility (Ewel 1999).

Processes of pine and oak colonization are inherent to ecosystems in the Mediterranean Basin and can therefore be viewed as a dynamic process at the landscape scale that is altering local ecosystems, even without recurring to the novel systems framework. Ecology has long acknowledged change as an important characteristic of ecosystems (Chapin et al. 2002; Hobbs et al. 2009), especially in ecosystems with a long history of human presence, such as in the Mediterranean Basin, where species composition are many times a result of human influence (Lindenmayer et al. 2008). It seems that in the last decades pine–oak dynamics have been changing dramatically, but the rate at which cross-colonization occurs is slow. Moreover, because these processes are slow and gradual research is delayed, maybe even late, in identifying the resulting formation of pine–oak ecosystems. Whether defined as altered, hybrid, or novel ecosystems, changes in these systems highlight the need to increase our understanding of the systems and how they are changing, attempt to predict their future development and manage them accordingly (Lindenmayer et al. 2008).

Changes in these Mediterranean ecosystems impose a need to examine the adequacy of current management policies and derive management and conservation implications accordingly. Once change is embraced, then management cannot aim at returning the systems to its historical state or removing the new colonists (Seastedt et al. 2008). Instead, adaptive ecosystem management approaches must be adopted, aiming at enhancing the formation and resilience of desired states while examining the current state of the system and projecting its future movement (Seastedt et al. 2008; Hobbs et al. 2009). Active management must be based on proper monitoring and on use of reference areas (when available, although not easy to select in disturbed landscapes of the Mediterranean Basin). Forest management trends in many developed Mediterranean countries have been shifting from the original productive and protective goals of plantations to aiming at increasing stand diversity and fostering the formation of mixed pine–oak stands (e.g., Perevolotsky and Sheffer 2009). New policies also reflect an understanding that emerging ecosystems may have an important role in providing additional ecosystem services (Hobbs et al. 2009), such as increasing biodiversity or recreation values (Brockerhoff et al. 2008). This review can be used as a first guideline to management strategies that can facilitate pine–oak ecosystem formation. Pine oak colonization can be improved by (1) promoting a proper landscape structure that would increase seed availability; (2) diversifying pine stand and oak maquis structure (e.g., light and water availability) so that more colonization niches will be opened; and (3) reducing the effects of competing factors (e.g., grazing, shrub encroachment, or disturbances) (see examples in Gonzalez-Moreno et al. 2011).

Calling for dynamic management is not an easy task for managers and stakeholders and necessitates a good collaboration with scientists (Seastedt et al. 2008). Future research is needed to uncover more key aspects in these dynamics and compose a basis of knowledge for projecting their future development and understanding their implications. Information is lacking about similar phenomena in more regions within the Mediterranean Basin (e.g., Greece, Italy, North Africa). More research is required to elucidate the basic operating processes, such as (1) oak seed dispersal, (2) oak establishment vs. vegetative regeneration, (3) survival of underground oak parts and their role in vegetative regeneration, and (4) dramatic pine encroachment in some areas. The ramifications of pine–oak ecosystems should be further examined, comparing mixed ecosystems that had been formed through different pathways (e.g., different starting conditions), found at different developmental stages, or in differing habitats. Finally, a proper understanding of the implications of past land-use changes is crucial as more ecosystems in the world are being damaged and restored, but the long-term and large-scale implications of these actions are seldom considered.

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