

Appendix S2: characteristics of Mediterranean ecosystems

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Climatic constraints and diversity of habitats (linked in particular to orographic and soil diversity), as well as diverse disturbances linked to human activities, have contributed to a wide diversity of evolutionary trajectories in Mediterranean marine and terrestrial ecosystems and socio-ecosystems. A remarkable endemic biodiversity coexists with widely distributed species at a global scale, which are often keystone species in terrestrial communities (e.g. oak and pine forests, shrublands like "garrigue" or "maquis"), olive groves) and marine environments (Posidonia meadows, coralligenous assemblages, planktonic assemblages in pelagic ecoregions).

Below we present adaptive characteristics of 7 selected Mediterranean ecosystems, detailing current knowledge for each of them on:

- context and pressures: what are the main current and future threats (if any);
- demography: what are the putative demographic trends in the context of global change (usually based on demographic models that do not take adaptation into account);
- adaptive abilities: differences in the response to major stressors, with a focus on their origin (acclimatisation or genetic adaptation). This includes:
 - population genetics: genetic diversity is the fuel of genetic adaptation that powers the engine of natural and man-made selection. This can be studied indirectly through neutral markers or directly by searching for adaptive loci through genomic approaches. Genetic structure and connectivity will also be important to understand range shift and the potential dispersal of adaptive alleles.

This material is the base for Table S1, which summarises the adaptive characteristics for 8 Mediterranean ecosystems and provides an estimate of their overall expected adaptive potential to environmental changes.

1. MARINE SYSTEMS

A. Phytoplankton and zooplankton

The basis of marine food webs is a set of small stream-dependent organisms - plankton - whose diversity and functions are still under-documented compared to higher trophic levels such as fishes or marine mammals. The biodiversity of plankton is immense and includes a very wide variety of living organisms, stemming from all branches of evolutionary history - virus, bacteria, archaea, unicellular and multicellular from different eukaryotic lineages (Brierley, 2017). The diversity of these planktonic microorganisms is also characterized by a very large size spectrum in depth spanning across several orders of magnitude (10^{-7} to 100 m), by metabolic diversity (photo-, mixo-, heterotrophy), and by complex life cycles of very variable duration (hour to several years) (Carlotti, 2019). Hereafter, we focus on phytoplankton and zooplankton adaptive characteristics, as structural and functional adaptation of the smaller marine forms has generated intense research in the last decades (Fuhrman & Caron, 2016).

A1. Phytoplankton

Context and pressures

Marine phytoplankton is the base of the marine food web. Their production is determined by light availability and access to nutrients. Developing in epipelagic waters due to their light dependence, phytoplankton and their associated microbial food webs are under multiple pressures, whose cumulated roles are partially unknown, including temperature (with their associated consequences on stratification and heat waves), acidification, changes in light (UV) and nutrient inputs from continents and atmosphere.

Temperature, stratification, deoxygenation

Earlier studies (e.g. Behrenfeld et al., 2006) reported an overall inverse relationship between anomalies in sea surface temperature and phytoplankton chlorophyll concentrations during the last decades. It is suggested that future climate change would decrease phytoplankton stocks and thus reduce ocean productivity (Boyce et al., 2010). This view has been largely challenged in the last decade, and there is now no consensus about the future projections of global ocean productivity (e.g. Behrenfeld et al., 2016). In theory, it is expected that increased stratification will reduce the mixing of nutrients necessary for photosynthesis, leading to a reduction of primary productivity, but also of the biologically-mediated carbon export to the deep ocean. In the Mediterranean Sea, the spring phytoplankton bloom is related to the intensity of previous winter mixing of the water column, and future water density changes are key players to project the evolution in primary productivity (Macias et al., 2015).

Nevertheless, a recent modelling study in the western Mediterranean Sea suggested that climate-change may not significantly modify the pelagic planktonic ecosystem (despite small impacts on plankton phenology and size spectrum), nor its associated carbon cycle (Herrmann et al., 2014). Basin-scale modelled projections for the end of the 21st century documented a stable net community production. This results from an increase in metabolic rates due to warming temperatures, leading to an increase by 5% of the gross primary production, which is compensated by increased community respiration rates and reduction of biomasses (Lazzari et al., 2014). Understanding and projecting how oceanic productivity will evolve under future climate requires further evaluation of how the multifaceted stressors of a warmer, higher-CO₂ world will impact the overall activity and adaptation of plankton communities, as well as carbon sequestration.

When considering the natural nutrient limitation characterising the Mediterranean Sea, that could increase due to increased stratification, the direct effect of sea surface warming on phytoplankton growth and productivity may be smaller than anticipated because resource limitation overrides temperature effects (Marañón et al., 2014). Increased stratification may also lead to reduced oxygen dissolution. Deoxygenation potentially impacts all oceanic life, from microbes to higher trophic levels; its consequences range from ecological shifts (Levin, 2018 and references therein), adaptation (Levin, 2003), changes of biogeochemical activity (Breitburg et al., 2018), to mass mortality events through hypoxia (Diaz & Rosenberg, 2008) and biodiversity restructuring (Vaquer-Sunyer & Duarte, 2008). Although still not detected in

the open Mediterranean Sea, deoxygenation is underway in the Black Sea (Capet et al. 2016) and affects Mediterranean lagoons seasonally (Dedieu et al 2007).

UV

The sensitivity of plankton to UV depends on nutrient status, pre acclimatisation, mixing regime (mixing depth vs UV transparency), inherent optical properties of dissolved organic matter and particles (photoreactivity, absorption, diffusion, backscattering), presence of radical precursors, and community composition. From ecosystem-level experiments, it is difficult to discriminate between direct UV effects and cascading effects propagated through the food web (e.g. prey or grazer/predator, viruses, bacterial utilization of derived-detritus or DOC), and mesocosms experiments help analyse such questions (Belzile et al., 2006). UV-B generally leads to reduced Net Community Production (NCP) (Regaudie-de-Gioux et al., 2014; Agustí et al., 2014) by enhancing respiration more than photosynthesis, as warming does.

Acidification

Acidification directly affects photosynthesis and decreases calcium carbonate saturation states. Thus it might affect calcareous microorganisms directly. Indirectly, through cascade effects, it can impact multiple components of the plankton food web. Acidification effects are mainly studied through artificial pH decrease in enclosed sea water (from pure cultures in batch cultures to communities in enclosed mesocosms). The initial species diversity largely influences the outcome of acidification experiments (Eggers et al., 2014), as well as initial conditions of nutrient enrichments. Indeed, the nutrient limitation overrides a potential effect of ocean acidification (Maugendre et al., 2015). Thus, when maintaining oligotrophic conditions of the Mediterranean Sea, mesocosm acidification experiments show no clear effect of ocean acidification on plankton metabolic rates.

Aerosols

The Mediterranean Sea is submitted to significant pulsed nutrient and trace metal inputs from the atmosphere, like Saharan dust from the South and anthropogenic sources from the North (Djaoudi et al., 2018; Guerzoni et al., 1999). It is suggested that the increased temperature and decreased humidity will promote soil drying, and will increase dust emissions, particularly in the eastern Mediterranean. After few hours of addition of artificially aged Saharan dust in mesocosms, an increase in chlorophyll a production was observed, but heterotrophic bacteria were more impacted by dust deposition than primary producers, resulting in a more heterotrophic natural assemblage. The sinking of particulate organic carbon (POC) through DOM/dust ballast effect and aggregation processes was favoured under dust deposition, decreasing the residence time of nutrients in the euphotic layer by several days (Guieu et al., 2014). A dust deposition event of 10 g m⁻² simulated at the surface of minicosms triggered the abiotic formation of transparent exopolymer particles (TEP), leading to the formation of organic-mineral aggregates. The amount of exported POC increased (Louis et al., 2017). Modelling the impact of atmospheric deposition of inorganic nutrients (ammonium phosphate and nitrate) on the whole Mediterranean Sea, Richon et al. (2018) calculated the fertilising effects of phosphate from dust to be low on average (6–10%)

for the period 1997-2012 but an increase of up to 30% in primary productivity could be observed during the months when surface water stratification occurred.

Adaptive abilities

Because of their huge population sizes and short generation time (hours to days), phytoplankton species should display a high potential for genetic adaptation (Reusch & Boyd, 2013). Indeed these populations should have high levels of genetic diversity (both from mutation supply and sexual recombination when relevant), very low genetic drift and high efficiency at natural selection. Additionally, observed patterns of temperature optima suggest the possibility of adaptation to local conditions across distant latitudes in phytoplankton (Thomas et al., 2012), which remains to be better understood and tested (Peijnenburg & Goetze, 2013).

The adaptive abilities are often studied through changes in plankton functional types (Quéré et al., 2015) rather than taxonomic composition, as they are corresponding to simplified phytoplankton groups having characteristic nutrient requirements, growth capacities and fate (nitrogen fixing, calcifying organisms, pico, nano, and micro phytoplankton groups including silica-requiring phytoplankton). For example diatoms, developing during spring bloom specifically in some Mediterranean regions are mostly responsible for carbon export through sedimentation of particles (cf the silica pump, (Leblanc et al., 2005)). However, damming resulted in reduced silica inputs from rivers in the Mediterranean Sea. Theoretically, this means that silica-requiring phytoplankton, like diatoms, will be progressively replaced by other nano- and pico-sized microphytoplankton redirecting food webs towards small grazers and carbon export via dissolved organic matter. Nevertheless, diatoms can persist and adapt in changing Mediterranean Sea by developing in a micro niche (for instance a persistent fucoxanthin and biogenic silica accumulation layer was documented below the deep chlorophyll maximum depth in summer even in the eastern Mediterranean Sea (Crombet et al., 2011)), or by reducing in size (the nano sized diatom *Nannochloropsis* can bloom in the North western Mediterranean (Leblanc et al., 2018)). Long-term natural phytoplankton changes can be estimated from oceanographic time series at fixed points, but these are rare in the Mediterranean (Estrada & Vaqué, 2014) and the older ones mainly focus on chlorophyll stocks (or plankton functional types) derived from pigment distribution or size-fractionation of chlorophyll (Marty et al., 2002), and not on phytoplankton taxonomy (however see the REPHY initiative at <https://www.seanoe.org/data/00361/47248/> or the LTER time series at <http://www.iobis.org/explore/#/dataset/3500>). Moreover, their analysis based only on a few decades is difficult due to the large interannual variability in thermohaline circulation, mixed layer dynamics, coastal effects or mesoscale variability.

Potential effects of climate change on phytoplankton are often based on experimentally artificial and abrupt changes of forcing factors (alone or in combination) in experimental enclosures (Guieu et al., 2010, Gazeau et al., 2017) or cultures. This may not reflect what will occur in nature. It has been shown for instance that the initial species composition largely influences the outcome of some acidification experiments (Eggers et al., 2014), and clearly little attention has been paid to the composition-functional relationships in these experiments. Not only taxonomic but also exploration of the total functional potential of

communities – with meta genomic approaches - coupled to such short-term manipulation of forcing factors on natural communities would help to interpret biogeochemical analysis based on marine waters' origin. Nevertheless existing experiments provide important information to study adaptive processes in marine phytoplankton (Reusch & Boyd, 2013). They can be used to study reaction norms and have revealed inter-clonal differences in several species. In agreement with the aforementioned properties of phytoplankton populations, an important variability of physiological traits exists within various phytoplankton species, traits that are important for adaptive abilities (Reusch & Boyd, 2013). Phenotypic plasticity has also been observed, which complements the adaptive abilities of phytoplanktonic species. Indeed experimental evolution, even if restricted in time and space, has demonstrated such possibility of adaptation in a few cases. Some pending questions remain to extrapolate this to the real world, including the possible interferences between genotypes and between selection regimes, or the importance of dispersal (Reusch & Boyd, 2013).

A2. Zooplankton

Context and pressures

Zooplankton (here defined as planktonic metazoans >200 µm) exhibits a very large taxonomic diversity at the level of holoplankton (continually living in full water) or meroplankton (larval stages of many benthic groups, and fish eggs and larvae). Because ocean currents provide an ideal mechanism for dispersal over a broad range of distances (from m to 1000 km), almost all marine animals have planktonic stages in their life cycles. Their diversity provides the main functions at the base of marine food webs in controlling primary production, linking microbial food webs to higher trophic levels and cycling and transporting biogenic elements in the ocean (Brierley, 2017). Climatic and anthropogenic forcing impact zooplankton vital rates, life cycles, population distributions and community structure and *in fine* the efficiency of these functions (Carlotti & Poggiale, 2010). Unlike other marine groups, such as fish and many intertidal organisms, zooplankton are generally not commercially exploited (with the exception of krill and some jellyfish species), and consequently studies of long-term trends in response to environmental changes are generally not confounded with trends in exploitation. The Mediterranean Sea presents strong hydrographic and biogeochemical characteristics, and environmental gradients that seem to allow the development of a wide variety of planktonic organisms, at different organisation levels, characterised by different environmental preferences (Durrieu de Madron et al., 2011).

Demography: zooplankton community changes in response to environmental changes

Data describing the diversity and composition of zooplankton in the Mediterranean Sea are widely dispersed in time and space (Siokou-Frangou et al., 2009) and regional patterns of planktonic biodiversity are still poorly understood, although the Mediterranean is one of the first basins to be studied (Bianchi & Morri, 2000). Copepods form the emblematic group of zooplankton. It is the most abundant multicellular metazoan group in the oceans, or even on earth (Bron et al., 2011), and dominates the composition and biomass of zooplankton in all oceans, as well as in the Mediterranean (Frangoulis et al., 2004; Mazzocchi et al., 2014; Siokou-Frangou et al., 2009). According to the copepod database <http://copepodes.obs->

banyuls.fr/en (last accessed on May 10, 2019), about 560 different species of copepods are listed in the Mediterranean Sea. Most individuals are located in the 200 upper meters of the water column, at the deep maximum of chlorophyll a, and relatively few species perform large-scale diel migrations (Andersen et al., 2001; Brugnano et al., 2012; di Carlo et al., 1984). The bulk of the Mediterranean copepod communities is composed of small (< 2 mm) species belonging to very diverse genera.

Quantitative synthesis of the literature (including observed oceanic data, models and satellite analyses) shows that climatic changes will induce major changes in the Mediterranean sea, such as hydrographic properties including surface circulation, deep water winter convection and extended seasonal stratification, in addition to changes in temperature, pH, salinity,... all of which is expected to deeply modify zooplanktonic distributions as zooplankton is generally very sensitive to these changes (Richardson, 2008). However Mediterranean zooplankton time series are too few and too dispersed, with relatively short overlapping periods, some of them too close of coastal anthropogenic influence masking the climate signal, in highly spatially differentiated regional climate patterns, to allow drawing a clear pattern of planktonic spatial and temporal shifts at the Mediterranean scale, which could be comparable to the North Atlantic with the CPR data analysis (Beaugrand et al., 2002). At times, abrupt and dramatic changes in ecosystems occur in response to subtle climate or physical oceanic forcings. Such abrupt reorganisation, known as a regime shift, can transform systems from one stable state to another (Hare & Mantua, 2000). Comparative studies of physical and biological time series in the eastern and western Mediterranean Sea for several decades (Berline et al., 2012; Conversi et al., 2010) converge to show an abrupt period of change in the late 1980s, that involved Mediterranean surface circulation and pelagic biotic and abiotic properties. Larger scale climate indexes (NHT and NAO) changed around that time as well (Conversi et al., 2010), and results from zooplankton time series in the northwestern Mediterranean have shown that inter-annual abundance patterns fitted the inter-annual pattern of the winter NAO (Fernández de Puelles & Molinero, 2007; Molinero et al., 2005; Molinero et al., 2008). However, these Mediterranean "biological" time series are not yet sufficiently extensive in time, or do not have a sufficient taxonomic resolution (Berline et al., 2012) to confirm an impact of climate change neither on the community composition, nor on changes in phenology. At present, it is impossible to say which species (or functional groups) will be advantaged or disadvantaged by future temperature rises in the Mediterranean.

Mechanisms underlying this zooplanktonic community change are still poorly known. Global warming is expected to have great repercussions for marine ecosystems because temperature influences the water column stability, nutrient enrichment, and the degree of new production, and thus the abundance, size composition, diversity, and trophic efficiency of zooplankton (Richardson, 2008). The effects of variations within the ocean climate system on zooplankton populations and their phenology (Ji et al., 2010; Richardson, 2008) can be direct (rising temperature, rising salinity, rising CO₂, decreasing pH, and decreasing O₂) through alteration of physiological functions and life-history traits and consequently the fitness of individual zooplankters (Dam, 2013), and indirect for effects exerted through vertical density stratification, which alters phytoplankton abundance and size as well as changes in phytoplankton community structure (Doney, 2013; Litchman et al., 2012). These variables affect individual fitness, predator-prey dynamics, and competition among

zooplankton species. Other indirect effects are exerted through altered circulation patterns, which can in turn impact zooplankton spatial distribution (Reid, 2000). Projections of community changes based on key mechanisms (i.e. impact of temperature) have been realised using new approaches of ensemble niche modelling. The application of a population thermal preference curve of 106 copepod species in oceanic temperature fields in the Mediterranean projected by hydro-climatic model (Adloff et al., 2015) has been used to project changes between present and future distribution of zooplanktonic assemblages (Benedetti et al., 2018). Their projections contrasted with those reported for higher trophic levels (Albouy et al., 2015), suggesting that a more complex ecosystem based approach is required.

Adaptive abilities: physiology and life-history traits

Marine species often have complex life-cycles, as many have a dispersive planktonic stage, with distinct life stages potentially occupying different habitats, each with different exposure and sensitivity to changing climate (Rijnsdorp et al., 2009). Despite this apparent complexity, which could be seen as a disadvantage to resist climate and associated ecosystem changes, it is in reality an advantage because it gives a flexibility through modifications of the life cycle (by reducing some critical planktonic phases). Recent evidence suggests that many of the meroplanktonic life stages are even more sensitive to climate change than their holozooplanktonic neighbours living permanently in the plankton (Richardson, 2008).

Zooplankton are characterised by physiological and behavioural traits that affect their ecological function and influence their interactions with other trophic levels (Litchman, Ohman, & Kiørboe, 2013). Changes in species composition are for a large part the consequence of species-specific behavioural changes, as change in behaviour results in changes in the main demographic parameters, birth and mortality (Halsband-Lenk et al., 2004; Ohman, 1990), and consequently in the success or failure of the species in a changing ecosystem.

From a physiological point of view, zooplanktonic organisms are excellent sentinels of climate change for several reasons. Because zooplankton are poikilotherms, their physiological functions (ingestion, respiration, excretion, defecation, growth) and life-history traits (e.g. short time to maturity in the order of weeks to months, fecundity up to 1000 eggs/female, and flexible development rate) are strongly sensitive to temperature (Mauchline, 1998). Maximum rates of ingestion, growth, and respiration double or even triple in many zooplankters with a standardized temperature increase of 10°C (Halsband-Lenk et al., 2002; Hansen et al., 1997), and with typical generation times of weeks to months zooplankton populations can respond quickly to environmental changes by means of phenotypic plasticity and natural selection (Dam, 2013). Despite previous statements on the low capacity of evolution of zooplankton, there are several traits which are favourable to evolution and adaptation facing climate change (Peijnenburg & Goetze, 2013): as for phytoplankton, huge population sizes, along with the previously mentioned short generation time, are important traits favouring genetic adaptation through natural selection. Another important trait is that zooplankton nutrition and trophic interactions with phytoplankton, microzooplankton and other zooplankton are quite flexible (Kiørboe et al., 2018), even for zooplankton species identified as herbivorous, because most of the time phytoplankton species dominate for short duration. The change in individual size during the ontogenic

development (ratio 1 to 100 from egg size to adult size) makes this feeding flexibility as a rule.

One particular very flexible behaviour of zooplankton to limit predation and maximize feeding and reproduction in changing environments is its ability to swim vertically between surface and deep layers either by diel vertical migration (DVM) (Hays, 2003) or by ontogenic migration (Hidalgo et al., 2005). As in other oceans, zooplankton in the Mediterranean sea presents a high variability in diel vertical migration (several hundred of meters) within the same planktonic community (Andersen et al., 2001; Brugnano et al., 2012; Halsband-Lenk et al., 2002), and between different phases of their ontogenic life cycle for each species. Ontogenic migrations, generally for a long phase (overwintering or oversummering) to deep waters is another major behavioural trait. The high flexibility of these behavioural traits allows to swim across a variety of water layers of different physical and chemical characteristics, which allows zooplanktonic species to maximize their metabolic and developmental rates in response to rapid environmental changes (Bonnet et al., 2005; Carlotti & Nival, 1991; Halsband-Lenk et al., 2001; Halsband-Lenk et al., 2004; Halsband-Lenk et al., 2002; Svetlichny et al., 2000). Finally, the wide variety of coastal and deep-sea habitats, from continental shelf areas to canyons and mesopelagic and bathypelagic habitats, offer to these flexible organisms the capacity to overcome major climate changes in terms of adaptive abilities.

Population genetics and genomics

Although the number of studies that have rigorously tested for genetic adaptation in marine zooplankton is small, and limited to estuarine and coastal taxa that are amenable to laboratory experimentation (reviewed in Dam, 2013), unequivocal evidence exists for genetic adaptation in marine zooplankton. One example is the case of grazer populations exposed to toxic algal blooms that show higher fitness than non-exposed populations when facing toxic prey (Colin & Dam, 2007). The use of the water flea *Daphnia* also led to a lot of studies regarding adaptive evolution for this freshwater model species (e.g. Pantel et al., 2015). For open ocean zooplankton, the majority of which cannot be cultured in the laboratory, evolutionary responses to global change are important to study and have been explored for limited number of taxa (e.g. *Calanus* in the Nordic Seas). This should rely on a precise species delimitation and identification, which may require genetic confirmation (Choquet et al., 2018; Choquet Marvin et al., 2017). Most population genetics studies for Mediterranean zooplanktonic species have been carried out in comparative studies with populations in North Atlantic and Black sea, such as the copepod *Calanus helgolandicus*, the euphausiid *Meganyctyphanes norvegica*, the jellyfish *Pelagia noctiluca*, or the chaetognath *Sagitta setosa* (Peijnenburg & Goetze, 2013). Such studies are still at the infancy, and clearly the Mediterranean pelagic habitat present obvious geographic isolating barriers that would be necessary for speciation in allopatry, the most common geographic mode of speciation.

Regarding the huge population sizes and geographical ranges of planktonic species, as well as their high adaptive potential, management tools are probably neither realistic, nor necessary.

B. Seagrass meadows (*Posidonia oceanica*)

Context and pressures

Seagrass meadows are one of the most productive coastal ecosystems, whose ecosystemic value has been estimated at a global scale to be one of the highest (29000 US\$/ha/yr ; Costanza et al., 2014). Most seagrass species are ecosystem engineers and can act as ecological sentinels (Boudouresque et al., 2009; Boudouresque et al., 2012; Boudouresque et al., 2016). Six native seagrass species are present in the Mediterranean Sea, the endemic *Posidonia oceanica* (Linnaeus) Delile being the most common in the open sea (Boudouresque et al., 2009). We will focus here on *P. oceanica*, which is a key engineer species that forms dense meadows from sea level down to 40-45 m depth depending on water transparency (Boudouresque et al., 2012; Telesca et al., 2015). The structure constituted by live and dead parts of rhizomes, together with the sediment that fills the interstices, is called 'matte' (Boudouresque et al., 2009; Boudouresque et al., 2016). This structure is essential to stabilize coastal sediments and attenuate coastal wave action. Its photosynthetic activity plays an important role in carbon sequestration (Fourqurean et al., 2012; Marbà et al., 2014; Pergent et al., 2014) given its very high biomass production (Pergent & Pergent-Martini, 1991). While a little proportion of *P. oceanica* leaf primary production and associated epibiota is consumed by herbivores (Peirano et al., 2001), the majority is exported in the form of dead leaves that is consumed by detritus feeders and is then transferred to higher trophic levels (Guidetti, 2000; Pergent et al., 1997; Personnic et al., 2014; Boudouresque et al., 2016). This habitat also provides food and shelter, allowing high quality settlement and nursery habitats for many fish and invertebrate species (Boudouresque et al., 2012; Hughes, Williams, Duarte, Heck, & Waycott, 2009).

Due to its particular sensitivity to environmental perturbations and anthropogenic stresses, *P. oceanica* and its ecosystem are used as bioindicators to assess the quality of the environment (Montefalcone, 2009; Personnic et al., 2014). A regression of *P. oceanica* meadows has been observed in different regions of the Mediterranean Sea (Boudouresque et al., 2009). This species is impacted by direct and indirect effects of human activities such as coastal development, trawling, beach replenishment, increasing turbidity (Boudouresque et al., 2009; Boudouresque et al., 2012; Francour et al., 1999; González-Correa et al., 2008; Montefalcone et al., 2010; Pergent-Martini et al., 2006; Ruiz & Romero, 2003), and potentially by non-native species (but see discussion in Boudouresque et al., 2009). Regarding climate change, Marbà & Duarte (2010) observed an increase in shoot mortality following two heat waves (2003 and 2006). Additionally the rise in sea level could lead to a withdrawal of *P. oceanica* at its lower limit (Boudouresque et al., 2017a).

Demography

Posidonia oceanica is a long-lived species (up to several thousand years for some clones; see below), with a very slow growth of the rhizomes (a few cm per year). Its recolonisation abilities, either via asexual propagation or by seeds, are very low (Boudouresque et al., 2009 and references therein). Indeed full-recovery of *P. oceanica* meadows may not be possible at a human-time scale (Telesca et al., 2015). *P. oceanica* mainly reproduces asexually, through rhizome splitting and elongation (Marbà & Duarte, 1998), forming meadows that occupy between 2.5 and 5 x 10¹⁰ m² (Pasqualini et al., 1998). This flowering plant also reproduces

sexually. Sexual reproduction seems locally sporadic in time, and has therefore been considered as inefficient. Flowering records compiled for the second half of the twentieth century across the Mediterranean Sea showed that flowering occurs on average every 5 years and involve 8% of the shoot of any one meadow (Diaz-Almela et al., 2006). The survey of Diaz-Almela et al. (2006) indicated that the proportion of flowering meadows was on average 17%, but varied from 3 to 86% of meadows depending on the years. Flowering prevalence and intensity was shown to coincide with peaks of sea surface annual temperature maxima (Diaz-Almela et al., 2006).

Population genetics

One major characteristic of the genetic diversity of *Posidonia oceanica* is clonality: one population can be composed of different clones with different spatial extent. The level of clonality (estimated by the clonal diversity), can be very variable depending on the meadows (Arnaud-Haond et al., 2007; Procaccini et al., 2001; Serra et al., 2010), with at the lower end some monoclonal populations (Ruggiero et al., 2002). Identical multilocus genotypes (MLGs, i.e. clones) can be observed at up to several kilometres of distance, potentially indicating a high longevity (hundreds to thousand years) and plasticity, or dispersal following fragmentation (Arnaud-Haond et al., 2012; Migliaccio et al., 2005). At higher spatial distances, *P. oceanica* from the western and eastern Mediterranean basins are well differentiated with a contact zone around the siculo-tunisian strait (Arnaud-Haond et al., 2007; Serra et al., 2010).

Adaptive abilities

Posidonia oceanica can be found in contrasted conditions, with populations dwelling in low salinity and low temperature areas (e.g. the Marmara Sea) and in high salinity and high temperature areas (e.g. the El-Biban Lagoon) (Meinesz et al., 2009; Tomasello et al., 2009; Vela et al., 2008), which suggests that adaptability is higher than previously expected. Information on the potential impact of warming comes from *in situ* correlations between shoot mortality and maximum sea water temperature (Marba & Duarte, 2010), and lepidochronology (Mayot et al., 2005). Experimental studies have shown that acidification seems to have no or reduced beneficial effect, which could buffer the effect of thermal stress (Cox et al., 2015; Cox et al., 2016). When considering the possible future warming trend, concerns about the future of this species along with climate change (Jordà et al., 2012) could have been overestimated. Regarding range shift, Boudouresque et al. (2017a) discussed if the warming could lead to a shrinking of the range of this species in its warmest locations (eastern Mediterranean), but also to an expansion at its cold limit (e.g. Adriatic, Gulf of Lions). Differences in thermotolerance have been demonstrated between depths or regions, which will influence the future evolution of this species (Marín-Guirao et al., 2018; Marín-Guirao et al., 2016). This could modulate the expected important range loss deduced from ecological niche modeling (Chefaoui et al., 2018).

From an adaptive point of view, asexual reproduction via clonality raises important questions. On one side, it might be expected that sexual reproduction should be important for adaptive evolution by the creation of important genetic diversity at each generation. Flowering could be induced by thermal stress in *P. oceanica*, which may enhance the production of new genotypes along with climate change (Marín-Guirao et al., 2019). In other

seagrasses some experiments also suggested a putative direct effect of genotypic diversity on the response of community to disturbances (Hughes & Stachowicz, 2004). On another side, very large and old clones could correspond to « general purpose genotypes » with important plasticity allowing them to cope with spatial and temporal environmental variations (Arnaud-Haond et al., 2012). The observation of very old clones means that some of them were indeed able to cope with past environmental changes. Such mixed reproductive mode, along with its long term persistence in the Mediterranean area, suggests higher adaptive abilities than expected for *P. oceanica*. The persistence of *P. oceanica* in the Mediterranean Sea, before and after the Messinian crises (5 to 6 million years ago), and during the Pleistocene 30 glaciation-deglaciation cycles, with abrupt changes in sea level and temperature, suggests that *P. oceanica* presents high adaptive characteristics and that it could be one of the most resistant species to climate change.

C. Coralligenous ecosystems (including marine animal forests)

Coralligenous assemblages are biogenic emblematic ecosystems of the Mediterranean Sea mainly built by calcareous encrusting algae (CEA). They are one of the biodiversity hotspots of the Mediterranean Sea (Ballesteros, 2006) and provide a wide variety of ecosystem services (de Ville d'Avray et al., 2019). Marine animal forests correspond to habitats structured by long-lived sessile metazoans, such as gorgonian octocorals, which also provide some habitat for other species (Paoli et al., 2017). In the Mediterranean these communities can be deeply intertwined, for example with octocorals and *Cystoseira* forests in coralligenous habitats (Boudouresque et al., 2017b). We will therefore group the study of these habitats here, with a focus on CEA and octocorals, i.e. the sister group of hexacorals that includes reef-building scleractinians. Nevertheless, there are specific characteristics to each of them such as ecological range (such as depth), main pressures, life history traits, or state of knowledge that can be very different depending on the species. Therefore we will separate the corresponding information whenever necessary.

Context and pressures

Coralligenous ecosystems (including marine animal forests) could be deeply impacted by climate change. Octocoral populations, along with other sessile organisms, have suffered in the last decades from mortality events induced by Marine Heat Waves (MHW) (Garrabou et al., 2009; Perez et al., 2000; Garrabou et al., 2019). The first reported mortality events in the Mediterranean dates back to 1983, and one of the most impressive mortality events was observed in 1999, followed by other ones with different impacts (Garrabou et al., 2019; Rivetti et al., 2014). Depending on the area and the date, the impact of the mortality could extend down to 70 m depth, and up to 1 000 km of coastline (Rivetti et al., 2014). The occurrence of such mortality events was linked with short acute thermal stress or longer milder stress (Crisci et al., 2011). The length of MHW may have increased after 2003 in the North-Western Mediterranean and in the Adriatic (Garrabou et al., 2021). The frequency and intensity of MHW is also expected to increase in the future in these areas along with climate change (Garrabou et al., 2021).

Calcareous encrusting algae produce carbonate structures and are particularly sensitive to ocean warming and acidification (Martin et al., 2013; Martin & Gattuso, 2009; Linares et al.,

2015; Lombardi et al., 2011; Nash et al., 2016; Rodríguez-Prieto, 2016). The red coral *Corallium rubrum*, a calcifying species, may also suffer from acidification (Bramanti et al., 2013).

Coralligenous habitats are jeopardized by other pressures such as physical damage (e.g. storms), chemical pollutants, increased sedimentation and invasive species (Balata et al., 2005; Balata et al., 2007; Ballesteros, 2006; Boudouresque et al., 2017b; Hong, 1980). Octocoral populations suffer from pollution, damages from fishing nets, detachment induced by recreational diving or mucilage development (Coma et al., 2004; Sini et al., 2015; Topçu & Öztürk, 2015). The red coral is harvested for jewellery, which led to an important reduction of the size of colonies in over-exploited populations (Garrabou et al., 2017).

Demography

On a long timescale, the accumulation rate of coralligenous constructions is very low ($0.006\text{--}0.83\text{ mm a}^{-1}$) and varies according to depth and time period (Sartoretto, 1996). The growth rates for two major species of CEA builders are very low: from 1.5 and 4.0 mm to 1.3 and 2.5 mm a^{-1} *in situ* (Garrabou & Ballesteros, 2000), and even slower when measured in the laboratory (Rodríguez-Prieto, 2016). The generation time of CEA is difficult to estimate: the age at first reproduction probably exceeds one-year old, and longevity probably exceeds one dozen, maybe several dozens of years. Thus the turnover of individuals is likely to be slow and suggests a generation time in the order of the decade. As far as *Cystoseira zosteroides* is concerned, it is a long-lived species : more than 50 years (Ballesteros et al., 2009), maybe centuries.

The growth rate of octocorals is variable depending on species, but very low for *C. rubrum* (less than 0.5 mm.a^{-1} for basal diameter (Marschal et al., 2004). The age at first reproduction is around 3-5 years for *C. rubrum* (Torrents et al., 2005), and this species could live more than 100 years (Garrabou et al., 2017). Nevertheless, harvesting has deeply modified the demographic structure of red coral populations towards small size colonies (Garrabou et al., 2017). These demographic characteristics question the future of coralligenous and octocoral species facing environmental changes. Modelling the demography of two Mediterranean octocorals (*Paramuricea clavata* and *C. rubrum*) following mortality events suggested possible recovery depending on the species (Santangelo et al., 2015). Conversely, Linares & Doak (2010) deduced high extinction risk for *P. clavata* populations following recurrent mortality events. Interestingly, long-lived species such as *C. rubrum*, may lead to demographic stability, but could also increase their sensitivity to mortality events (Montero-Serra et al., 2018). Immediate impacts of mortality events lead to an increase in the frequency of necrosis, and a decrease in population density (Garrabou et al., 2021). Sublethal effects can have long-term consequences on gorgonian populations for example through detrimental effects on reproductive success (Garrabou et al., 2021). A monitoring of *P. clavata* populations over 10 to 14 years after mortality events in France has shown that after an important initial decline in biomass, no sign of recovery was observed (Garrabou et al., 2021).

Population genetics and genomics

To date, data indicate frequent cases of significant genetic structure at short distances in metazoans from coralligenous habitat, with short estimated dispersal distances (Costantini et al., 2018; Ledoux et al., 2010), which is quite unusual among marine species with larval dispersal. Nevertheless, this observation may be driven by a taxonomic bias in the studied species. Among the main species of marine animal forest, a strong genetic structure has been observed in Mediterranean octocorals, with significant differentiation at short to moderate distances, including between depths at a same site in several cases (Costantini et al., 2011; Gazulla et al., 2021; Ledoux et al., 2010; Masmoudi et al., 2016; Mokhtar-Jamaï et al., 2011; Pérez-Portela et al., 2016; but see Padron et al., 2018 on *Eunicella singularis*). Recent studies on the bryozoan *M. truncata* also revealed a high genetic structure even at small spatial scale (Cahill et al., 2017, De Jode et al. pers. com.). Regarding CEA, De Jode et al. (2019) revealed the presence of several cryptic species among the engineering CEA of coralligenous reefs. The most abundant of these species harboured low genetic diversity and high genetic structure even at small spatial scales.

The observed genetic differentiation is often discussed with respect to the deep refugia hypothesis: as deeper populations may be less affected by extreme thermal events, they could "reseed" shallow sites (e.g. Bongaerts et al., 2017) provided dispersal from deep to shallow sites is frequent enough. The observation of significant genetic differentiation between depths or sites (as observed in the aforementioned cases), is sometimes interpreted as a lack of recolonisation abilities between populations. Nevertheless, such interpretation is far from straightforward. First, the different depth populations could correspond to different species (Pantel et al., 2015; Prada & Hellberg, 2013). Second, genetic differentiation is the result of interaction between gene flow and genetic drift, which depends on effective population size (Luikart et al., 2010). Low effective size can be an important factor leading to high differentiation. Third, current exchanges can be limited by available space and colonisation effects (Orsini et al., 2013): studies of recruitment on natural and artificial substrates show that recolonisation abilities may be important in Mediterranean octocorals (Cánovas-Molina et al., 2018; Aurelle et al., 2020), when free habitat is available. When different sites or environments are occupied by different cryptic species (as in CEA), the question of recolonization abilities remains: could the local loss of one species open the way to colonisation from a related one in a neighbouring site? Apart from demographic effects, the previously mentioned decline in population biomass following mortality events may have genetic consequences as well: depending on its intensity and duration, this decline may increase genetic drift in gorgonian populations. The genetic analysis of a declining population of red coral in Spain did not evidence any difference in population effective size compared to a pristine-like population (Ledoux et al., 2020). Nevertheless this last study suggested an higher biparental inbreeding in the declining population (Ledoux et al., 2020). Regarding the generally generation time of Mediterranean gorgonians, genetic effects may be visible on longer time intervals.

Microbial diversity and climate-linked diseases

Adaptation of an organism to different environments should be understood at the hologenome level. Similarly to tropical reef-building scleractinian corals, temperate octocorals are holobiont entities inhabited by a diverse bacterial assemblage (Bayer et al., 2013; La Rivière, et al., 2013; van de Water et al., 2018a). However, in contrast with the

ubiquitous association of scleractinian corals with the dinoflagellate alga *Symbiodinium*, *Eunicella singularis* is the only Mediterranean octocoral hosting symbiotic *Symbiodinium*.

The bacterial microbiomes of the Mediterranean octocorals are species-specific, although closely related hosts like *Eunicella cavolini* and *E. singularis* share some common bacterial phlotypes (La Rivière et al., 2015; van de Water et al., 2017). With the exception of *C. rubrum*, the octocoral microbiome is mainly composed of members of the Proteobacteria phylum, and largely dominated by a gammaproteobacterial symbiont affiliated to the genus *Endozoicomonas* (order Oceanospirillales) which can represent more than 90% of the microbiome (La Rivière et al., 2013). *Endozoicomonas* are also detected in the microbiome of *C. rubrum*, but the main associates of this species belong to the Spirochaetes phylum (van de Water et al., 2016).

Endozoicomonas are predominant bacteria in the microbiome of a wide range of tropical reef corals and have been suggested to play an important role in host fitness (Peixoto et al., 2017), which may rely on their potential capacities in nutrient acquisition or production of antimicrobial compounds (Neave et al., 2016). Their presence within the host tissues is also indicative of an intimate biological relationship, possibly resulting from a long-term coadaptation process (La Rivière et al., 2016; Neave et al., 2016). The abundance of *Endozoicomonas* decreases under altered environmental conditions, including climate stress, and in health-compromised colonies of various coral species (McDevitt-Irwin et al., 2017). In Mediterranean octocorals, a decreasing dominance by *Endozoicomonas* is observed in the microbiome of *P. clavata* populations subjected to anthropogenic impacts (Vezzulli et al., 2013). The loss of *Endozoicomonas* may trigger or facilitate a microbial shift toward opportunistic or disease-associated microorganisms such as vibrios. In *P. clavata*, microbial infection by *Vibrio coralliilyticus* has been identified as the cause of tissue lysis during mortality outbreaks induced by heat waves (La Rivière et al., 2016). This bacterium has previously emerged as a thermo-dependent pathogen of tropical corals, and its occurrence in the Mediterranean is correlated with the seawater temperature (Vezzulli et al., 2010). Susceptibility to pathogens under temperature stress may also be related to the down-regulation of some components of the immune defence system. For example, a mannose-binding lectin involved in recognition of a variety of bacteria, including *V. coralliilyticus*, is down-regulated in heat-stressed hexacorals (Kvennefors et al., 2008). Although a putative link between temperature stress and immune response has yet to be elucidated in Mediterranean octocorals, the overexpression of a lectin homologue observed in shallow colonies of *C. rubrum* may suggest the implication of adaptive mechanisms to counteract a higher pathogen pressure in warmer, low-depth environmental conditions (Pratlong et al., 2015).

In addition to the *Endozoicomonas*-dominated “core” microbiome consistently associated with each species, unique combinations of other bacterial taxa are present in different locations (van de Water et al., 2018b). In *Eunicella* species, the abundance and the diversity of locally stable bacterial associates increase in locations submitted to anthropogenic disturbances. In contrast, the relative amount of the core bacterial taxa in the octocoral *Leptogorgia sarmentosa* was greater in a disturbed site, indicating that each host species may exert different control over their microbial partners (van de Water et al., 2018). Notably, changes in diversity and abundances of various *Endozoicomonas* phlotypes were

observed in the microbiome of *Eunicella* spp. and *L. sarmentosa* from different locations, suggesting that the most adapted ecotypes are favoured in a given environment. In *C. rubrum*, changes in the microbiome were also evidenced at spatial scale, consisting in the readjustment of the relative abundance of members of the Spirochaetales and Oceanospirillales (van de Water et al., 2016). Overall, this suggests that octocoral holobionts may fluctuate in their microbial composition in response to environmental conditions, raising the question of the potential contribution of microbiome flexibility in local adaptation. This research area is emerging as a major topic in the future, which should be extended to other engineer species.

Research and management implications

Interactions between environmental diversity, especially along depth, and intrinsic dispersal abilities, have generated complex genetic and adaptive patterns, including at short distances, among coralligenous and animal forests in the Mediterranean Sea. Observations of mortality events mostly coincide with areas where warming trends are already recorded, and also with areas where other cumulative impacts are present (Rivetti et al., 2014). This raises several questions regarding the potential adaptive abilities of the affected species facing climate change. On the positive side, the available studies documented an important genetic diversity among populations, and in some cases an important adaptive diversity. Indeed a signal of local adaptation to depth has been shown (Ledoux et al., 2015) and more resistant individuals have been observed during mortality events (Garrabou et al., 2021). These results suggest a potential for acclimatisation or genetic adaptation with time. The presence of a given species along a depth gradient could also allow its persistence in deep refugia less affected by warming, but possibly at the expense of a range contraction (Galli et al., 2017). On the negative side, the slow growth rate and demographic dynamics of some engineer species could limit the rate of adaptive evolution, resulting in a slower adaptation than the environmental changes driving it. The reduced dispersal abilities could limit the exchange of adaptive alleles between populations (conversely, natural selection can increase their frequency). Interactions between pressures can be problematic as well, as demonstrated for acidification and temperature (Prada et al., 2017), but other non-climatic effects could act. For example, a reduction of population size through habitat destruction or harvesting could impact genetic drift.

There are several management tools for coralligenous or animal forests that could take this information into account in order to sustain adaptive evolution. Marine Protected Areas (MPAs) should be designed by favouring connectivity between populations (Palumbi, 2003). In the case of red coral, the modelling study of Montero-Serra et al. (2019) has shown that while MPAs can increase population growth if mass mortality events are rare, they are not efficient when the frequency of such events increases, as expected under future climate conditions. This is in line with observations on recent mass bleaching events in the Great Barrier Reef, where local protection had little effect on the resistance to bleaching (Hughes et al., 2017). Transplantations are increasingly proposed by environmental consulting firms as tools to sustain or recover octocoral populations in the Mediterranean Sea (Aurelle & Bally, pers. com.). This could be used to sustain the demography of populations or to restore gene flow for isolated populations. Nevertheless, such proposals usually do not take the possible adaptation to local conditions into account, nor do they fully estimate the required efforts. The potential effects of such practices and the best modalities sustaining biological

evolution could be evaluated through simulation approaches (Bay et al., 2017). In the case of tropical coral reefs, the possibility of using assisted evolution (i.e. acceleration of natural evolutionary processes, here to increase thermotolerance) in management plans is discussed (van Oppen et al., 2015). In all cases knowledge gaps remain. One major point is the determinism of adaptation and its heritability (with questions on genetic architecture, epigenetic effects, transgenerational acclimatisation, holobiont evolution): this will have major consequences on the possibility of evolution and on the corresponding management strategies. This is an evidently highly complex task which only starts to be understood in non-model species, e.g. Bay et al. (2017) on corals; and Perrier & Charmantier (2019) for examples and potential pitfalls with birds. These last examples show that this is now a timely and possible research line for Mediterranean marine species.

Adaptive abilities

The study of the possibility of adaptation to temperature or pH changes in non-model marine species, can take advantage of environmental gradients to study the current adaptive diversity. Indeed in the Mediterranean Sea, temperature regime can vary sharply along a short depth range (Haguenaer et al., 2013), which allow testing for local adaptation. Natural pH gradients were used to study the impact of acidification (Prada et al., 2017). In octocorals, higher thermotolerance levels were observed for shallower colonies (from 11 or 20 m depth) compared to deeper ones (40 m depth) in *C. rubrum* (Torrents et al., 2008) and *Eunicella cavolini* (Pivotto et al., 2015). Nevertheless in *P. clavata*, Crisci et al. (2017) did not observe a correlation between thermotolerance and the original thermal regime experienced *in situ* by colonies. This could be the consequence of genetic drift counter-acting local adaptation, or of the protocol: colonies were fed during the experiment, whereas energetic constraints during summer have been proposed as a factor shaping mortality events (Coma & Ribes, 2003). In *Eunicella singularis*, a reverse pattern of thermotolerance was observed with shallower colonies being less thermotolerant than deeper ones (15 vs 35 m depth) (Ferrier-Pagès et al., 2009). This could be due to the photosynthetic activity of *Symbiodinium* symbionts in this species (*Symbiodinium*), which could interact with thermal stress at lower depths. Additionally, it is not clear whether such diversity in thermotolerance corresponds to acclimatisation, to local, genetic adaptation, or to interactions between both processes. Acclimatisation could buffer the impact of environmental changes for long-lived species with long generation time as suggested for tropical corals (Munday et al., 2013a). There is little information on acclimatisation abilities of Mediterranean octocorals: one experiment in *C. rubrum* has shown a reduction of the expression of HSP70 in experimental thermal stress following a first similar stress (Haguenaer et al., 2013), but a reverse signal was observed for another temperate octocoral after acclimatisation to temperature (Lopes et al., 2018). In all cases, for such long lived species, acclimatisation abilities should be explored on a longer time interval, especially over different years. Transplant studies on the bryozoan *Myriapora truncata* showed that, at low pH, individuals were able to survive, but not to grow (Lombardi et al., 2011). Rodolfo-Metalpa et al. (2010) showed that under elevated pCO₂ one event of prolonged high seawater temperature triggered the death of all individuals in the experiment. These last experiments on *M. truncata* were not dedicated to study the diversity of responses, but they showed the potential impact of acidification on this calcifying metazoan.

Laboratory studies on CEA species showed that their survival rate, calcification rate, photosynthesis declined with increased temperature and acidification (Rodríguez-Prieto, 2016; Martin et al., 2013). Thus, engineering species of coralligenous habitats have limited acclimatization abilities, especially when facing a combination of stresses (see also Prada et al., 2017; Rodolfo-Metalpa et al., 2011).

The possibility of genetic adaptation to local thermal conditions is supported by reciprocal transplant experiments between depths in *C. rubrum*, but in only one of the two investigated regions (Ledoux et al., 2015). Gene expression differences between depths have been demonstrated for this species at the transcriptome level (Pratlong et al., 2015). Some of the differentially expressed genes are involved in stress response in other coral species, but a demonstration of their role in adaptation is still lacking in *C. rubrum*. A population genomic study indicated a signal of local (genetic) adaptation to depth in the red coral (Pratlong et al., 2018). Nevertheless, in such species with important genetic differentiation, false positive induced by genetic drift are really problematic, and additional work is required to study genetic adaptation in this species (Pratlong et al., 2018). Regarding depth gradients, genetic studies have shown that CEA species community composition vary along a depth and light gradient suggesting that different species are adapted to different niches (De Jode et al., 2019). The case of CEA underlines that the diversity of adaptation should be considered at different levels: from within species to between related species.

At higher distances, different octocoral species are present in different parts of the Mediterranean Sea (North – South, East – West). It would be interesting to study the differences in adaptive abilities according to the different basins. In all cases, for such long-lived species with sometimes long generation time, the possibility of genetic adaptation along with environmental changes seems difficult, especially if extreme events strongly impact the population dynamics. The study of recurrent bleaching events in the Great Barrier Reef, conversely indicated that previous bleaching events could reduce the impact of new events, possibly as a consequence of selective effects (mortality affecting the most sensitive individuals or species) or of acclimatisation (Hughes et al., 2018). Additional studies would be required for a better understanding of this effect and its potential consequences on corals' evolution.

2. LAND SYSTEMS

D. *Microbial soil communities of pine and oak forests*

Drivers of forest soil diversity

Soil represents a huge reservoir of biodiversity including microorganisms (mainly bacteria, fungi and protozoa) and invertebrate animals (Gobat et al., 2004), all of which are actively involved in organic matter transformation. This fundamental ecosystem process sustains major ecosystem services, such as primary production and biogeochemical cycles (Bardgett et al., 2008). Forests are essential biomes in providing such services. The abundance and diversity of soil microorganisms is particularly high in such ecosystems (Buée et al., 2009; Lladó et al., 2017). Both bacterial and fungal communities are key soil components that produce extracellular enzymes involved in nutrient turnover and humification, leading to CO₂

emission and carbon storage (assimilation in the biomass, aggregation...) in soil. Forest soils can indeed act as both sinks and potential sources of carbon (Bardgett et al., 2008; DeAngelis et al., 2016) and this balance is driven by various environmental factors acting at different spatial scales. At a global scale, temperature and mean annual precipitation (Tedersoo et al., 2016) and edaphic properties - mainly pH - (Fierer & Jackson, 2006) have been identified as main drivers of soil microbial diversity, while locally it varies greatly according to above ground plant diversity (Haichar et al., 2008; Roesch et al., 2007; Tardy, 2015). At a local scale, soil microbial activities indeed depend on the nature and quantity of organic input coming from root exudates, litter fall or fire residues (Schmidt et al., 2011) as well as on physico-chemical processes (e.g. organo-mineral association, freezing and thawing) and interactions between soil organisms mainly related to trophic relationships (Scheu, 2002).

The Mediterranean context

The dynamics of Mediterranean forest stands react to various environmental drivers acting at different spatio-temporal scales. Of all these drivers, land use legacy and specific edaphic and climate conditions, play an important role (Ertlen et al., 2015). The surface and composition of European Mediterranean forests have been strongly structured by wildfires and human activities leading to agro-silvo-pastoral systems during the last century (Quezel & Médail, 2003). From the 1930s, abandonment of land previously devoted to agriculture and increasingly frequent wildfires promoted massive colonisation of natural spaces by resinous species such as *Pinus halepensis* Mill. and *Pinus sylvestris* (Tatoni & Roche, 1994), resulting in pure stands. The Mediterranean region is characterized by particularly dry summer periods that have selected plants producing leaf litters containing particularly high amounts of secondary metabolites (Chomel et al., 2016; Hashoum et al., 2017) and of recalcitrant phenolic compounds (Rovira & Ramón Vallejo, 2007) that were both shown to affect litter decomposition and soil nutrient cycling. In forests, vegetation assemblages are known to deeply impact soil organic matter composition. Broadleaved species, such as *Quercus* spp., enhance soil organic matter quality, increasing easily-degradable compounds and thus enhancing microbial metabolism (Polyakova & Billor, 2007). Conversely, some plant species that are specific to the Mediterranean area such as *Pinus* spp. contain particularly high amounts of recalcitrant molecules (such as cutin or lignin) and are poor in nutrients, which induces lower rates of decomposition. When both type of species (broadleaves and coniferous) are mixed, the tree-species identity and the function traits associated can strongly modify the stand 'print' on soil properties and thus on soil chemical signature (Laganière et al., 2009; Matos et al., 2010; Prescott & Grayston, 2013). This has been described as additive or non-additive (synergistic or antagonistic) effects (Brunel et al., 2017; Scheibe et al., 2015).

Mediterranean forest soil functioning may be threatened by additional pressures linked to environmental changes. The Mediterranean basin, considered as a hotspot of biodiversity (Quezel & Médail, 2003), has also been identified as one of the most prominent "Hot-Spots" in climate change projections (Giorgi, 2006; Giorgi & Lionello, 2008). Climate scenarios project changes in the spatial and temporal distribution of precipitation as well as increased frequency and intensity of extreme events (heat waves, droughts, wildfires) that will impact ecosystem functioning (Giorgi & Lionello, 2008), including through soil-related processes.

Forest soil responses to drought stress

Soil ecologists are now extensively focusing their research on how climate change effects may alter soil diversity and functions (Kéfi et al., 2007). Most litter decomposition experiments have investigated litters from plants artificially exposed to global change factors such as warming, drought or elevated CO₂ (Suseela & Tharayil, 2018). Some studies have used field-scale experiments via rainfall exclusion to mimic drought constraints (Rodríguez-Ramirez et al., 2017; Santonja et al., 2017), while others are now using transplantation experiments across natural climate gradients to investigate the impact of climate conditions on forest soils *in situ* (Berger et al., 2016; Keiser & Bradford, 2017; Makkonen et al., 2012).

Previous studies showed that microbial communities frequently exposed to drought stresses are more resistant to drying/rewetting cycles than less exposed communities (Butterly et al., 2009; Farnet Da Silva et al., 2016; Fierer et al., 2003; Fierer & Schimel, 2002; Schmitt et al., 2010; Van Gestel, Merckx, & Vlassak, 1993), which has been interpreted as resulting from natural selection (Sparling et al., 1987). Several authors detected a shift in microbial composition towards fungal-dominant communities after repeated drying (Cleveland et al., 2004; Evans & Wallenstein, 2012; Yao et al., 2011), suggesting that this microbial group can resist to drought stress better than bacteria. More precisely, fungi may be more tolerant to drought stresses (fungal hyphae can transfer moisture from water-filled micropores) than bacteria, which are more connected to their immediate surroundings and require water films for motility and substrate diffusion as described above (Evans & Wallenstein, 2012). In fact, based on morphology and life history strategies (inherent resistance and acclimatisation abilities) of microbial groups, stresses linked to drying/rewetting cycles are likely to favour Gram-positive bacteria (with a strong, thick, interlinked peptidoglycan cell wall) and fungi rather than Gram-negative bacteria (with a single-layer cell wall and an outer membrane) (Schimel et al., 2007). Production of intracellular osmolytes is often observed as a physiological response to water potential stresses (Kakumanu & Williams, 2014), which is particularly energy-consuming for microorganisms and thus impacts their metabolism. However, the stability of decomposer microbial communities after stress also relies on other factors that shape community structure, composition and diversity, such as organic matter quality and quantity (Loreau et al., 2001; Loreau Michel, 2010; Wardle & Jonsson, 2014). Mixed forests have long been considered essential for sustainable forestry management (Gartner & Cardon, 2004; Rodríguez-Loinaz et al., 2008). Increased biodiversity creates more diverse habitats, produces more above-ground biomass (Vilà et al., 2007) and enhances resilience to stress and to disturbances like diseases (Pautasso et al., 2005), fires (Wirth, 2005) or extreme weather events (Dhôte, 2005).

Numerous previous studies (Rodríguez-Ramirez et al., 2017; Setiawan et al., 2016; Zimmer, 2002) have shown higher decomposition rates in mixed litter compared to monospecific litters, depending strongly on litter species within the mixture (Brunel et al., 2017; Cuchietti et al., 2014; Prescott & Grayston, 2013; Wu et al., 2013). The diversity of plant species within litter mixtures is also thought to maximize the diversity of nutrient resources, which in turn favours microbial diversity and abundance (Santonja et al., 2017, 2018). Any alteration of the plant species diversity should thus drive strong cascading effects on microbial decomposer communities. In other words, diversity begets diversity (Chapman & Newman, 2010). This can be related to the ecological concept of complementary ecological niches, underlying

better microbial exploitation of organic matter and better stability (Loreau et al., 2001; Loreau Michel, 2010). A meta-analysis by Cornwell et al. (2008) suggests that plant species traits have a strong effect on resistance to stresses and could be considered as a predominant driver of soil functioning within biomes worldwide. However, another concept based on the redundancy of functions in soil microbial communities supports the fact that there is no clear relationship between microbial diversity and the stability of function 'decomposition'. Many authors have indeed assumed that there is a high level of equivalence in functions within decomposer communities and thus a substantial potential of resilience in functional capacity. In other words, the loss of any group of species may not strongly impact decomposition processes since other microorganisms can sustain its function (Nannipieri et al., 2003; Swift, Izac, & van Noordwijk, 2004).

Many research outputs point to the need to take drivers at different spatio-temporal scales into account (mainly stress legacy, land use history, climate conditions at various spatial scales and litter chemical signature) to improve our projection capacity of functional and structural microbial community responses to environmental changes, and their consequences for ecosystem functioning and stability. This is particularly challenging for microbial communities of soils since only a very small fraction of the existing species diversity is known. Yet, it is crucial for the above ground communities that depend on soil biodiversity, such as forests.

E. Semi-arid and arid Mediterranean steppes

Mediterranean steppes host a unique biodiversity with rare and threatened species. Among them, steppe bird species (e.g. *Chersophilus duponti*, *Tetrax tetrax*, *Otis tarda*, *Pterocles alchata*, *Falco naumanni*) represent the most threatened group of birds in Europe (Laiolo & Tella, 2006). Steppes also host rich assemblages of arthropods with many species typical of oligotrophic and arid areas (Fadda et al., 2007), also including some endemic taxa (e.g. the grasshopper *Prionotropis rhodanica* Uvarov in the Plaine de La Crau, France). North African steppes are exceptionally rich with more than 2600 plant species of which 25% are endemic (Le Houerou, 1995). In North Africa, arid steppes potentially cover over 630 000 km² (Le Houerou, 1995). Today, only fragmented and reduced surface of semi-arid and arid steppes occur in the Mediterranean basin, especially in the western Mediterranean (Iberian Peninsula, and North Africa).

The openness of steppes confers them a long history of traditional agricultural practices such as sheep grazing, especially the gramineous steppes of *Stipa tenacissima* that are often the result of the degradation of former Mediterranean open forests (Gauquelin et al., 1998). However, arid and semi-arid ecosystems are especially prone to state changes as a result of scarce, variable rainfall and low soil fertility, and among the most sensitive ecosystems to global climate change (Kéfi et al., 2007; Reynolds et al., 2007). In North and South Mediterranean, recent industrial development, agricultural intensification, changes in agricultural practices or changes in fire regimes pushes arid and semi-arid ecosystems towards the edge of extinction (Kéfi et al., 2007; Puigdefábregas & Mendizabal, 1998). Desertification, land degradation in arid, semi-arid and dry sub-humid areas results from various factors, including climatic variations and human activities (Reynolds et al., 2007).

Many studies have reported the consequences of climate and land use changes in steppes on biodiversity. In North Africa, (Le Cuziat, et al., 2005) showed that human presence and pastoral activity affect the distribution of a steppe bird species, the Houbara bustard. Similar projections for steppe bird species in Spain showed a strong impact of land use on their potential distribution range (Brotons et al., 2004). Agricultural intensification also impacted the composition of steppe vegetation (Römermann et al., 2005). Trait-based modelling of plant abundances in the arid steppes of eastern Morocco showed that stress-tolerant subshrubs will become the dominant functional group in the next decades whatever the climate change scenario used, suggesting a process of desertification (Frenette-Dussault et al., 2013). In North Africa, a vegetation model simulating an increase of atmospheric CO₂ (500 ppmv) and of annual temperature (+2°C) with stable precipitation showed that a woody xerophytic vegetation might occupy a more extensive territory than today, and would replace part of the present steppe area (Cheddadi et al., 2001). The phenomenon of shrub encroachment, i.e. the increase in the density and cover of shrubs in former grassland, triggered by many factors ranging from climate change to grazing to fire suppression, has been largely reported. *Stipa tenacissima* - when preserved - might also have a direct key role of facilitation on these introduced shrubs in some arid and semi-arid steppes (Maestre et al., 2001).

In this context, the authors recommend enlarging the network of protected areas to prevent any further habitat degradation and to implement agri-environmental measures as well as active transnational management measures for the maintenance and survival of viable bird population (Brotons et al., 2004; Buisson & Dutoit, 2006) and biodiversity in general.

F. Forests

F1. Thermophilic oak-pine forests and shrubland

Downy oak (*Quercus pubescens* Willd.), Holm oak (*Quercus ilex* L.) and Aleppo pine (*Pinus halepensis* Miller) are the three most widespread forest tree species of the western part of the Mediterranean. They form vast monospecific or mixed forests as do many species of oaks and pines across the altitudinal vegetation belts throughout the region (Quezel & Médail, 2003). They are adapted to the long summer droughts of the Mediterranean and will probably increase their ecological role and distribution area as climate gets hotter and summers get drier throughout the 21st century.

Total forest cover of Aleppo pine is estimated to be approximately 3.5 million hectares (Fady et al., 2003; Mauri et al., 2016). *P. halepensis* is mainly found at lower elevations in the thermo- and meso-Mediterranean belts, and up to 2 000 m above sea level in Morocco. Total forest cover of downy oak is at least 2.5 million hectares, with over 1.7 million hectares in France and Italy alone. Downy oak is a northern Mediterranean oak that can grow from coastal plains up to 1200-1300 m above sea level while it is most often found on hillsides between 200 and 800 m. Downy oaks prefer lime-rich and well drained soils in the northern part of their range, while they may also be common on acidic soils in its southern part (Pasta, de Rigo, & Caudullo, 2016). Total forest cover of holm oak is over 6 million hectares, with the largest forests in the western Mediterranean (Quezel & Médail, 2003). Holm oak is mostly found from 0 to 1000 m above sea level but can reach elevations of 2500 m in areas

where competition with other broadleaves is limited such as in Morocco and Spain. Holm oak can be the keystone species of various ecosystems, from open matorral type to late successional (de Rigo & Caudullo, 2016). It prefers well drained sites and is insensitive to soil pH.

The current distribution of these thermophilic, drought resistant forests and their associated biodiversity results from millennia of human disturbance and it is actually difficult to precisely characterize the limits of the ecological niche of these species (Covas & Blondel, 1998; Doblas-Miranda et al., 2017; Henne et al., 2013). Fire and land use change are the main drivers of their distribution and their recolonisation of low elevation sites has been spectacular during the second half of the 20th century onwards (Quezel & Médail, 2003).

The major challenge for these species during the 21st century will be to adapt to increased periods of summer drought and heat. Widespread mortality of *Quercus pubescens* in southern France over the past years, for example, have alarmed forest management agencies. Ongoing experiments in flux tower sites measuring gas exchange rates over Mediterranean oak and pine ecosystems reveal numerous adaptation potentials. In the O3HP Oak Observatory in Provence (France), rain exclusion experiments helped better understand the capacity of *Q. pubescens* to resist recurrent droughts projected by climatic models. After 4 years of reduced rain (30%), although water potential (Ψ) and net photosynthesis (P_n) were noticeably reduced, trees showed no reduced growth and no oxidative stress. Defences such as Volatil Organic Compound emissions actually decreased. However, growth decrease was observed at longer term (5th year) and antioxidant contents (carotenoids and isoprene) started to change (Saunier et al., 2018). Although *Q. pubescens* is a highly drought-resistant species that possesses efficient antioxidant mechanisms (tocopherol, xanthophyll cycle) to cope with oxidative stress, we can anticipate substantial decreases in gas exchange, adjustments of the photosynthetic pigment composition (chlorophylls, carotenoids), impaired growth in the long-term and maybe stronger compensatory mechanisms between antioxidants. The wide distribution of this taxon often occurring in the transition of several climatic influences (Quezel & Médail, 2003) still requires further research on its entire range in order to test its phenotypic plasticity.

Other effects of experimental reduction of rainfall in *Q. ilex* forests (in Catalonia (Spain) and Puechabon, near Montpellier, France) have included significant shifts in community composition of ectomycorrhizal communities (Richard et al., 2011), decreased soil enzyme activity (Sardans & Peñuelas, 2005), decreased species richness of recruited seedlings in a Mediterranean shrubland (Lloret et al., 2004) and phenological changes (Misson et al., 2011; Ogaya & Peñuelas, 2004). In the long run these shifts may offset the increased productivity projected by mechanistic process-based models focusing on CO₂ fertilisation (Keenan et al., 2011). Varying phenotypes under different environmental conditions are better projected by phenotypic plasticity than by genetic diversity (Valladares et al., 2002).

Increased risk of wildfires is another major challenge. Fire is a dominant ecosystem process of low elevation pine and oak forests, likely to become more prevalent under climate warming in the 21st century. Low elevation pines have developed serotinous cones that make them particularly adapted to recurrent fires at a frequency of over 20-30 years. It is likely that recurrent fires have impacted the genetic diversity of Aleppo pine, making it a relatively

low diversity species amongst pines. Oaks are resprouters and are also well adapted to fire. Nonetheless, an increase in fire frequency and intensity may negatively affect pine and oak forest composition, recovery rate and suitability as a habitat for other communities of plants and animals (Doblas-Miranda et al., 2017; Puerta-Piñero et al., 2012; Regos et al., 2015), with complex feedback loops associated to other changes such as drought and land-use (see review by (Doblas-Miranda et al., 2017).

Despite some sensitivity to late frosts and winter freezing, Aleppo pine is likely to resist and be one of the winners of climate warming in the Mediterranean. From an evolutionary ecology perspective, this eastern Mediterranean origin pine re-occupied its current distribution after the Glacial cycles from a few refugial areas via local diffusion and long-distance dispersal processes. The genetic diversity of this species is one of the lowest for trees worldwide, indicating strong past demographic bottlenecks (such as cold episodes and large wildfires) (Fady, 2012; Fady & Conord, 2010; Grivet et al., 2009; Grivet et al., 2011). Aleppo pine displays several strategies to withstand severe drought, including high resistance to embolism and a capacity to reduce wood-formation rates as water availability decreases (e.g. Camarero et al., 2015). However, water shortage can limit growth and productivity of Aleppo pine forests and increase tree mortality (del Río et al., 2014; Dorman et al., 2013). Depending on the origin of the populations in the vast and contrasted climatic zones the species occupies, from semi-desert to temperate climates, climate-growth response functions are highly variable (Luis et al., 2013). Although some evidence of differentiation for survival (xylem hydraulic conductance and resistance to embolism) has been found in semi-arid common gardens (David-Schwartz et al., 2016; Klein et al., 2013; Schiller & Atzmon, 2009), signatures of local adaptation are limited (Gómez et al., 2001; Grivet et al., 2011). This suggests that most of the variation is due to phenotypic plasticity (Baquedano et al., 2008; Chambel et al., 2007).

Similarly, *Q. ilex* is likely to be among the winners of environmental changes in the Mediterranean. Although there are fewer molecular studies in this oak than in other oak species or Aleppo pine, its genetic diversity is higher than that of Aleppo pine and among the highest within the oaks. *Quercus ilex* is made of three major genetic clusters: eastern, central and western Mediterranean (Vitelli et al., 2016). *Quercus ilex* has its highest diversity in the eastern Mediterranean cluster, similarly to Aleppo pine and many species in the Mediterranean (Conord et al., 2012).

F2. Beech-fir forest

Ecology

Some of the typical mixed broadleaf conifer forests of the mountain belts of the Mediterranean region are *Abies* sp. and *Fagus* sp. Forests, collectively names beech-fir forest in this section. *Abies* sp. forests are found from 700-900 m and up to 2300 m above sea level while *Fagus* sp. forests are found between 700 and 1800 m in the Mediterranean. Their occurrence is highly dependent on soil and air moisture and the lowest elevation presence of beech is often associated with riverine forests (Quézel & Médail, 2003). While approx. 10 species of *Abies* have been described in Mediterranean mountains, there are only two for the genus *Fagus* (*F. sylvatica* and *F. orientalis*), and they are often considered as sub-

species level taxonomic entities (Quézel & Médail, 2003) (Table S1). *Abies* and *Fagus* species form both mixed and single species dominated forests.

Most *Abies* species occupy reduced distribution areas in isolated mountains except *Abies alba*, the European silver fir whose European distribution spans from Spain to Romania (Valladares et al., 2002; Wolf, 2003). In the westernmost part of its Alpine distribution, *Abies alba* grows under various biogeographical (from inner to outer Alps), bioclimatic (from Mid-European to Sub-Mediterranean influences) and edaphic conditions, with scattered locations under strict Mediterranean climate (Ozenda, 1981). Mediterranean climate occurrences of *Abies alba* are rare outside of France. Similarly to *Abies alba*, *Fagus sylvatica* is a typically medio-European forest tree, requiring moist habitats and able to colonise mountain belts under Mediterranean climate (i.e. where adaptation to summer drought is an issue) in Catalonia, southern France, southern Italy, Sicily and central Greece (Quézel & Médail, 2003). It has the same longitudinal span as *Abies alba* and is replaced by its more drought resistant congener, *Fagus orientalis*, in scattered places in northern Greece and Bulgaria and large forests in Turkey (Kandemir & Kaya, 2009; Von Wuehlisch, 2008).

Table S1 : Distribution and bioclimatic preferences of Mediterranean *Abies* (a) and *Fagus* (b) species, compiled from (Quezel & Médail, 2003) unless indicated otherwise. A sub-humid bioclimate receives between 600 and 800 mm of precipitation a year, a humid bioclimate over 800. Temperature variants are as follows: fresh when mean temperature of coldest month (m) is $0^{\circ}\text{C} < m < 3^{\circ}\text{C}$, cold: $-3^{\circ}\text{C} < m < 0^{\circ}\text{C}$, very cold: $-7^{\circ}\text{C} < m < -3^{\circ}\text{C}$. Data for *A. alba* and *A. bornmuelleriana* are limited to their Mediterranean distribution. Elevation and surface data for *A. equi trojani* are from Kaya et al. (2008) and data for *A. bornmuelleriana* are from Özel & Erteki,(2012). MECC* (national forest inventory) data provided for Greece are from P. Dimopoulos and the project: National Cadastre & Mapping Agency S.A. & Ministry of the Environment and Climate Change (2015). Distribution data for *Fagus orientalis* in Turkey are from Ozturk et al. (2010). Distribution data for *Fagus sp.* in Greece were provided by P. Alizoti using the reference: Results of the first national forest inventory, 1992. Ministry of Agriculture, General Secretariat for Forests and Natural Environment, General Directorate for Forests and Natural Environment, Athens.

(a)

Species	Occupied surface (in ha)	Country of occurrence	Altitudinal range (in m) (and extremes)	Bioclimate type and temperature variants	Substrate	Summer drought duration (months)
ABIES SPECIES						
<i>A. cephalonica</i>	200 000 (130 000 according to MECC*)	Greece	700 - 2000 (400 - 2300)	sub-humid to humid, fresh to cold	Limestone and dolomites	1 - 5
<i>A. borisii regis</i>	57 000 (according to MECC*)	Greece	1100 - 1900 (600 - 2000)	sub-humid to humid, cold to very cold	Limestone and serpentine	Probably between <i>A. cephalonica</i> and <i>A. alba</i>
<i>A. bornmuelleriana</i>	200 000 (entire range)	Turkey	1200 - 2000	humid, cold to very cold	Schists and gneiss	0 - 2
<i>A. equitrojani</i>	3600	Turkey	1300 - 1500 (400 - 1600)	humid, cold to very cold	Metamorphic bedrock	0 - 2
<i>A. cilicica</i>	350 000	Lebanon, Syria and Turkey	1200 - 2100 (1100 - 2200)	humid, cold to very cold	Limestone and dolomites (some serpentines)	1 - 3
<i>A. pinsapo</i> and <i>A. marocana</i>	2300 (Spain) and 7000 (Morocco)	Spain, Morocco	900 - 1800 in Spain, 700 - 2200 in Morocco	humid, fresh to cold	Limestone and dolomites	1 - 4
<i>A. numidica</i>	300	Algeria	1750 - 2000	humid, cold	Limestone and dolomites	1 - 3
<i>A. nebrodensis</i>	150	Italy	1400 - 1600	humid, cold	Schists	0 - 1
<i>A. alba</i> (Medit. range)	20 000	France, Italy, Spain	1100 - 1600 (600 - 2000)	humid, fresh to cold	Limestone and dolomites	0 - 1

(b)

Species	Occupied surface (in ha)	Country of occurrence	Altitudinal range (in m) (and extremes)	Bioclimate type and temperature variants	Substrate	Summer drought duration (months)
FAGUS SPECIES						
<i>F. sylvatica</i> (Mediterranean range)	295 290 (in Greece)	France, Italy, Spain, Greece	800 - 1700 (600 - 2200)	sub-humid to humid, cold to very cold (locally, fresh)	Limestone and dolomites (locally acidic)	0 - 1
<i>F. orientalis</i> (Mediterranean range)	85 000 (in Turkey), 41 350 (in Greece)	Greece, Turkey (mostly)	1000 - 1800	sub-humid to humid, cold to very cold	Limestone and dolomites	0 - 1

Evolutionary history

Fir and beech survived the last glacial cycle of the Pleistocene and the Late Glacial Maximum (LGM) in refugia located in the Mediterranean, giving rise to highly differentiated and genetically rich local populations. The LGM refugial and Holocene colonisation history is rather well known for both *Fagus sylvatica* and *Abies alba*, the most largely distributed of all Euro-Mediterranean firs (Liepelt et al., 2009; Magri et al., 2006). Magri et al. (2006) showed using both paleoecological and genetic data that beech survived the last glaciation in at least 10 different refugia. Most of them were in the Mediterranean but did not contribute to the recolonisation of Europe, which instead sprung from refugia further north in the Massif Central, Slovenia and possibly Carpathians. The Mediterranean refugia may in fact be a long-term area of persistence for beech throughout the last two glacial / interglacial cycles of the Pleistocene. Liepelt et al. (2009), also using both paleoecological and genetic data, showed that *Abies alba* survived in multiple refugia during the LGM. As for beech, few of the Mediterranean refugia were effective sources for Holocene recolonisation, which sprung from refugia further north in the Apennines, Dinaric Alps and at least two areas in the northern Balkans (Gömöry et al., 2012). The Mediterranean refugia may again indicate areas of long-term persistence during the glacial periods of the Pleistocene.

Mediterranean *Abies* species are well differentiated, with few detected events of admixture and gene flow, indicating that Mediterranean *Abies* species have probably survived in separate refugia during the Pleistocene (Liepelt et al., 2010). *Abies* type pollen dating back to the late Miocene and the Pliocene are widespread in paleoecological archives, an indication of the long presence of firs in the Mediterranean. As for *Fagus* forests, their presence is attested in sediments since the Oligocene (Quézel & Médail, 2003).

Importance and effect of land use and management

Due to their importance for industry, from ship building as early as pre-Roman times, to mining and construction throughout recent history, both *Abies* sp. and *Fagus* sp. dominated forests have seen their distribution areas shrink considerably over historical times. They reached their lowest coverage during the 19th century on Europe's side of the Mediterranean (Lander et al., 2011), while they remain threatened by land use change to these days in North Africa and the Middle East (Awad et al., 2014). In Mediterranean Europe, the demographic dynamics are still towards habitat recolonisation despite increasing decline due to environmental changes.

Adaptation to environmental changes - decline

Reports of decline due to environmental changes and associated factors such as insect outbreaks (bark beetles for example) are alarming. In the words of Gazol et al. (2015): "Climate warming is distinctly modifying growth patterns and responses to climate in silver fir across most of the species' European distribution area. In south-western Europe the reduction in growth of many populations is related to an observed increase in aridity, whereas in more temperate areas warming is enhancing growth. Our results confirm a decline in the growth of silver fir at its south-western distribution limits as a consequence of climate warming". There are similar reports for beech, although the adaptive capacity of marginal populations located at the southern limit of this species' distribution is unclear. Some reports indicate strong growth decline (up to 49% compared to pre-climate change levels), whilst others highlight that sensitivity and low resistance to drought is greater at the core of the species range than at the xeric range edge (Cavin & Jump, 2017; Jump et al., 2006). Just as local differences were found at tree and plot level for water stress sensitivity in *A. alba* at range margins, it is likely that the same applies to beech (Cailleret et al., 2014). Their conclusion that "this study highlights the importance of local site and stand conditions on mortality and decline processes..." can probably be generalised to the entire range margins of the two species and their communities. There, drought is a strongly limiting factor that can be compensated by high local habitat heterogeneity, thus offering options for adaptation to increased drought under environmental changes.

Long standing variability in local site conditions has triggered local adaptation under natural selection processes, as identified in genomic signatures in both silver fir and European beech (Brousseau et al., 2016; Lagüe et al., 2014; Roschanski et al., 2016). In these studies, stress related candidate genes (mostly cold resistance and drought resistance) showed significant population differentiation along environmental gradients both within and amongst sites. Despite relatively limited dispersal abilities, their habitat heterogeneity and their high diversity in stress related genes make Mediterranean populations of beech and fir both museums of past diversity and a cradle of possible adaptation to environmental changes of high conservation value.

G. Agrosystems

The terrestrial Mediterranean hotspot of biodiversity is dominated by agricultural lands, evergreen woodlands and shrubland habitats. Several traditional Mediterranean agroecosystems are multifunctional mosaic associations of diverse annual and perennial crops, grazing and semi-natural areas. The potential evolution of these systems under climate

change is deeply shaped by interactions management choice and land uses, and will have important consequences on associated landscapes and biodiversity. Agro-silvo-pastoral systems are present on both sides of the Mediterranean Sea. The design of such heterogeneous systems shapes a man-made landscape diversity and can support a rich specific biodiversity (Bagella et al., 2016; Blondel & Aronson, 1999). Blondel (2006) points out that the exceptional richness of annual plant species in the Mediterranean flora is due to long-standing but constantly changing human activities and heavily grazed areas.

In the Mediterranean region like everywhere else, a decrease in biodiversity has accompanied the changes in land use and farming practices throughout the 20th century. In productive areas, agricultural intensification implies first a reduction of the diversity of cultivars and livestock varieties, while landscape simplification (Pinto-Correia & VO, 2004), mechanisation and the use of chemicals are responsible for the decrease of the biodiversity within the whole agricultural landscape. The extinction of arable weeds (Chamorro et al., 2016; Saatkamp et al., 2009), or the declining populations of farmland bird species often with a high conservation status (Sirami et al., 2008) are particularly significant examples for the Mediterranean. Beside intensification, land abandonment in remote (often mountainous) areas of Mediterranean Europe is mostly followed by landscape closing due to woody encroachment, which affects negatively plant species diversity due to competition on light and water, or by inhibiting seed arrival and germination (Gabay et al., 2008). Even the disappearance of livestock in forests might reduce the biodiversity of understorey plant communities on a regional scale because of a greater homogenisation of plant composition (Fortuny et al., 2014). Rural land abandonment may lead to the return of forest birds when forests spreads (Gil-Tena et al., 2009) and it proves to be the most effective way to recover both habitat and bird populations in Mediterranean steppes (e.g. Laiolo & Tella, 2006). In contrast, Papanastasis et al. (2002) report that overgrazing in the mountains of Crete may have a negative impact on plant biodiversity, especially when associated with burning.

Regarding intensification, despite the continuous general use of synthetic fertilizers and pesticides in Mediterranean agroecosystems (like worldwide), agroecological practices that rely more on functional agrobiodiversity of the ecological system and less on external inputs are on the rise (Stojanovic, 2019) and has become an objective now supported by various institutions. More specifically, agroecology aims at enhancing species biodiversity delivering important services for agriculture, like pollination, soil fertility, or biological pest control (Gaba et al., 2018). For example, organic orchards in southern France hold a lot more earthworms - soil engineers - than other orchards (Sauphanor et al., 2009). Besides, the maintenance of on-farm diversity allows the conservation of threatened species, like the Great bustard *Otis tarda* that benefits from cereal/fallow rotations in Portugal (Moreira et al., 2004). Policies enhancing low-intensity management techniques such as organic farming are also the main way to promote plant diversity in dryland cereal fields of the Iberian Peninsula (José-María et al., 2010), or to favour bird communities and their resilience to climate change in the Mediterranean vineyards (Rollan et al., 2019).

Threats by environmental changes to Mediterranean agro-ecosystems are related to the increasing drought and heat stress in the first place (see part C in Main manuscript). More and more studies show how a change towards farming practices that favour the soil capacity to hold and keep water, like conservation farming, with the objective of stabilizing or

enhancing yields under Mediterranean climates (Jemai et al., 2013; Mrabet, 2011), may have a beneficial effect on biodiversity (e.g. arthropod population under no-tillage maize in Spain (Rodríguez, Fernández-Anero, Ruiz, & Campos, 2006)). The use of herbicides consequent to many no-tillage systems (used to fight competition by arable weeds) contradicts the agro-ecological objectives. Research now investigates organic conservation agriculture by using agro-ecological service crops and improved technology (Canali et al., 2013; Navarro-Miró et al., 2017). For example, conservation farming in organic systems often rely on the use of legume intercrops for both increasing soil fertility and reducing weed competition. Such systems increase biodiversity both within and at the surface of the soil (see e.g. (Henneron et al., 2015; Rypstra et al., 1999)). Organic systems have a greater abundance and diversity of arbuscular mycorrhizal fungi (Oehl et al., 2004), which play a crucial role in nutrient acquisition and soil fertility. Gianinazzi et al. (2010) highlight the fact that arbuscular mycorrhizas fungi alleviate stress salinity both in olive tree plantations in Spain, and in palm groves in arid North Africa where yields are considerably affected by drought and soil salinity (Bouamri et al., 2006; Porrás-Soriano et al., 2009). Arbuscular mycorrhizas fungi also improve resistance of clover to hydric stress in arid Morocco (Meddich et al., 2000). Under climatic fluctuations, intercrop systems in Mediterranean environments have a greater land use efficiency than monocrops (Lithourgidis et al., 2011a), and are more stable to disturbances, this later effect being attributed to the larger on-farm diversity (Lithourgidis et al., 2011b). Under projected increase water stress, Falco & Chavas (2008) estimate the resilient ability of the south Italian cereal agro-ecosystem to be positively related to crop diversity.

Agroforestry and silvopastoral systems (crops and trees or livestock and trees association) that were partly abandoned (Eichhorn et al., 2006) are now rediscovered, thanks to a better understanding of their multiple ecosystem services. They appear to be well adapted to the Mediterranean climate (Joffre et al., 1999), providing a better temperate and less dry microclimate for crops or livestock between trees, and allowing a better water and nutrient availability due to tree roots plasticity (Cardinael et al., 2015), therefore increasing total productivity (Graves et al., 2007). At the same time, the land use mosaic of the silvopastoral systems in the Iberian Peninsula (named “Montado” in Portugal and “Dehesa” in Spain) supports a wide diversity of plant and animal species (Diaz et al., 1997). The appropriate management of such system benefits both farmland and forest bird species (Godinho & Rabaça, 2011; Leal et al., 2011), as well as plant and invertebrate diversity (Bugalho et al., 2011a; Bugalho et al., 2011b).

This review highlights the fact that the pressures on Mediterranean agroecosystems due to environmental changes may accelerate changes toward agroecology (already required to counter soil erosion, pollution, and biodiversity loss), bringing together enhanced sustainability and biodiversity in a positive feedback loop. In a nutshell, the best configuration for biodiversity is a mosaic landscape composed of open and woody patches (Gabay et al., 2008).

in order to complement the adaptive capacity expected from a progressive shift toward agroecological management, work to improve the selection of cultivars better adapted to the Mediterranean climate is ongoing (e.g. for drought tolerance (Cattivelli et al., 2008)). Anticipating future droughts, Habash et al. (2009) discuss the potential of designing a climate

change ready durum wheat through genomic approaches. Plant breeders must consider strategies to retain diversity from wheat landraces (Lopes et al., 2015), especially Mediterranean durum landraces, which represent a particularly important group of genetic resources because of their extensive genetic variability, and their documented tolerance to drought (Kyzeridis et al., 1995), resilience to pests, resistance to diseases (Talas et al., 2011), and adaptability to low-input farming systems (see Chapter 6 by Srivastava and Damania in Brown et al. (1989)). Not only the quantitative production is looked at, but also its quality. In order to avoid grapevine ripening during very hot days, (Costantini et al., 2008) show that breeding new late-ripening varieties is a way to increase the existing genetic variability and to adapt the grapevine phenology to environmental changes.

3. OVERVIEW

Table S2: characteristics of the different Mediterranean ecosystems examined and overall expectation according to authors' opinion as to their adaptive potential under changing environmental conditions. Cells in grey include a high level of uncertainty.

MEDITERRANEAN ECOSYSTEMS		ADAPTIVE MECHANISMS					OVERALL ADAPTATIVE POTENTIAL
NAME	ECOLOGICAL DIVERSITY	ACCLIMATIZATION	GENETIC ADAPTATION	RANGE SHIFT	COMMUNITY COMPOSITION MODIFICATIONS	MANAGEMENT	
MARINE ECOSYSTEMS							
Plankton (phyto and zoo)	Coastal and oceanic	Medium to High	High	High	High	Low	High
Seagrass meadows (Posidonia oceanica)	Coastal (depth gradient 1-40m)	High	Low	Medium to High	High	Low	Medium / High
Coralligenous ecosystems and marine animal forests	Mostly coastal (depth gradient. <i>C. rubrum</i> : 10 - 1000 m Corallinaceae: 20-120 m)	Low to Medium	Low	Low	Low	Medium	Low / Medium
LAND ECOSYSTEMS							
Microbial soil communities of pine and oak forests	Similar to thermophilic oak-pine forests	High	High	High	High	Medium	High
Semi arid and arid steppes	High (altitude from sea level up to 3500 meters)	Data deficient	Data deficient	Low	Low	High	Unclear
Thermophilic oak-pine forests	High (altitude from sea level up to 2000 meters)	High	Medium (oaks) Low (pines)	High	Medium	High	High
Beech-fir forests	High (altitude from 800 up to 2200 meters)	Medium	Medium	Low	High	High	Medium
Agrosystems	High (altitude from sea level up to 2000 meters)	Low	High	High	High	High	Medium

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