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Food for Thought

Foreseeing the future of *Posidonia oceanica* meadows by accounting for the past evolution of the Mediterranean Sea

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The current warming of the Mediterranean Sea has been forecast to lead to the shrinkage of seagrass meadows. We agree that rising sea temperatures most likely will have immediate negative effects on them because present-day asexually reproducing clones of *Posidonia oceanica* were likely selected as a form of resistance under suboptimal conditions during the colder temperatures of the last glaciation. However, since the evolution of *P. oceanica* has happened under tropical/subtropical conditions for tens of millions of years, some kind of evolutionary resilience to high temperatures is to be expected. We suggest that the ability of *P. oceanica* plants to reproduce sexually when water temperature is >27°C might lead in the future to the selection of warm-loving plants (as warm-sensitive clones decline), with an associated increase in genetic variability in the species gene pool. Predictions focused exclusively on the future decline of cold-selected (warm-sensitive) clones may result in short-sighted forecasts because the deep history of the taxon is overlooked. We suggest that an evolutionary-based approach should be more often considered when analysing the present declines of animal and plant species. We provide some additional examples of cases in which this could be done.

Keywords: clonal reproduction, deep history, Mediterranean warming, Pleistocene selection, resilience, seagrass meadows, sexual reproduction.

Population projections and management decisions are often based on snapshots of observations made in the present. However, many species are several million years old and have especially deep origins in geological time. Over their existence, species may have gone through all sorts of changing environmental conditions. Past records of species presence and ecology (i.e. either fossils for deep history or historical records for a more recent past) can help us better understand present distribution and ecology and foresee future changes (see, e.g. Silliman *et al.*, 2018). We use here the case of *Posidonia oceanica* reef-forming seagrass meadows, to illustrate how a historically informed observation (i.e. an observation on present-day reproductive strategies in a seagrass, informed by past temperatures of the planet) may lead to very different conclusions, compared to uninformed ones.

A bit of a background

A large clone of *P. oceanica* was discovered in 2006 on the island of Ibiza (Balearic Islands, Spain), being highlighted as one of the largest and oldest clones on Earth (Arnaud-Haond *et al.*, 2012). We will argue here that *P. oceanica* clones, beyond being record-breaking cases in biology, may convey relevant historical information, most likely the occurrence of detrimental environmental conditions for the marine plant during millennia. We base our argument on the fact that clonal growth provides increased capacity for resource sharing (i.e. clonal integration), which allows clones to act as a cooperative system, buffering stressful conditions (Jónsdóttir and Watson, 1997; Saitoh *et al.*, 2002). Hence, the benefits of clonal reproduction seem especially relevant in unfavourable environments (Liu *et al.*, 2016). In this sense, clonal reproduction may act as persistence insurance outside optimal tolerance limits, compensating for the lowered relative prevalence of sexual reproduction associated with adverse environmental conditions, such as cold in this case (Eckert, 2001; Herben *et al.*, 2015).

The genus *Posidonia* is a very old one. European fossils are known from the Cretaceous (145–166 million years ago; Aires *et al.*, 2011), and seagrass is known to have evolved in the former Tethys Sea, the tropical ancestor of the Mediterranean Sea. More specifically, *P. oceanica* is an endemism from the Mediterranean Sea that evolved after the Tethys eastern closure in the Miocene (Aires *et al.*, 2011). The genus evolved under water temperatures that were much warmer than those currently present in the Mediterranean and has been subjected to those conditions during the largest part of its history, except for the major events of extreme cooling during the Pleistocene. Current cold-tolerant (i.e. warm-sensitive) dominant genotypes must necessarily have been heavily selected during the recent Plio-Pleistocene cooling. Indeed, temperatures >27°C trigger massive plant flowering presently (Díaz-Almela *et al.*, 2007; Ruiz *et al.*, 2018; Marín-Guirao *et al.*, 2019). The Würm glaciation (ca. 115000–11700 years ago) may have been extremely harsh for this seagrass, which evolved under tropical and/or subtropical conditions. Hence, the Ibiza clone and all others might simply reflect the difficulty of recently cold-selected plants to reproduce sexually under the sea-water conditions of the last tens of thousands of years (Fig. 1). In fact, clonal growth is more common in cold environments (Klimes *et al.*, 1997; Klimešová *et al.*, 2021), where a high degree of clonal integration has been reported (Jónsdóttir and Callaghan, 1990).

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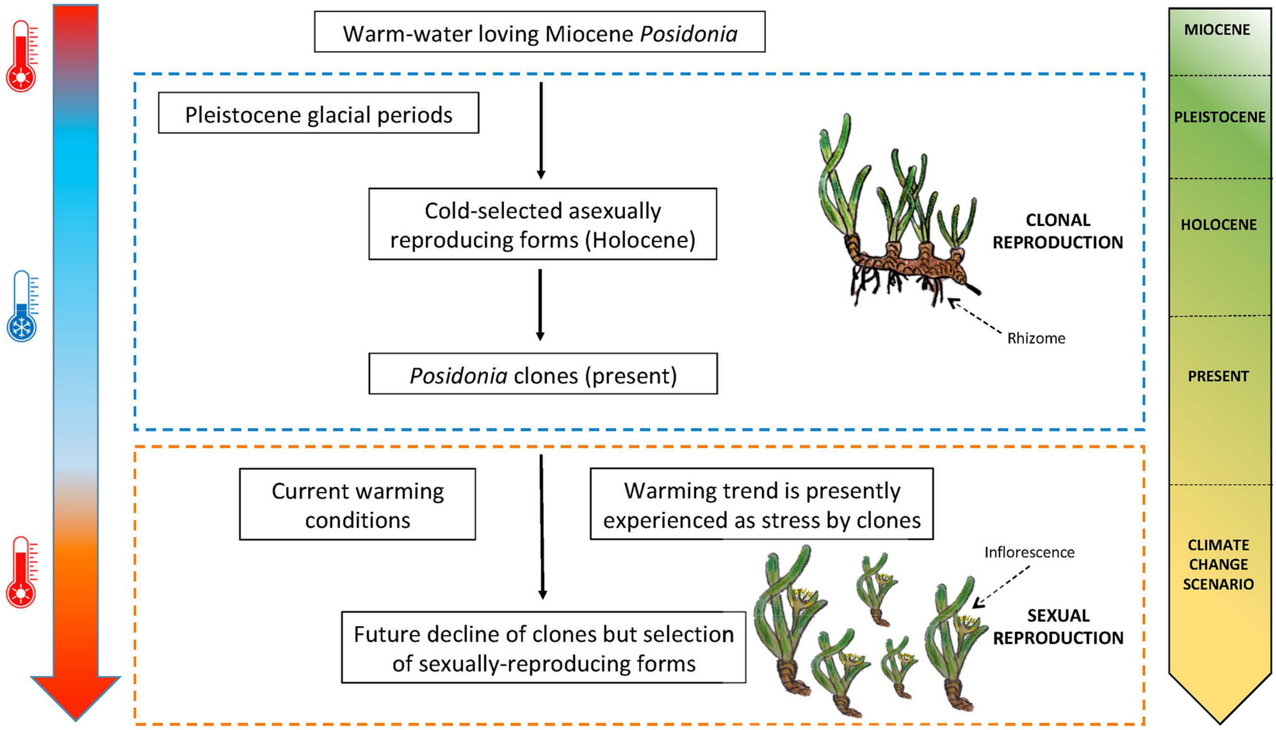

Figure 1. Diagram showing *P. oceanica* reproduction and Mediterranean temperature over time in support of the idea that current clones may represent the selection of cold-tolerant ecotypes of this marine plant.

Forecasting the future of *P. oceanica*

The current increase in water temperature associated with global warming has been predicted to have a negative effect on *P. oceanica*, causing a drastic spatial reduction of clones in the short run (Jordà *et al.*, 2012). This projected spatial reduction makes full sense since current clones may have been selected under the colder conditions of the last ice age. However, and importantly, increasing temperatures could also bring about the generalization of sexual reproduction (Marín-Guirao *et al.*, 2019), promoting increased genetic variability in the gene pool of the species in the medium and long runs.

We propose that the relatively cold temperatures experienced by *P. oceanica* during the Plio-Pleistocene selected for clonal reproduction as the optimal strategy for the harsh prevailing conditions, until very recently. Moreover, under a warming situation, conditions could be propitious for a shift to a generalized sexual reproduction strategy. That change does not need to be continuous and most likely will follow non-linear threshold-like dynamics. Importantly, from our perspective, it makes full sense that current cold-selected clones now perceive the current warming as a physiologically stressful situation (Marín-Guirao *et al.*, 2019).

Hence, we agree with the idea that this marine plant will "adapt" (*sensu lato*) to a warming sea (Marín-Guirao *et al.*, 2019), but not as an "unexpected response", but rather as an expected outcome, when the history of the taxon is taken into account. Recently, the resilience to warming of this Mediterranean seagrass has been suggested to be a consequence of deep "pre-Mediterranean" evolutionary legacies (Bennett *et al.*, 2022a, b), which clearly goes along the same line of thought as our claim that deep geological time needs to be accounted for in order to understand the present ecology of seagrass meadows and to correctly foresee its future.

Fortunately, *P. oceanica* seems to preserve enough plasticity (via epigenetic mechanisms) to recover sexual reproduction when warm environmental conditions are back (Marín-Guirao *et al.*, 2019). From a population dynamics point of view, clonal reproduction may mainly affect local dynamics (persistence), while sexual reproduction could also foster increased regional dispersal capabilities of the species, favouring the spreading to new areas (Bonte *et al.*, 2012).

As a corollary of our idea, we hypothesize that if *P. oceanica* genetics/genomics/epigenetics were to be studied along an east–west gradient in the Mediterranean basin, a higher susceptibility to shifting more readily to generalized sexual reproduction could be found in the eastern (warmer) extreme of the gradient. This is to be expected because the western end of the basin is, and has been, the point of incoming colder Atlantic waters that may have selected more strongly for cold-adapted *Posidonia* clones.

Some additional applied considerations

The historical perspective we are adopting here for the *P. oceanica* case study has indeed many implications for other current changes associated with the warming trend of the planet's atmosphere and hydrosphere. To provide just another example of the generalized relevance of accounting for past conditions to understand the present and properly forecast the future, let's think of phenological changes. The ongoing process of change towards earlier dates of terrestrial plant flowering or insect reproductive timing (see e.g. Donoso *et al.*, 2016) could be seen as a return to physiological schedules prevailing before the onset of the so-called Little Ice Age (LIA) of the 14th–19th centuries, instead of as a catastrophe. It is to be expected that the currently changing phenologies represent a return to the warmer conditions of the Medieval Climate Optimum (950–1250 BP), interrupted by the cold temperatures of the LIA. Similar considerations regarding plant and insect phenology could be done if we go farther back in time to the Roman Climate Optimum of the period 650–400 BP. Adopting a historical perspective may substantially change the way we interpret currently observed changes and allow us to expect that populations and species will have some sort of physiological resilience (i.e. genetic variability, epigenetic plasticity) in relation to past prevailing conditions. Going back to our plant-insect decoupling example, depending on whether one takes the past into account or not, an earlier phenology is seen as having an impact or, alternatively, as a return to past ecological strategies. Unfortunately, the former, less rigorous option, is more commonly adopted than the latter. This is a perfect example of the well-known Pauly's Shifting Baseline Syndrome (Pauly, 1995; Soga and Gaston, 2018) applied at the time scale of a few centuries. We think there is a lot of room for scientific improvement along these lines of thought.

Competing interests

The authors declare not to have any competing interests.

Author contributions

AMA developed the initial idea and wrote the main part of the paper. IC provided relevant literature, wrote some parts of the manuscript, and helped answer reviewer queries. SR designed the file figure, wrote part of the paper, and helped in preparing the reviewed versions.

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Data availability statement

No new data were generated or analysed in support of this research.

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