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Biodiversity, climate change, and adaptation in the Mediterranean

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Abstract

Potential for, and limits to, adaptation to environmental changes are critical for resilience and risk mitigation. The Mediterranean basin is a mosaic of biodiversity-rich ecosystems long affected by human influence, whose resilience is now questioned by climate change. After reviewing the different components of biological adaptation, we present the main characteristics of marine and terrestrial biodiversity in the Mediterranean basin and of the pressures they face. Taking climatic trends into consideration, we discuss the adaptive potential of a range of ecosystems dominated by species without active dispersal. We argue that the high heterogeneity of Mediterranean landscapes and seascapes constitutes a laboratory for the study of adaptation when environmental conditions change rapidly and may provide opportunities for adaptation and adaptability of species and ecosystems. Adaptive management in the Mediterranean can and should harness the nature-based solutions offered

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by both ecological and evolutionary processes for increasing the resilience of ecosystems to climate change.

KEYWORDS
adaptive management, biodiversity, biological adaptation, climate change, marine ecosystems, Mediterranean, terrestrial ecosystems

INTRODUCTION

Land-use change, overexploitation, pollution, and biological invasions have strong detrimental effects on biodiversity globally (Halpern et al., 2019). It is now clear that climate change also impacts biodiversity at all levels of organization, both on land and at sea, affecting genes, populations, species, ecosystems, and thus, human livelihood (Burrows et al., 2011, 2014; Isbell et al., 2015; Pecl et al., 2017; Titeux et al., 2017). Such detrimental effects on biodiversity, though difficult to model, will probably increase with climate change (Bellard et al., 2012; Urban, 2015). Parties to the 2015 United Nations Paris agreement on climate change have pledged to keep global temperature increase well below 2°C above preindustrial averages (aiming at +1.5°C). A warming of 2°C or higher would lead to deep changes in Mediterranean land ecosystems (Guiot & Cramer, 2016), and projections with the highest emission scenarios along with increased human pressures point to important modification of Mediterranean biodiversity, including numerous species extinctions (Balzan et al., 2020).

The Intergovernmental Panel on Climate Change (IPCC) defines adaptation as "the process of adjustment to actual or expected climate and its effects" (Hewitson et al., 2014). This general definition can be extended to any environmental change and concerns all ecosystems and social–ecological systems (Schoon & Van Der Leeuw, 2015). Here, we will focus on biological adaptation, which is the adaptation of living organisms, from individual to population and ecosystems levels. Biological adaptation can be envisioned through different individual, ecological, and evolutionary components, which are detailed in the Section "Adaptive responses of ecosystems and social–ecological systems to environmental change." Adjustment can also be driven by a change in management and/or a change at organismal, population, and community assembly levels. We will not consider here societal adaptation, which is changes in human societies aiming at facilitating adjustment to climate change (IPCC, 2014).

We will focus here on the Mediterranean region. The marine part of this area is easily defined, whereas several definitions exist for its land part. Even if our review is more about ecosystems than geography, one can consider here the geographical scope used in the MedECC report, which is similar to the MED zone in other IPCC reports. It relates to the following latitude–longitude limits: 29°N–47.5°N and 10°W–39°E (Lange et al., 2020). The Mediterranean region is a mosaic of ecosystems rich in endemic species with a millennia-long history of human–nature interactions, which is currently undergoing ever-increasing human pressures (Coll et al., 2010, 2012; Lejeusne et al., 2010; Médail & Quézel, 1997). Continuous evolution in the context of anthropogenic pressures and steep terrestrial and marine ecological gradients is thus an ancient characteristic of Mediterranean biodiversity (Blondel & Aronson, 1999). Such gradients may explain the relatively lower velocity of climate-related change in Mediterranean biomes compared with other biomes (Loarie et al., 2009). Yet, climate-change-related pressures add significant constraints on Mediterranean ecoregions, projected to be second after northern latitudes in terms of rates of temperature changes (Li et al., 2013; Micheli et al., 2013).

Previous studies on Mediterranean biodiversity have focused on the effects of environmental change (e.g., Thiébault et al., 2016), particularly spatial shifts (e.g., Klausmeyer & Shaw, 2009) and changes in phenology, but without specifically considering adaptation processes in most cases. Conversely, studies on adaptation in the Mediterranean have mainly targeted specific ecosystems or species, such as forests (Dorado-Liñán et al., 2019; Fady, 2012; Peñuelas et al., 2017; Prober et al., 2012), anthozoans (Pivotto et al., 2015; Pratlong et al., 2015; Rodolfo-Metalpa et al., 2014), birds (Bonamour et al., 2019), or drylands (Valencia et al., 2016). In this study, we review the potentials and limits of the adaptive capacity to environmental change of both terrestrial and marine Mediterranean biodiversity, considering adaptation as a central process that can mitigate species extinctions and drastic ecosystem modifications similarly on land and at sea (Bell & Collins, 2008; Otto, 2018). Parallel environmental challenges and processes to cope with them are at play both on land and in marine environments, providing similar types of opportunities and threats for resilience in the context of climate change.

Our review is organized as follows: Section "Adaptive responses of ecosystems and social–ecological systems to

environmental changes" describes the definition of adaptive mechanisms; Section "The Mediterranean region: a special context for a highly diverse biodiversity" describes the highly diverse environment and biodiversity of the Mediterranean basin; Section "Mediterranean environmental trends and consequences for adaptive potential" describes quantitative trends of historical and predicted Mediterranean environmental changes and interactions with adaptive mechanisms; Section "Adaptive potential of exemplary Mediterranean ecosystems" describes the possibility for key Mediterranean ecosystems to adapt; and Section "Adaptation and perspectives for management of Mediterranean ecosystem" describes management suggestions to enhance the adaptive potential of ecosystems. Our aim is to demonstrate that along with climate-change-related threats, Mediterranean ecosystems, present in sharply contrasted environmental gradients, are laboratories of high significance when considering adaptation to climate change.

We did not aim at an exhaustive review of all Mediterranean ecosystems. We focused our work on species with important ecological roles (such as engineer species) and for which sufficient data on adaptation are available in different ecosystems. Our case studies are also mainly species without the possibility of important active dispersal, such as sessile species or planktonic species (passive dispersal). Such species are directly susceptible to the modifications of their environment, making them flagship species for studying adaptation to face environmental changes.

ADAPTIVE RESPONSES OF ECOSYSTEMS AND SOCIAL–ECOLOGICAL SYSTEMS TO ENVIRONMENTAL CHANGES

Environmental change can induce massive modifications at organism, species, community, and eco- and agrosystem levels (Figure 1; Parmesan, 2006), from change in individual reproduction or survival rate to shifts in ecosystem structure. Climate change can have a direct effect on

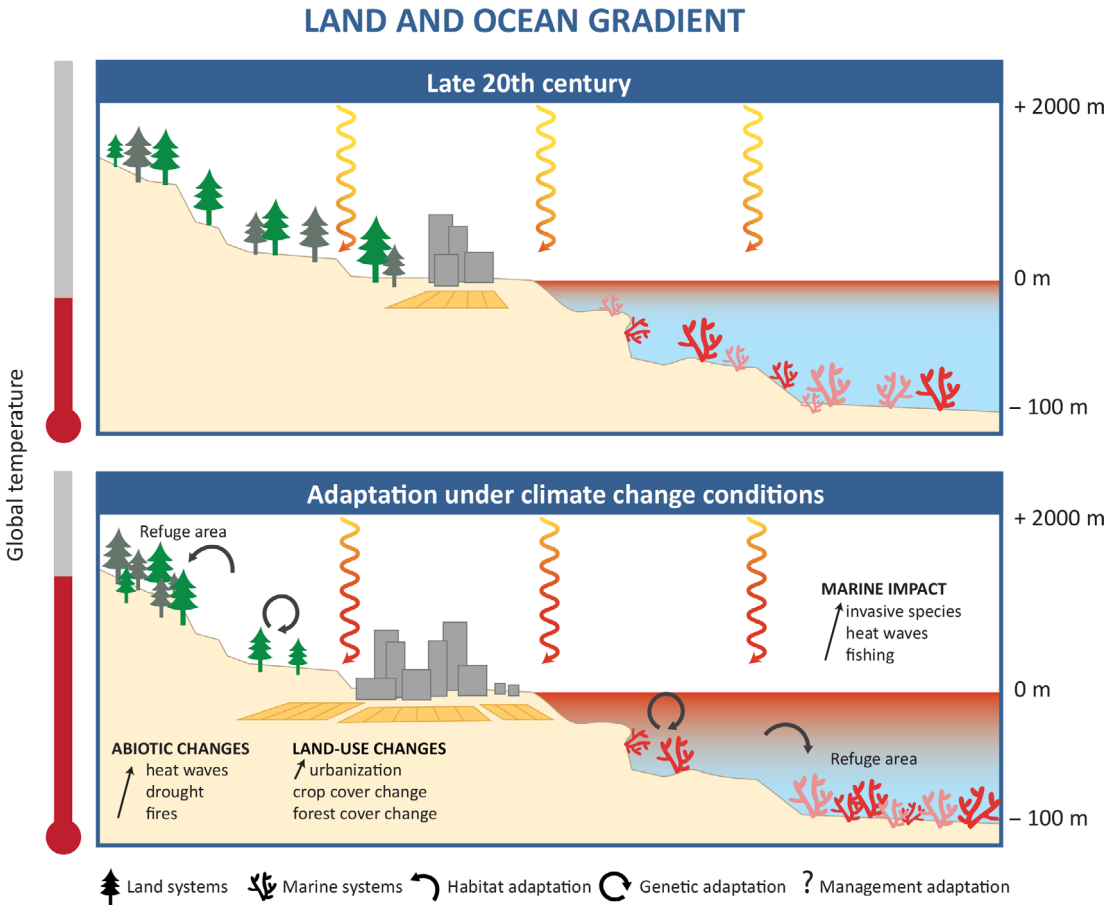


FIGURE 1 Possible responses of Mediterranean biodiversity to climate and environmental changes. The figure illustrates marine and terrestrial environmental gradients, main pressures (climatic, anthropogenic, and others) that may affect adaptive capacity, in situ adaptation through genetic adaptation and acclimatization (with darker colors for higher thermotolerance), and range shift. Range shifts are symbolized by curved arrows directed toward higher altitudes (on land) or deeper zones (at sea). Range shifts toward higher latitudes also occur (not shown here)

mortality, through change in the organism's environment beyond its physiological limits, or an indirect effect through changes in species interactions such as competition or parasitism (Allen et al., 2010; Cahill et al., 2013; Cailleret et al., 2017; Garrabou et al., 2009). Adaptation can counteract these outcomes via five main interrelated adaptive mechanisms (Figure 1). Before developing these mechanisms, we must point out that the various organism or ecosystem modifications induced by environmental change are not necessarily adaptive but can correspond to a disruption in the ecology of the species (Visser, 2008). Therefore, adaptation remains a hypothesis to be tested. Evaluating if a change is adaptive should rely on a precise understanding of the involved mechanisms.

Acclimatization via phenotypic plasticity happens when modifications in key fitness traits (physiology, behavior, or phenology) allow an organism to cope with environmental change without genetic change. Acclimatization allows immediate buffering of environmental changes at individual level and is particularly important for long-lived organisms (Boutin & Lane, 2014; Charmantier et al., 2008; Nicotra et al., 2010). The capacity of acclimatization varies within and among populations and species (Matesanz & Ramírez-Valiente, 2019). However, phenotypic plasticity per se will not always improve adaptation (Auld et al., 2010; Chevin et al., 2013; Hendry, 2016). For example, plasticity can hinder genetic adaptation (see below) by shielding some phenotypes from natural selection (Fox et al., 2019). Plasticity may also not be adaptive under new environmental conditions (Bonamour et al., 2019). Whenever the current acclimatization range or process does not allow adaptation, a genetic evolution of acclimatization may allow adaptation (Visser, 2008).

Genetic adaptation results from changes in allele frequencies at population level under the action of natural selection over several generations. It can be slowed down or hindered by gene flow and genetic drift (Hendry, 2020). The current rate of environmental change is often hypothesized as overtaking the maximum sustainable rate of natural selection of species with long generation times or reduced population sizes (Bell, 2013). However, rapid genetic adaptation has repeatedly been shown to occur in various taxa (Skelly et al., 2007), such as the frog *Rana sylvatica*, the fruit fly *Drosophila melanogaster*, various Mediterranean plants (Matesanz & Valladares, 2014), and others reviewed by De Meester et al. (2018). Demonstrating the possibility of temporal genetic adaptation remains difficult for nonmodel species, as it requires temporal surveys of fitness-related traits or of genomic variations. The observation of genetic adaptation to different climate habitats can be used as a space-for-time substitute (Waldvogel et al., 2019), but with uncertainties regarding the projection of current to future conditions.

Range shift, which can be considered as geographic adaptation, is probably the best-known adaptive mechanism to environmental change. Range shift has been repeatedly documented for terrestrial and marine species (Beaugrand, 2009; Burrows et al., 2014; Parmesan, 2006; Pecl et al., 2017; Poloczanska et al., 2013), including in the Mediterranean region (Parravicini et al., 2015). Typically oriented poleward or upward on land, range shifts can also occur as depth shifts at sea (Poloczanska et al., 2016). Range shifts can be constrained by time and habitat fragmentation, whether natural or due to anthropogenic activities. Limited in their dispersal abilities, which occur at least over one generation, range shift may not allow sessile species to cope with environmental change (Bertrand et al., 2011). Northward range shift of Mediterranean marine species is also limited by the geography of this sea (e.g., Ben Rais Lasram et al., 2010).

Climate change can induce important modifications of community compositions through trophic, parasitic, and mutualistic networks, and reorganization of species assemblages (Cahill et al., 2013; Hays et al., 2005; Walther et al., 2002). Depending on how communities change, ecosystem functions may be conserved, thus resulting in ecosystem adaptation. Conversely, important functional traits or functions can be modified or lost, especially if changes affect engineer or ecologically key species (Gómez-Gras et al., 2021; Verdura et al., 2019). Such changes can even lead to regime shift (e.g., Wernberg et al., 2016). Changes in the composition of microbial communities can also have important adaptive consequences: biotic interactions among macroorganisms and microorganisms can facilitate adaptation thanks to the shorter generation time and higher population sizes of microorganisms (Rosenberg & Zilber-Rosenberg, 2018). The potential role of microbiomes in the adaptation of their hosts is a growing research area.

For social–ecological systems such as forests, agrosystems, or fisheries, adaptation can consist of changes in management, in particular to ensure the sustainable provisioning of goods and services. Such changes range, for example, from developing water-saving practices in agriculture or forestry, fixing harvest quotas (Astruch et al., 2018; Miller et al., 2019), using species or varieties that are presumably resilient to new climatic conditions, enforcing specific harvest regulations to creating protected areas that facilitate a spontaneous adaptation of ecosystems (Benito-Garzón et al., 2019; Lindner et al., 2010; Pecl et al., 2017).

Adaptation is, therefore, at the crossroad of a diversity of different biological and management mechanisms by which populations, species, ecosystems, and social–ecological systems may escape, resist, or adjust to environmental changes, including those due to climate change (Figure 1). These adaptive mechanisms interact with each other in multiple ways, are not mutually exclusive, and

can lead to phenotypic changes such as changes in gene expression, physiology, morphology, behavior, and phenology of organisms (e.g., Anderson et al., 2012; Charmantier et al., 2008; Mills et al., 2018; Peijnenburg & Goetze, 2013). Range shifts also interact with genetic adaptation (Ronce & Kirkpatrick, 2001) as they require adaptation to new environments, even in a similar climate, and can also lead to modified dispersal abilities (De Meester et al., 2018). Whether adaptation can take place, and with which modality (i.e., phenotypic plasticity, genetic adaptation, or range shift) is then inherently hard to predict. It will depend on the genetic diversity available for the traits under selection (e.g., Hendry, 2020), on the plasticity and constraints of the traits related to fitness, and on the connectivity among available habitats (De Meester et al., 2018; Hendry, 2020; Ronce & Kirkpatrick, 2001).

THE MEDITERRANEAN REGION: A SPECIAL CONTEXT FOR A HIGHLY DIVERSE BIODIVERSITY

The Mediterranean basin is one of 34 species diversity hotspots worldwide, characterized by both high species endemism and severe threats on natural ecosystems (Myers et al., 2000): its terrestrial area covers less than 2% of the Earth's surface while sheltering 20% of global flowering plants and ferns species (Fady & Médail, 2004). The Mediterranean Sea covers less than 1% of the global ocean surface and contains 4% (sponges) to 17% (brown algae) of global marine species (Boudouresque, 2004; Coll et al., 2010). The Mediterranean basin also hosts many wild relatives of agronomic, horticulture, and forestry plants of high economic value (Kell et al., 2008). The complex history and the highly variable hydro-climatic, morphological, geographical, historical, and social features of the Mediterranean basin are key drivers of this exceptional biodiversity. Evolution in the context of anthropogenic pressures and steep terrestrial and marine ecological gradients is also an ancient characteristic of Mediterranean biodiversity, which will impact the possibility of future adaptation (Blondel & Aronson, 1999).

The Mediterranean Sea is almost completely closed, and its thermohaline circulation induces a tight link between physical and biogeochemical conditions (Lascaratos et al., 1999; Millot & Taupier-Letage, 2005). Surrounded by high mountains, Mediterranean landscapes and seascapes are characterized by sharp local soil and climate gradients, especially, but not only, along altitude and depth. For example, maximum summer sea temperatures near Marseille vary by more than 3°C between 8 and 40 m depths, with much higher temperature variability for shallow compared with deeper depths (Pratlong et al., 2021). On Mont Ventoux, north of Marseille, elevation increases rapidly from 400 to almost 2000 m over just 10 km, leading to sharp vegetation changes from thermo-Mediterranean type forests to Alpine and arctic type meadows (Barbero et al., 1978). Such gradients are also present in many other Mediterranean mountains such as Sierra Nevada or Mount Olympus. These sharp gradients generate strong local winds (e.g., mistral and bora) that affect both terrestrial evapotranspiration and marine circulation. The sea topography is similarly complex with deep subbasins interconnected by shallow straits, creating highly turbulent currents. The strong surface influx of Atlantic waters through the Gibraltar Strait, the freshwater inputs, the evaporation/precipitation budget, and the general circulation in the Mediterranean Sea create and maintain strong gradients of temperature and salinity, with surface differences of ~10°C and ~3 practical salinity unit (psu), respectively, between the eastern and western basins (Millot & Taupier-Letage, 2005). Local deviations from these large-scale gradients are ubiquitous, and although the Mediterranean climate is characterized by generally warm to hot dry summers and wetter cold winters (Daget, 1977), its high regional variability, along with other local factors such as edaphic conditions, for example, may induce contrasted biodiversity responses to changes.

The Mediterranean basin hosts one of the highest genetic diversity within population, worldwide (Fady, 2005). Significant genetic differentiation is observed for various species between eastern and western marine populations (Arnaud-Haond et al., 2007; Marzouk et al., 2017), or with their Atlantic counterparts (Patarnello et al., 2007; Tine et al., 2014). Marked phylogeographic divergence also occurs on land (Conord et al., 2012; Migliore et al., 2011; Viruel et al., 2020), as Mediterranean peninsulas were refugia for many terrestrial species during the cold Pleistocene periods (Hewitt, 1999; Médail & Diadema, 2009). Patterns of genetic diversity and genetic structure are often correlated with environmental contrasts (Conord et al., 2012), as observed in the red coral *Corallium rubrum* (Pratlong et al., 2021) or the blue tit *Cyanistes caeruleus* (Szulkin et al., 2016). Although often understudied, the link between genetic structure and environmental gradients is pivotal in the understanding of the response to climate change.

MEDITERRANEAN ENVIRONMENTAL TRENDS AND CONSEQUENCES FOR ADAPTIVE POTENTIAL

While the rich biodiversity of the Mediterranean results from a complex evolutionary history in a context of sharp environmental contrasts, it has also been shaped by human

activities since the emergence of agriculture. The intensity and severity of human impact have recently increased. Below we summarize historical (since preindustrial era, around 1850–1900) and projected (by ~2100) trends for major environmental changes due to climate and anthropogenic changes in the Mediterranean (details in Appendix S1; summary in Table 1). We also examine how these modifications interact with adaptive mechanisms.

Air and sea temperature

On land, air temperature and rainfalls are major predictors of ecological niches and thus major drivers of species distribution and vegetation belts (Barbero et al., 1978; Quézel & Médail, 2003). Jump et al. (2009) estimate that an additional increase of 1°C compared with early 20th century conditions could lead to an altitudinal shift of species distribution of ca. 160 m and to a latitudinal shift northward of ca. 150 km under Mediterranean latitudes. At the current rate of increase of +0.2°C/decade and a predicted rate between 0.2 and 0.45°C/decade for the 21st century depending on the scenario (Table 1), warming could cause an important reshuffling of species, potentially involving all five adaptive mechanisms described above. For example, Mediterranean pines show signs of genetic diversity in response to drought at local and large scales (Grivet et al., 2013). At sea, beyond consequences due to general warming, marine heat waves (MHWs; see Hobday et al., 2016 for a precise definition) can lead to important mortality events in sessile species (Garrabou et al., 2009). The frequency of MHW is expected to increase along with climate change, also becoming longer and more intense MHWs (Garrabou et al., 2021). This could lead to a

TABLE 1 Synthesis of observations and projections on abiotic and land-use changes linked to climate and social changes in the Mediterranean region, based on the references detailed in Appendix S1

Climate or environmental variable	Historical data	Projections
Land		
Air temperature		
	Mean ~0.1°C/decade	(Range: 0.2–0.45°C/decade)
	Extremes: increased intensity, duration, and frequency	Extremes: increased intensity, duration, and frequency
Precipitation	No clear trend	Unclear negative trend difficulty to project
Surface solar radiation	(Range: −2 to +5 W/m^2/decade)	General increase difficulty to project
Sea		
Sea temperature		
	Surface mean: 0.37°C/decade (range: 0.09–0.61)	0.22°C/decade (range: 0.21–0.26)
	Upper water mean: 0.03°C/decade (range of local data: 0.008–0.26)	Order of 0.2
	Intermediate water mean: (range of local data: 0.02–0.67)	Order of 0.1
	Deep water mean: (range of local data: 0.035–0.04)	Order of 0.01
	Extremes: Increase of marine heat waves frequency and duration	Increase of marine heat waves frequency and duration
Salinity	No clear trend	No clear trend
Sea level	1.2 cm/decade	(range: 1.2–8 cm/decade) difficulty to project
pH	Order of −0.01/decade	Negative trend (unclear value)
Society		
	Urban use: ~6%/decade	~3%/decade
	Land use: Intensification, loss of crop diversity forest[a]: increase in the Northern Mediterranean, decrease in the Southern and Eastern Mediterranean	Forest[a]: decreasing trend

[a]Trends for forests are based on (FAO et al., 2018). Values reported in Table 1 are medians of data shown in Appendix S1, unless stated otherwise (e.g., range). Only regional data were used to calculate the medians, and local data (shaded in gray Appendix S1) were not included to calculate the trends of Table 1. Urbanization refers to population residing in urban areas.

reduction in the depth range of some species (e.g., *C. rubrum*) and have potential consequences on other species through community interactions (Galli et al., 2017; Verdura et al., 2019). Thermotolerance is a key adaptive trait in this context, and its variation is linked to the interaction between genetic adaptation and acclimatization (Haguenauer et al., 2013). The effect of extreme events may be increased through enhanced stratification of the water column, leading to reduced food availability for sessile filter feeders and increased sensitivity to thermal stress (Coma et al., 2009).

Salinity

Salinity does not show any clear trend of change across the Mediterranean basin (Table 1), except at lower depth and in the Adriatic Sea and the Levantine basin, where an increase is either already observed or expected (Adloff et al., 2015; Rixen et al., 2005). Some species are able to cope with different levels of salinity (e.g., fishes migrating between lagoons and open sea). This is the case for the Sea Bream *Sparus aurata*, where subtle selective effects of salinity on genetic diversity have been demonstrated (Rey et al., 2020). Experimental approaches have shown that an increase in salinity might reduce leaf growth and increase mortality in two Mediterranean seagrasses (Fernández-Torquemada & Sánchez-Lizaso, 2011). Depending on the projected trends, the effects of salinity on Mediterranean marine species should be more precisely studied. Changes in salinity could also impact water circulation and therefore modify planktonic communities and associated trophic networks (Calvo et al., 2011). In coastal regions as well as in brackish lagoons and estuaries, changes in freshwater discharges will likely influence stenohaline species.

Sea level rise

Deleterious effects caused by sea level rise (1.2 cm/decade so far in the Mediterranean with large regional variations and predicted to remain in that range or above; Table 1) are anticipated for systems living at the land/sea interface. In the Mediterranean, coastal algal rims are identified as vulnerable (Blanfuné et al., 2016). Seal level rise should have large effects on coastal ecosystems such as plant communities in salt marshes, which can also be impacted by drought and heatwaves (Noto & Shurin, 2017; Vicente & Boscaiu, 2020). Sea level rise can impact other terrestrial coastal ecosystems through coastal erosion, salinization of wetlands, or regression of habitats such as "pocket beaches" (Médail, 2017). The main adaptive mechanism against sea level rise is expected to be range shift, which may be limited by growth rate for algal rims. The impact of sea level rise on adaptive abilities should interact with other human pressures such as drought stress and urbanization (Kaniewski et al., 2014).

pH

Experimental studies indicate that a drop in seawater pH level could impact various marine calcifying organisms (corals, mollusks, and calcifying macroalgae) at different levels: survival, growth, development, etc. (Bramanti et al., 2013; Kroeker et al., 2013; Martin & Gattuso, 2009). Observed and projected rates of pH change in the Mediterranean are in the order of −0.02/decade (Table 1). Most marine organisms already undergo natural cycles of pH variations in the order of 0.2 on a daily to seasonal cycles (due, for instance, to hydrodynamics or biogeochemical activity, e.g., Wootton et al., 2008; Hofmann et al., 2011; and references therein), which may suggest a possibility of acclimatization to acidification. Cornwall et al. (2020) have exposed a (non-Mediterranean) coralline crustose alga (*Hydrolithon reinboldii*) to potential future pH conditions (pH 7.7): they have observed an increase in the tolerance to acidification after six generations. Such results suggest the possibility of an adaptive response to acidification, but the underlying mechanisms (acclimatization or genetic adaptation) remain unknown, as well as the generality of this response. In contrast, range shift and management are unlikely to play an important role.

CO_2, nitrogen, and O_3

Mediterranean plants can benefit from an increase in atmospheric CO_2, which enhances photosynthesis (Walker et al., 2021). Its mitigating effects could be beneficial in the Mediterranean where droughts are important drivers of ecosystem functioning (Allard et al., 2008). Indeed, CO_2 fertilization increases water use efficiency (Keenan et al., 2013) and thus facilitates the usual plasticity mechanisms to cope with drought. On the other hand, this positive effect of CO_2, which will saturate at some point, will limit the effect of natural selection and probably delay genetic adaptation.

Nitrogen deposition is particularly high in the Mediterranean area and is expected to increase by 2050, with 12.6% area of the region exceeding deposition of 10 kg N ha^{-1} yr^{-1} in 1991 and 68.9% projected in 2050 (Phoenix et al., 2006). Nitrogen deposition can stimulate plant growth (Quinn Thomas et al., 2010), but also differentially impact species and thus diversity (Ochoa-Hueso et al., 2011). As with the increase in CO_2, this can facilitate

plasticity mechanisms to the detriment of longer-term genetic adaptation.

Ozone pollution is pronounced in regions with strong photochemical activity, such as the Mediterranean basin and it may increase forest defoliation and decrease plant growth (see Paoletti, 2006). By altering stomatal function, ozone can limit phenotypic plasticity.

Urbanization and land-use change

With 507 million people (in 2010) over three continents, the Mediterranean is an ecoregion in which human and economic development is largely dependent on scarce and mostly overexploited natural resources (Birot et al., 2011). Following a historical positive trend of 19% per decade and a projected increase of 8% per decade (FAO et al., 2018), the human population of the 21 countries surrounding the Mediterranean basin is predicted to increase some 30% by 2050, intensifying pressure on ecosystems and agrosystems, particularly in all coastal areas and in southern and eastern Mediterranean countries. The combination of a growing population with climate warming and associated risks (heatwaves, droughts, and fires) creates strong adaptive challenges for biodiversity, involving both biological mechanisms and management requirements. This demographic increase is spatially heterogeneous, with higher growth in southern countries and urban centers (FAO et al., 2018). On land, genetic adaptation and community composition change can trigger the emergence of increased fire-tolerant and drought-resistant species (Budde et al., 2014). Nevertheless, the possibility of a rapid genetic adaptation of Mediterranean plants to fire is still discussed (Romero & Ganteaume, 2020; Torres et al., 2018). Overall, management options such as modifying variety assemblages, using assisted migration or enforcing quotas, and implementing spatial regulations (e.g., Cramer et al., 2018; Giakoumi et al., 2012; Manea et al., 2020; Moreira et al., 2011) could help sustain ecosystems services.

Effects of environmental changes on the possibility of adaptation

The environmental changes listed above will affect Mediterranean biodiversity during the 21st century, and subsequent ecosystem responses will depend on habitat availability, biotic interactions, connectivity, and adaptation processes. Generally, practices favoring acclimatization, natural or artificial selection are expected to support biodiversity persistence and sustainability. Local variations in environmental change could also affect species persistence positively and create refugia useful for species persistence and adaptation (Suggitt et al., 2018). Conversely, practices that reduce population size and/or genetic diversity are expected to harm biodiversity persistence (e.g., overfishing in marine ecosystems, crop variety reduction on land, forest monoculture). Changes in connectivity networks, for example, through habitat fragmentation, can also negatively impact adaptive abilities through effects on genetic diversity or possibilities of range shift.

Table 2 summarizes the adaptive mechanisms for different levels of community organization and time scales, together with Mediterranean ecosystems examples. From a temporal point of view, acclimatization represents a particularly important buffering mechanism, especially for long-lived sessile species such as trees and various anthozoans, and range shift is commonly viewed as a complement to acclimatization over several generations. We argue here that genetic adaptation could be important as well to help species adjust in Mediterranean areas where ecological gradients are strong. As previously suggested, the diversity of environmental conditions and responses sometimes observed at short distances creates sites where adaptation may take place and be facilitated via current adaptive diversity, gene flow, short-range shift, and local refugia (see "Adaptive potential of exemplary Mediterranean ecosystems"). Finally, management options are explored given that the region has millennia-long and increasing human influence (see "Adaptation and perspectives for management of Mediterranean ecosystems"). See main text for general information and appendices for detailed information on each case.

ADAPTIVE POTENTIAL OF EXEMPLARY MEDITERRANEAN ECOSYSTEMS

In this section, we discuss the threats and adaptive potential of emblematic Mediterranean ecosystems and social–ecological systems to highlight the determinants of adaptation. These case studies are detailed in Appendix S2 (summarized in Table S2 including an estimate of the overall adaptation capacity for each Mediterranean system) and illustrated in Figure 2. This section does not aim at giving a definite answer on adaptive abilities. The objective is rather to analyze the main drivers of adaptive potential by considering contrasted case studies. This qualitative analysis is based on current knowledge and should stimulate further discussions and research.

Octocorals

Octocoral populations form "marine animal forests." They are directly impacted by heatwaves (Garrabou et al., 2009, 2021) and human pressures (pollution, fishing nets, etc.;

TABLE 2 Adaptation mechanisms, population and temporal scale, and examples in the Mediterranean region

Adaptation mechanism	Population scale	Temporal scale	Mediterranean example
Acclimatization	Individual	Individual lifetime but possibility of transgenerational effects	Microbial soil Oak-pine forests *Posidonia oceanica* meadows Unknown for plankton, octocorals
Genetic adaptation	Population	Several generations	Plankton Microbial soil Agrosystems
Range shift	Population	Individual lifetime to generations	Plankton Oak-pine forests *Posidonia oceanica* Range reduction for octocorals
Community composition	Several populations	Individual lifetime to generations	Plankton Microbial soil Agrosystems
Social–ecological systems management	Several populations	Current and next generations	Oak-pine forests Agrosystems

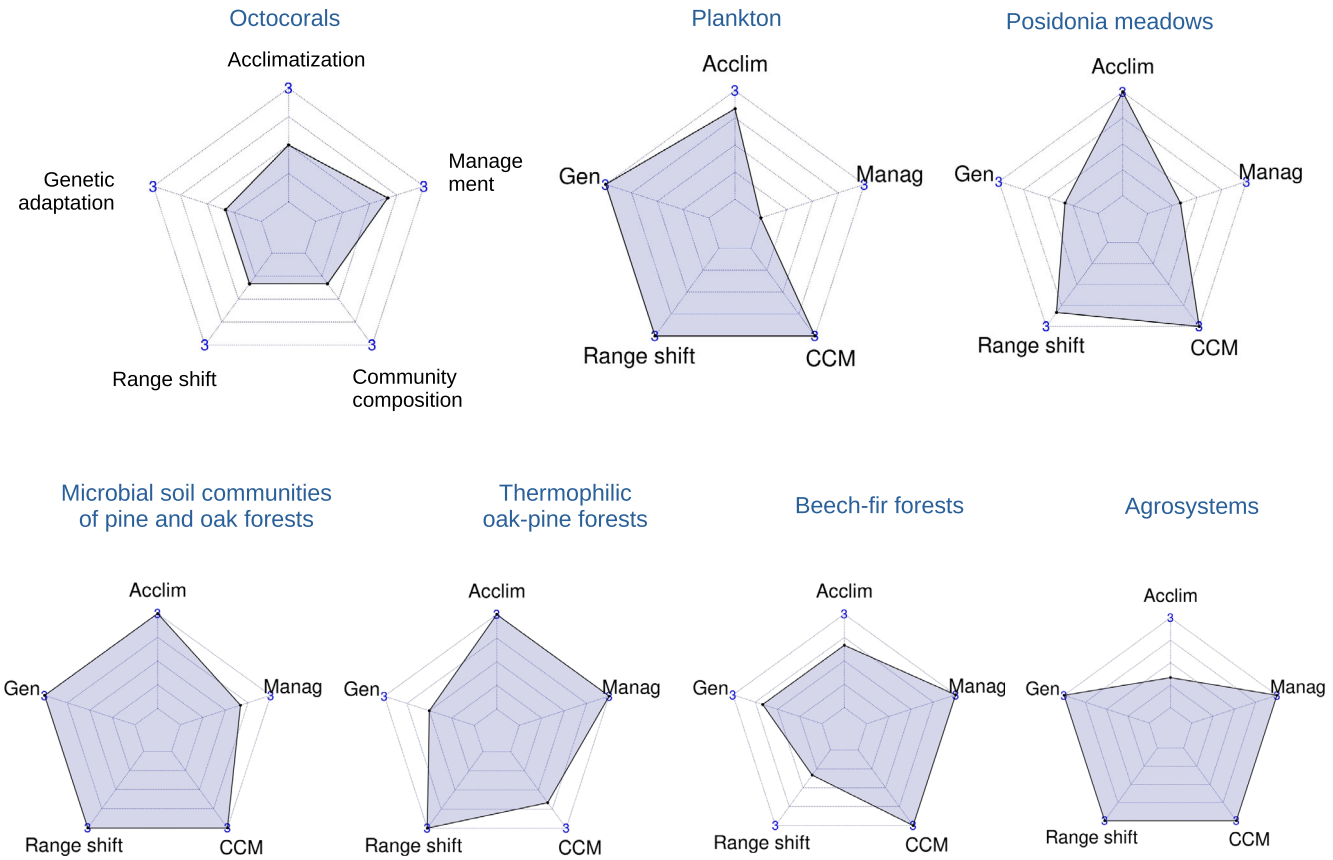


FIGURE 2 Relative weight of adaptive mechanisms for various Mediterranean ecosystems. The components estimated values of 1, 2, and 3 correspond to low, medium, and high potential for acclimatization (Acclim.), genetic adaptation (Gen.), range shift, community composition modification (CCM), and management (Manag.) to support adaptation. Scores are inferred from Table S2 in Appendix S2. These radars provide a qualitative analysis of the different adaptive mechanisms for Mediterranean ecosystems as per the authors' opinions. This analysis is not predictive but underlines factors that are either enhancing or hindering biological evolution toward resilience in the context of expected environmental changes. Steppes are not represented due to a lack of available information

Coma et al., 2004; Sini et al., 2015; Topçu & Öztürk, 2015). Mediterranean octocorals can be observed over a large depth range, for example, 10–1000 m for *C. rubrum* (Knittweis et al., 2016) due to different levels of thermotolerance (Haguenauer et al., 2013; Pivotto et al., 2015). Shallow populations are usually more thermotolerant than deeper ones, but also more impacted by heatwaves (Garrabou et al., 2009; Pivotto et al., 2015). Despite thermotolerance and acclimatization potential, the late reproductive age of these long-lived species may hinder genetic adaptation if facing repeated extreme events. Additionally, the link between local thermal regime and thermotolerance is not always clear as in the red gorgonian *Paramuricea clavata* (Crisci et al., 2017). The depth range of these species could allow deep populations to act as refugia reseeding shallow ones, although warming could simply restrict the vertical extension of the species. Finally, the lack of demographic recovery several years after mortality events could further limit the adaptive potential of these species (Garrabou et al., 2021). Overall, important uncertainties remain regarding the adaptive potential of Mediterranean octocorals, which are under severe threats.

Plankton ecosystems

Because of their huge population sizes and short generation time (hours to days), phyto- and zooplankton species can respond quickly to environmental changes through phenotypic plasticity, natural selection, and genetic adaptation (Colin & Dam, 2007; Dam, 2013; Reusch & Boyd, 2013). Diatoms may acclimatize to nutrient variations, for instance (Crombet et al., 2011; Leblanc et al., 2018), while Reusch and Boyd (2013) observed a large variability of phytoplankton physiological traits that support adaptive abilities and phenotypic plasticity. The way phytoplankton genotypes—or selection regimes—interact between themselves and the importance of dispersal remains open questions (Reusch & Boyd, 2013). Zooplankton display additional physiology and life-history traits supporting adaptation: nutrition and trophic interactions with other plankton are quite flexible (Kiørboe et al., 2018); vertical swimming allows movement across a variety of water layers of different physical and chemical characteristics, thus maximizing growth in a rapidly changing environment (Bonnet et al., 2005; Carlotti & Nival, 1991; Halsband-Lenk et al., 2001, 2002, 2004; Svetlichny et al., 2000).

Overall, the wide variety of pelagic habitats in the Mediterranean used by these flexible organisms, along with their huge population size and short generation time, give them a high adaptive potential, without the need for unrealistic management actions.

Posidonia oceanica meadows

Posidonia oceanica meadows display a potentially important acclimatization capacity through thermotolerance (Marín-Guirao et al., 2016, 2018) and development in a wide range of salinity (Meinesz et al., 2009; Tomasello et al., 2009; Vela et al., 2008). Thermotolerance differs among regions (Marín-Guirao et al., 2019), which could modulate the possible range loss inferred from ecological niche modeling (Chefaoui et al., 2018) and experimental studies have shown that acidification would have no or slightly beneficial effects on this species (Cox et al., 2015, 2016). *P. oceanica* uses both sexual and asexual reproduction, and flowering could be induced by thermal stress, potentially increasing genotypic diversity, which can be beneficial for adaptation (Marín-Guirao et al., 2019). Very large and old *Posidonia* clones could also correspond to high plasticity "general purpose genotypes," tolerant to spatial and temporal environmental variations (Arnaud-Haond et al., 2012; Migliaccio et al., 2005). According to an approach of niche modeling, *P. oceanica* may lose an large part of its current range by 2100 (Chefaoui et al., 2018). Nevertheless, the persistence of Mediterranean *P. oceanica* meadows throughout the Pleistocene glaciation–deglaciation cycles with abrupt changes in sea level and temperature suggests that adaptive characteristics and resilience may be higher than first expected (Jordà et al., 2012), but the fate of *Posidonia* meadows depends on various pressures, primarily direct anthropic pressures (Boudouresque et al., 2017).

Microbial soil communities of pine and oak forests

Microbial soil communities of pine and oak forests frequently exposed to drought stresses appear to be more resistant to drying/rewetting cycles than less exposed communities (Butterly et al., 2009 and other references in Appendix S2), a sign of natural selection (Sparling et al., 1987). Soil microbial community composition has been shown to shift toward fungal-dominated communities after repeated drying, suggesting that fungi resist better to drought stress than bacteria (Cleveland et al., 2004; Evans & Wallenstein, 2012; Yao et al., 2011). Based on morphology and life history strategies (inherent resistance and acclimatization abilities), stresses linked to drying/rewetting cycles are likely to favor Gram-positive bacteria and fungi rather than Gram-negative bacteria (Schimel et al., 2007). Recent studies revealed consistent responses to warming in a group of ubiquitous soil microbes from a wide range of lineages (Oliverio et al., 2017). Their resistance and resilience responses to such disturbance were shown to depend on specific microbial traits related to the r-K-strategy

spectrum and environmental factors related to higher trophic levels and resource availability (De Vries & Shade, 2013). Regarding fires, experimental approaches have shown that it can importantly modify the bacterial composition of the soil with an effect depending on fire intensity (Lucas-Borja et al., 2019). A study on pine forests (*Pinus halepensis* and *P. pinaster*) has shown that recurrent fires can also modify the fungal communities, with a lower diversity of ectomycorrhizal species (Pérez-Izquierdo et al., 2020). Drought can also interact with fires, as shown experimentally on a *Cistus-Erica* system where microbial activity after fire was reduced by drought (Hinojosa et al., 2016). The study of the interactions among stressors (fire, drought, etc), plant and microbial communities now benefits from the output of up-to-date environmental genomics approaches (e.g., Pérez-Izquierdo et al., 2020).

Semiarid and arid steppes

Plants of semiarid and arid steppes are emblematic Mediterranean ecosystems, with data on response to climate change lacking for important species. A modeling study on *Stipa tenacissima* (alfa grass) has nevertheless shown that suitable habitats for this species in Tunisia may decrease importantly along with climate change (Ben Mariem & Chaieb, 2017). The seed germination of *S. tenacissima* is likely to be impacted by the interaction among temperature, drought, and salinity, which raises the question of the evolution and conservation of local populations of this species (Krichen et al., 2017). More generally, where steppes result from land exploitation such as grazing, a change of practice could lead to a transformation into shrub land or sparse forest, with water availability as a key issue (Fady & Médail, 2004).

Thermophilic oak-pine forests

Thermophilic oak-pine forests have high survival, high population growth, and demonstrate high phenotypic plasticity under different drought and temperature conditions; they display high dispersal abilities, excellent adaptation to fire, and a relatively low genetic diversity, which a priori implies a reduced capacity for genetic adaptation. As generalists, thermophilic Mediterranean oak-pine forests display limited local adaptation (Fady & Conord, 2010; Grivet et al., 2013; Taïbi et al., 2017, 2018) and occupy a wide range of ecological conditions, from sea level up to 1500–2000 m (Quézel & Médail, 2003). They thus have a high potential for range shift adaptation and are good examples of species with high plasticity to adapt to future conditions. They have spread spontaneously since the mid-19th century as agro-pastoral activities declined (e.g., a threefold to fourfold increase in France where Aleppo pine forests now cover over 230,000 ha, while they cover over 3.5 million ha in the Mediterranean; Fernandez et al., 2013). In this sense, oak-pine forests can respond positively to management and are overall good candidates for persistence and adaptation to environmental changes.

Marginal beech-fir forests

Abies sp. and *Fagus* spp. dominated forests, either mixed or monospecific, are typical of the mountain belts of the Mediterranean region, from 700 to 900 m and up to 2300 m above sea level, even if marginal compared with their range outside this region. Their occurrence is highly dependent on soil and air moisture. While approximately 10 species of *Abies* have been described in the Mediterranean mountains, there are only two for the genus *Fagus* (*F. sylvatica* and *F. orientalis*) (Quézel & Médail, 2003) (Appendix S2: Table S1). Their distribution has generally increased during the 20th century under agricultural land abandonment, except for marginal populations. Ecological genetic studies point to *Abies* spp. and *Fagus* spp. as being climate generalists (Frank et al., 2017), with somewhat limited risks of maladaptation to changing climate. However, long-standing variability in local site conditions has triggered local adaptation under natural selection processes particularly for stress-related candidate genes, leading to population differentiation along environmental gradients both within and among sites (Csilléry et al., 2020; Gauzere et al., 2020; Lalagüe et al., 2014; Roschanski et al., 2016). Despite relatively limited dispersal abilities, their habitat heterogeneity, their complex demographic history, and their high diversity in stress-related genes make Mediterranean populations of beech and fir both archives of past diversity of high conservation value and a cradle of possible adaptation to environmental changes. Management options such as density and mixture changes as well as assisted gene flow (AGF) and hybridization are also possible for these species of high economic value.

Agrosystems

Agrosystems differ from natural ecosystems regarding adaptation as they are the result of long-lasting human–nature interactions. Crops and livestock may already be vulnerable to future climate because they have been selected for maximum productivity under past and current climates. Phenological acclimation of some orchard crops has been observed (Eccel et al., 2009), but this is

clearly insufficient to resist the climate-driven rising risks of late-spring frosts (Lamichhane, 2021). Agrosystem adaptation will most likely come from genetic adaptation by breeding cultivars better adapted to expected climatic conditions and from management.

Short-term adaptation strategies deal with management conducted at the farm level, such as irrigation, conservation agriculture (reduced tillage, cover crops, mulching, etc), the use of protective sprays or heating against extreme weather, precise pruning (see, e.g., Jemai et al., 2013; Kassam et al., 2012; Fraga & Santos, 2018) including with Mediterranean crops (wheat, olive, vineyards, orchards, etc). Interesting synergies are provided by strategies that rely on soil management (resulting in an improved capability of absorbing and retaining water) both on the climate (carbon sequestration), on biodiversity, and on other environmental issues such as erosion avoidance. Long-term adaptations rely on the selection and development of varieties by breeders and on significant changes in the management from the farm level to the regional scale that need increased knowledge and/or financial support. We describe a few examples. Olive trees are typically Mediterranean, and it exists more than 2000 varieties. Facing the climate projections, drought-tolerant varieties can be selected in place of the currently used varieties (Cabezas et al., 2020; Zaied & Zouabi, 2016). Climate-resilient varieties are selected for further breeding, eventually with the combined selection of tolerance traits to climate-driven diseases and insects (Fraga et al., 2021). Similar research is done for all important crops. For example, Cattivelli et al., 2008 describe the breeding of drought-tolerant wheat, and Costantini et al., 2008 that of late ripening varieties of grapevine. The development of such new varieties of woody crops (olive, citrus, grapevine, etc) can be done with a portfolio of tools from hybridization and the use of wild relatives, to transcriptomics and proteomics (De Ollas et al., 2019).

Due to the nonsustainable overexploitation of groundwater for irrigation in many regions, the use of unconventional water sources is investigated. Reuse of wastewater is currently a much studied option that requires multidisciplinary analyses considering its low acceptation by farmers (Choukr-Allah, 2012). Desalination is another option, despite its costs, but it needs revised treatment standards for providing irrigation water that is not ion depleted (Yermiyahu et al., 2007). It is also very much energy intensive.

Agroforestry is considered to be an interesting adaptation strategy in the Mediterranean basin as it enhances the capability of the agrosystem to better use limited water resources as well as nutrients (Cardinael et al., 2015; Graves et al., 2007). It is also a mitigation strategy, as it increases soil organic carbon stocks (Cardinael et al., 2017), reduces fire-risks (Damianidis et al., 2021), and shapes the landscape with a human-made diversity that should sustain both patrimonial and functional biodiversity, providing adequate maintenance (Fernandes et al., 2019; Torralba et al., 2016). Traditional Mediterranean agroforestry systems like the Dehesa/Montado in Spain/Portugal are now recognized for their multiple ecosystem services, and some current policy measures promote agroforestry in Europe (Mosquera-Losada et al., 2018). Mediterranean agroforestry systems contribute to the rich biodiversity of Mediterranean agriculture: they are now becoming protected or are encouraged partly for climate reasons. We can conclude that sustainable climate adaptation in Mediterranean agrosystems is likely to enhance landscape diversity and biodiversity.

ADAPTATION AND PERSPECTIVES FOR MANAGEMENT OF MEDITERRANEAN ECOSYSTEMS

Mediterranean ecosystems have been greatly modified by human activities, yet they are diverse and occupy habitats that change rapidly over short distances. Pronounced elevation and habitat gradients in Mediterranean landscapes and seascapes may represent an opportunity for systems with low dispersal ability to adapt through limited range shift and gene flow. In places where elevation gradients are less pronounced, where habitat fragmentation is widespread or where agricultural influence is strong, ecosystems will probably depend primarily on acclimatization, genetic adaptation, and management for their long-term survival. However, acclimatization and genetic adaptation have biological constraints and metabolic costs that may intrinsically limit the adaptive rate needed for population persistence (Chevin et al., 2010; Futuyma, 2010). Adaptation to climate change may further be limited by the multiple components of global change. Additionally, when adaptive responses are observed, such as earlier bird reproduction or plant community modifications, it remains unclear whether these responses will allow keeping up with environmental changes and whether they will occur in other species (Bertrand et al., 2011; Radchuk et al., 2019).

Several management options can be used to promote evolutionary and adaptive processes facing climate change. Two categories of management actions exist: (1) direct actions to limit the impacts of climate change (review by Gattuso et al., 2018) and other pressures, or manipulate organisms and populations to sustain evolution—that is, develop assisted evolution; and (2) nature-based solutions (NBS) (Eggermont et al., 2015,

Filbee-Dexter & Smajdor, 2019), which aim at enhancing population or ecosystem evolution through various natural adaptive mechanisms. NBS range from no or low intervention actions, such as establishing protected areas or ecological corridors, to more intrusive actions such as creating artificial ecosystems (Eggermont et al., 2015). One should note that in all cases reducing human pressures on populations should be undertaken whenever possible in order to maximize the success of management and conservation actions. Below we discuss the main management options likely to favor adaptive processes in the Mediterranean basin.

Protected areas and connectivity

Terrestrial and marine protected areas appear as a low risk and feasible solution where space is available. Locations should be chosen based on specific, genetic, phenotypic (e.g., diversity of response to thermal stress), and habitat diversity for target species, and on connectivity to maximize the adaptation potential of protected populations (e.g., maps of larval dispersal potential; Rossi et al., 2014; Dubois et al., 2016). Indeed, if a population is negatively affected by global changes, connectivity is the main process to ensure its persistence by allowing demographic recovery, range shift, and/or genetic adaptation through the spread of advantageous alleles and/or providing access to refugia for reseeding. Moreover, the high heterogeneity in population responses to various pressures, as well as the high anthropic fragmentation, support the idea that connectivity between different habitats of a given species should be enhanced whenever possible. This means, for example, protecting populations along local environmental gradients (altitude, depth, different habitats, etc.) and from distant regions of the Mediterranean. While protected areas can be built for a single purpose (e.g., habitat protection), multipurpose protected areas are desirable (e.g., a remarkable habitat where target ecosystem engineer species also have their genetic diversity conserved), as done in Europe within the EUFORGEN in situ gene conservation network of forest trees (Koskela et al., 2013).

Assisted gene flow

AGF is the controlled movement of genes between different populations of individuals from a given species (e.g., corresponding to different climatic conditions) to sustain adaptation (Aitken & Whitlock, 2013). AGF can immediately increase the frequency of genotypes adapted to new environmental conditions and can introduce alleles linked with climate that themselves increase the genetic diversity required for selection and adaptation over generations (Aitken & Whitlock, 2013). Environmental gradients provide a theoretically favorable context for AGF because they allow AGF application over short geographical distances, potentially corresponding to relatively low genetic differences (e.g., along a depth gradient; Pivotto et al., 2015). This could limit the potentially negative genetic effects of the crossing of too divergent individuals, which is limiting the risk of outbreeding depression (Aitken & Whitlock, 2013). Using genomic data could help inform AGF, through the choice of the potentially most efficient genotypes, as proposed for the Californian valley oak *Quercus lobata* (Browne et al., 2019). Even if AGF becomes more feasible with new techniques, and a better understanding of related processes (required in most cases) and potential consequences, maintaining connectivity along environmental gradients constitutes an already-existing, low impact/high results method to support "natural" (not assisted) gene flow, with the added advantage that it is effective for several species at the same time.

Assisted evolution

Assisted evolution corresponds to a range of more intrusive actions than AGF (e.g., stress conditioning, hybridization) and aims at sustaining adaptation to environmental and climate changes. Assisted evolution may target acclimatization, modification of associated microbial communities (van Oppen et al., 2015), or genetic adaptation through selective breeding of crop species more tolerant to modified conditions (Kole et al., 2015). While the existing diversity of crops in the Mediterranean basin could facilitate selective breeding, the potential advantages of assisted evolution for the majority of wild species are unknown, and so is its feasibility at large geographical scales. Besides, assisted evolution corresponds to influencing evolutionary trajectories, which raises ethical issues and potential risk, and one should be cautious that the proposed solutions do not divert us from reducing the impact on biodiversity (Filbee-Dexter & Smajdor, 2019, and see below).

Evolutionary biology

These management avenues underline the importance of evolutionary biology in conservation, already flagged for several decades (e.g., Frankham et al., 2002; Mace & Purvis, 2008) and currently progressing as a tool for adaptive management (Garner et al., 2016). Evolutionary

biology, by studying processes such as natural selection, common descent, or speciation, has led to large knowledge accumulation. However, applications are still lacking, in particular for wild and nonexploited species (Shafer et al., 2016). We also believe that biodiversity assessment at genetic or specific levels is important for management. For example, it can identify cryptic species, lineages, or populations that might respond differently to environmental changes (e.g., De Jode et al., 2019; Pivotto et al., 2015). Developing knowledge of the diversity of adaptive phenotypes, or of fitness-related traits, in a species is also meaningful, for example, to undertake AGF or protected areas actions. It is possible, for instance, to assess the potential for genetic adaptation of trees through reciprocal transplants (Latreille & Pichot, 2017) or by measuring adaptive eco-physiological traits in "common gardens" (Bussotti et al., 2015; Frank et al., 2017). Indeed, there is a diversity of fitness-related traits, which vary along environmental gradients depending on the species such as thermotolerance, budburst date, and seedling survival (Gauzere et al., 2020; Latreille & Pichot, 2017; Pivotto et al., 2015). Data on the variability of these traits can be integrated in models allowing the study of the variation of selection and adaptation along gradients (Gauzere et al., 2020). Genomic data, from partial to whole genome sequencing now allow a better understanding of adaptive processes, even in nonmodel species (Gagnaire & Gaggiotti, 2016; Waldvogel et al., 2019): in this context, it is particularly interesting to compare populations in different climatic environments, the space-for-time substitute to study the potential response to climate change (Waldvogel et al., 2019).

With such information, adaptive management (e.g., a more active forestry) can be adopted, for example, to limit the risk of drought and fire in Mediterranean forests. The different sources of adaptation could also be integrated into ecosystem process-based models (Oddou-Muratorio & Davi, 2014) to improve the niche models on possible evolution of biodiversity in the face of environmental changes. This is the case in the ΔTraitSDM species distribution model, which takes into account local adaptation and phenotypic plasticity (Benito-Garzón et al., 2019). Genomic data can be useful to study species response to climate change as well (see review in the study by Waldvogel et al., 2019). Nevertheless, the integration of evolutionary approaches in models of response to climate change can be limited by a lack of knowledge regarding local adaptation or on the heritability of important traits related to fitness (Waldvogel et al., 2019). In the future, intraspecific genetic monitoring would be particularly useful to study evolutionary changes, but such surveys are lacking for wild species (Geijzendorffer et al., 2016; Graudal et al., 2014; Laikre et al., 2020; Waldvogel et al., 2019) including suggestions for indicators (but see Rossberg et al., 2017). These studies now need a temporal context, especially to characterize if an adaptive process is ongoing, the nature of the adaptive response, and if it may keep up with environmental and climate changes (Radchuk et al., 2019).

On the importance of limiting the impacts

Species with high gene flow and high population effective size, such as various tree or marine species, are inherently more prone to adaptive evolution (depending on generation time), and not easy to manipulate on realistic spatial scales. In such cases, assisted evolution may not be the best solution. More generally, however, the speed and intensity of warming combined with increasing anthropic pressures might overwhelm the adaptive potential of a wide range of small or isolated populations. In such cases, the reduction of impacts is most probably the first option to consider. Apart from the essential reduction in emissions of greenhouse gases, the reduction of other pressures is critical as well. As previously mentioned, climate change is not the most immediate factor of risk for many species. Additionally, other pressures, such as pollution, can interact, sometimes synergistically, with the effect of climate change (Cabral et al., 2019). Active intervention could then be considered more locally, for example, with specific objectives on the restoration of ecosystem services. More generally, these limits on the possibility of action underline the need for urgent measures to reduce major anthropic impacts on the biosphere (Ripple et al., 2017).

CONCLUSIONS AND RESEARCH PERSPECTIVES

The Mediterranean basin, with its high biodiversity and human concentrations, is a natural laboratory to study adaptation in a rapidly changing environment. It is also an ideal place to apply adaptive management actions that include evolutionary processes. Adapting human practices to the challenges of environmental change remains a priority, with the objective that warming combined with increasing anthropic pressures does not overwhelm the adaptive capacity of ecosystems. For many species, important knowledge gaps remain to better understand the future of biodiversity facing climate and to adapt to the previously mentioned human practices. Integrative studies on the different components of adaptation, taking into account the potential of acclimatization and genetic adaptation, the connectivity in heterogeneous

and fragmented landscapes, remain limited to a few species. Studies of adaptation should be applied to a wide range of species, with ecological, biological, or conservation interests. Developing temporal surveys of phenotypic and genetic response to climate change is also timely to detect potential tipping points in the evolution of target species and implement potential management actions. One key factor will be the speed of species evolution compared with the pace of climate change. Our work was also limited in its scope and could now be extended to more mobile species such as insects and birds, and other ecosystems that are particularly under pressure in the Mediterranean, such as freshwater or estuary ecosystems. As a final note, we recall that we did not aim at providing a definite answer on the adaptive potential of the cases discussed here, rather to stimulate reflections and further research studies, which could take into account the multiple facets of adaptation and their interaction with global change.

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CONFLICT OF INTEREST

The authors have declared no conflict of interest.

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