

Screening for Hyperthermophilic Electrotrophs for the Microbial Electrosynthesis of Organic Compounds

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Review

Bioinvasion impacts on biodiversity, ecosystem services, and human health in the Mediterranean Sea

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Abstract

Biological invasions have become a defining feature of marine Mediterranean ecosystems with significant impacts on biodiversity, ecosystem services, and human health. We systematically reviewed the current knowledge on the impacts of marine biological invasions in the Mediterranean Sea. We screened relevant literature and applied a standardised framework that classifies mechanisms and magnitude of impacts and type of evidence. Overall, 103 alien and cryptogenic species were analysed, 59 of which were associated with both negative and positive impacts, 17 to only negative, and 13 to only positive; no impacts were found for 14 species. Evidence for most reported impacts (52%) was of medium strength, but for 32% of impact reports evidence was weak, based solely on expert judgement. Only 16% of the reported impacts were based on experimental studies. Our assessment allowed us to create an inventory of 88 alien and cryptogenic species from 16 different phyla with reported moderate to high impacts. The ten worst invasive species in terms of reported negative impacts on biodiversity include six algae, two fishes, and two molluscs, with the green alga *Caulerpa cylindracea* ranking first. Negative impacts on biodiversity prevailed over positive ones. Competition for resources, the creation of novel habitat through ecosystem engineering, and predation were the primary reported mechanisms of negative effects. Most cases of combined negative and positive impacts on biodiversity referred to community-level modifications. Overall, more positive than negative impacts were reported on ecosystem services, but this varied depending on the service. For human health, only negative impacts were recorded. Substantial variation was found among Mediterranean ecoregions in terms of mechanisms of impact and the taxonomic identity of impacting species. There was no evidence that the magnitude of impact increases with residence time. Holistic approaches and experimental research constitute the way forward to better understanding and managing biological invasions.

Key words: alien species, cryptogenic, effects, experiments, expert judgement, modelling, systematic review

Introduction

The rate of human-mediated introduction of species to new areas is high and accelerating all over the world (Seebens et al. 2017; Pyšek et al. 2020), with heavy and rising associated economic costs (Diagne et al. 2021). Modern biological invasions constitute a unique form of global environmental change, profound enough to surpass natural drivers of selection and dispersal, creating novel biological communities that would have never emerged through natural processes (Ricciardi 2007). In the ecological domain, the integration of novel species in the ecosystems can generate fundamental alterations to the structure of native communities and ecosystem functioning (e.g., Vitousek et al. 1996; Kideys 2002; Pranovi et al. 2006; Galil 2007; Ehrenfeld 2010; Vilà et al. 2011; Katsanevakis et al. 2014a; Howard et al. 2019), often with detrimental losses of native biodiversity (e.g., Clavero et al. 2009; Sala et al. 2011; Harper and Bunbury 2015; Bellard et al. 2016; Doherty et al. 2016; García-Gómez et al. 2020). The provision of ecosystem services can also be strongly affected by the impacts of biological invasions (Vilà et al. 2010; Katsanevakis et al. 2014a; Vilà and Hulme 2017; Castro-Díez et al. 2019). Furthermore, invasive species pose a threat to human health through a variety of mechanisms such as pathogen transmission, intoxication, and envenomation (Schaffner et al. 2013; Hulme 2014; Galil 2018; Peyton et al. 2019; Bédry et al. 2021).

Recent works highlighted that biological invasions can also have positive outcomes (Katsanevakis et al. 2014a; Vimercati et al. 2020), for example by creating novel ecosystems that may support native biodiversity and ecosystem functioning (Hobbs et al. 2009; Schlaepfer et al. 2011; Evers et al. 2018), providing ecosystem services (Katsanevakis et al. 2018; Apostolaki et al. 2019), and contributing to human well-being (Shackleton et al. 2019; Sfriso et al. 2020). The positive impacts of alien species are dependent on societal perception and different cultural values and motivations (Simberloff et al. 2013) and are commonly underestimated (Katsanevakis et al. 2014a). Nevertheless, their study is receiving increasing attention (Vimercati et al. 2020) and, in some cases, alien species can even constitute targets for protection and conservation (Schlaepfer et al. 2011; Mačić et al. 2018).

Impact assessment (including both negative and positive impacts of biological invasions) is an important but challenging process aiming to quantify the magnitude of changes and prioritise management and mitigation of undesired effects (Parker et al. 1999; Kumschick et al. 2012; Ricciardi et al. 2013; Simberloff et al. 2013; Ojaveer et al. 2015). The utilisation of conceptual frameworks that classify in a standard way the effects of alien species on ecosystems is essential in the process (Blackburn et al. 2011; Bacher et al. 2018). Katsanevakis et al. (2014a) assessed the impacts of marine alien species on biodiversity and ecosystem services utilising a framework that emphasised the robustness of the reported evidence and

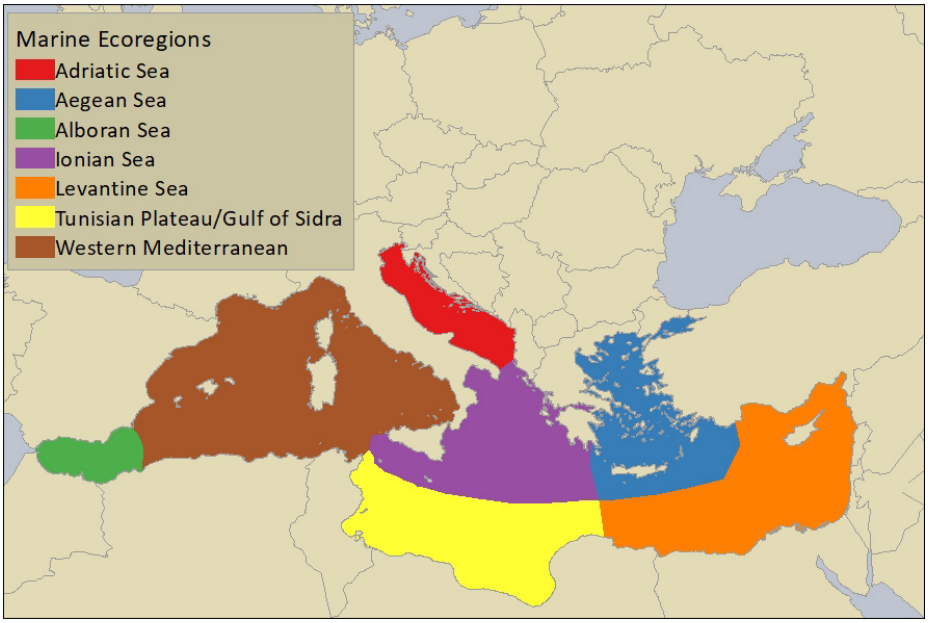


Figure 1. Mediterranean Sea ecoregions (*sensu* Spalding et al. 2007). The present review covered all seven Mediterranean ecoregions.

the ecological mechanisms of negative and positive impacts on both biodiversity and ecosystem services. Blackburn et al. (2014) proposed a classification framework of impact magnitude levels for a series of ecological mechanisms through which alien species impact individuals, populations, and communities. Difficulties that hinder impact assessments, such as a wide range of taxonomic groups, various types of affected habitats, estimation of impact magnitude, and spatial quantification of impacts, can be overcome through the application of such schemes (Kumschick et al. 2015; Katsanevakis et al. 2016; Nentwig et al. 2016; Galanidi et al. 2018).

The Mediterranean Sea is a hotspot of biodiversity with a high level of endemism (Coll et al. 2010). It is divided into seven marine ecoregions (Figure 1), each with a distinct suite of oceanographic and topographic features and relatively homogeneous species composition (Spalding et al. 2007). In addition, the Mediterranean is a hotspot of biological invasions, particularly throughout its eastern part, having the highest number of introduced species than any other sea region of the world (Costello et al. 2021). In the same easternmost sectors, under a rapid warming trend, many thermally-sensitive native populations have collapsed in the past few decades (Yeruham et al. 2015; Rilov 2016; Albano et al. 2021) and in some cases alien species are the only ones that can sustain ecosystem functions. Hence, a shift in conservation strategies from protecting native biodiversity to protecting ecosystem functions (thus also including some alien species as conservation targets) has been recently proposed (Katsanevakis et al. 2020a).

Approximately 1,000 species are estimated to have been introduced in Mediterranean ecoregions (Zenetos et al. 2010, 2012), with more than half

having established populations (Galil et al. 2016; Zenetos et al. 2017; Zenetos and Galanidi 2020) and exhibiting an accelerating rate of establishment success during recent years (Zenetos et al. 2022). Biological invasions in the Mediterranean have caused large-scale biogeographic modifications, range shifts of native species, population declines or even local extinctions (Galil 2007; Edelist et al. 2013; Katsanevakis et al. 2014a). Previous assessments of the spatial variation of impacts in the Mediterranean Sea indicated strong spatial heterogeneity, not significantly correlated to alien species richness (Katsanevakis et al. 2016). As the situation changes fast, with many new alien species becoming invasive and expanding rapidly in the last few years (e.g., Dimitriadis et al. 2020; Zenetos and Galanidi 2020), and as new knowledge accumulates, a regular reassessment of impacts is important to adequately inform management measures.

With the purpose to update the current knowledge on invasive alien marine species' impacts on Mediterranean ecosystems, a new systematic literature review was conducted building upon the work of Katsanevakis et al. (2014a). To accomplish this, we compiled and assessed published available information on alien and cryptogenic species impacts to: (i) identify impactful species for biodiversity, ecosystem services, and human health, updating previous knowledge, (ii) assess the magnitude and mechanisms of their impacts, and their variability across Mediterranean Sea ecoregions, and (iii) propose an inventory of the impactful marine alien species of the Mediterranean Sea.

Materials and methods

List of assessed species

A list of targeted taxa for impact assessments was compiled, including marine alien and cryptogenic species flagged as of "High Impact" in the European Alien Species Information Network (EASIN; Katsanevakis et al. 2012) or as high-impact or invasive in recently published reviews (e.g. Otero et al. 2013; Katsanevakis et al. 2014a; Karachle et al. 2017; Galanidi et al. 2018; Zenetos et al. 2018; Peyton et al. 2019; Tsiamis et al. 2020). Based on their expert knowledge, the authors added to the list further invasive species not previously considered by EASIN or the aforementioned reviews. Diatoms, dinoflagellates and other microalgae were not included in the initial species list, based on Gómez (2008, 2019) who argued about the difficulties and uncertainties in defining the native distribution of such species. Tsiamis et al. (2021) have agreed that there are large gaps in knowledge on unicellular plankton species and that more work is needed on marine non-indigenous phytoplankton species in Europe before tagging any phytoplankton species as alien. In total, 103 alien and cryptogenic species belonging to 16 different taxonomic groups were assessed for their impacts on biodiversity, ecosystem services, and human health in the Mediterranean Sea.

Literature review

A bibliographical review was performed for each targeted species, using the Scholar Google search engine, as it includes grey literature (i.e. technical reports, PhD and MSc theses, and conference proceedings) in addition to peer-reviewed journal articles. Species previously assessed by Katsanevakis et al. (2014a) were updated by searching for more recent publications (between 2013 and March 2021), whereas the bibliographic search was performed without chronological restrictions for those species not previously assessed. For each species, eligible documents were those with the following set of keywords (anywhere in the article): <species name> AND "impact" AND "Mediterranean". The search provided 62,043 articles (sum of the articles found for each separate species search) but included duplicates as some articles covered more than one target species. Potentially eligible papers to be included in the review were initially screened based on their titles and abstracts; for those that passed the initial screening, the full text was reviewed. At a later stage, taxonomic experts further enriched the list of selected studies with additional documents that had not been found through the literature search. In total, 593 studies that included relevant information on negative or positive impacts of alien and cryptogenic species were retained for the analysis.

From each retained paper, the following information was extracted and coded: DOI/link; short reference; year of publication; Mediterranean ecoregion (according to Spalding et al. 2007; Figure 1); species name and phylum following WoRMS (WoRMS Editorial Board 2021); and reported negative or positive impact on biodiversity, ecosystem services, and human health, type of evidence, mechanism of impact, magnitude of impact and ecosystem engineer type, if relevant (the latter two only for impacts on biodiversity). Only impacts referring to the Mediterranean Sea were included; potential impacts, e.g. based on evidence in non-Mediterranean regions, were not considered.

Framework for impact assessment

Type of evidence refers to the robustness of the methodological approach that was applied to assess the impact. As such, the robustness of the reported evidence was classified into six different types corresponding to three strength of evidence categories (Katsanevakis et al. 2014a, 2016). The six evidence types were: (i) manipulative experiments and (ii) natural experiments (high strength of evidence), (iii) direct observations, (iv) modelling, (v) non–experimental-based correlations (medium strength of evidence), and (vi) expert judgement (low strength of evidence). Manipulative experiments are field or laboratory experiments that include treatments/control and random selection of experimental units. In natural experiments, the experimental units (i.e. controls or impacted areas) are selected by nature

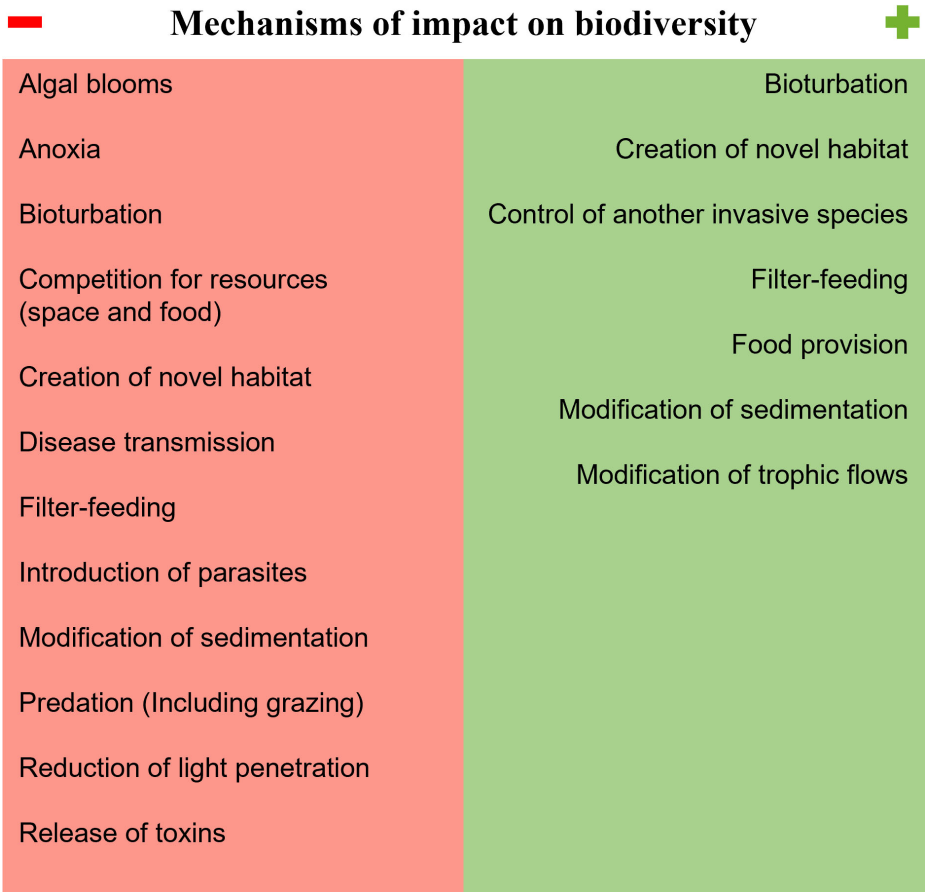


Figure 2. Main mechanisms through which marine alien species impact biodiversity (*sensu* Katsanevakis et al. 2014a). Red background refers to negative impacts and green background refers to positive impacts.

(i.e. not randomly). Direct observations are direct raw measurements of the impact about which there is no doubt (e.g. fouling in aquaculture or on fishing gear, new commodities in fish markets). Modelling refers to modelled consequences on biodiversity, ecosystem services and human health derived from ecosystem models. Non-experimental-based correlations refer to significant correlations between the targeted species and the investigated impact, but not based on an experimental design for data collection (e.g. there was a negative correlation between the biomass of an alien predator and the biomass of its native prey). Expert judgement is a qualitative or semi-quantitative assessment that relies on the empirical knowledge of experts based on the species' traits or the reported impact of similar or the same species in a different geographical region.

Each reported impact was linked to the underlying mechanism. Mechanisms of impact were classified according to Katsanevakis et al. (2014a), with some additions (see Figure 2 for biodiversity; Figure 3 for regulating and maintenance ecosystem services; Figure 4 for cultural, provisioning ecosystem services, and human health). The impact magnitude was classified following the five-level classification proposed by Blackburn et al. (2014), i.e. minimal, minor, moderate, major, and massive (Table 1),

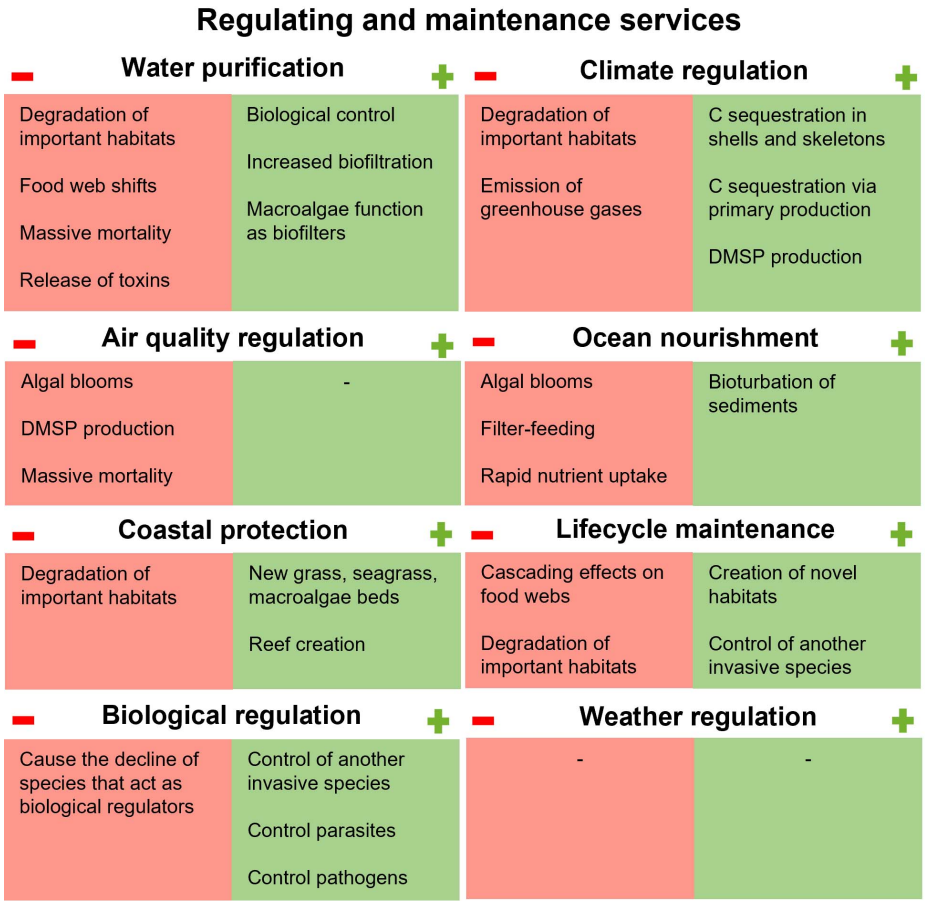


Figure 3. Main mechanisms through which marine alien species impact regulating and maintenance ecosystem services (*sensu* Liquete et al. 2013). Red background refers to negative impacts while green background refers to positive impacts. The classification of impacts on ecosystem services was based on Katsanevakis et al. (2014a).

considering also Volery et al. (2020). The selection of marine ecosystem services classification was based on Liquete et al. (2013), who proposed a classification of 14 marine ecosystem services grouped as "provisioning", "regulating and maintenance", and "cultural" (Table 2). Ecosystem engineers were categorised into four different types: structural, chemical, light engineers, and bioturbators (Wallentinus and Nyberg 2007; Berke 2010; Katsanevakis et al. 2014a; Figure 5).

Analyses

In addition to descriptive statistics, contingency table analyses were conducted to quantify the degree of association between selected pairs of variables. The hypothesis of independence between such pairs was tested via chi-square tests. To avoid having cells with < 5 observations, certain categories within each variable were grouped. Hierarchical cluster analysis, using Euclidean distance and square-root transformation of the number of impact records by each mechanism for each species, was performed to determine the similarities of the analysed species in terms of the mechanisms of their impacts for both negative and positive records.

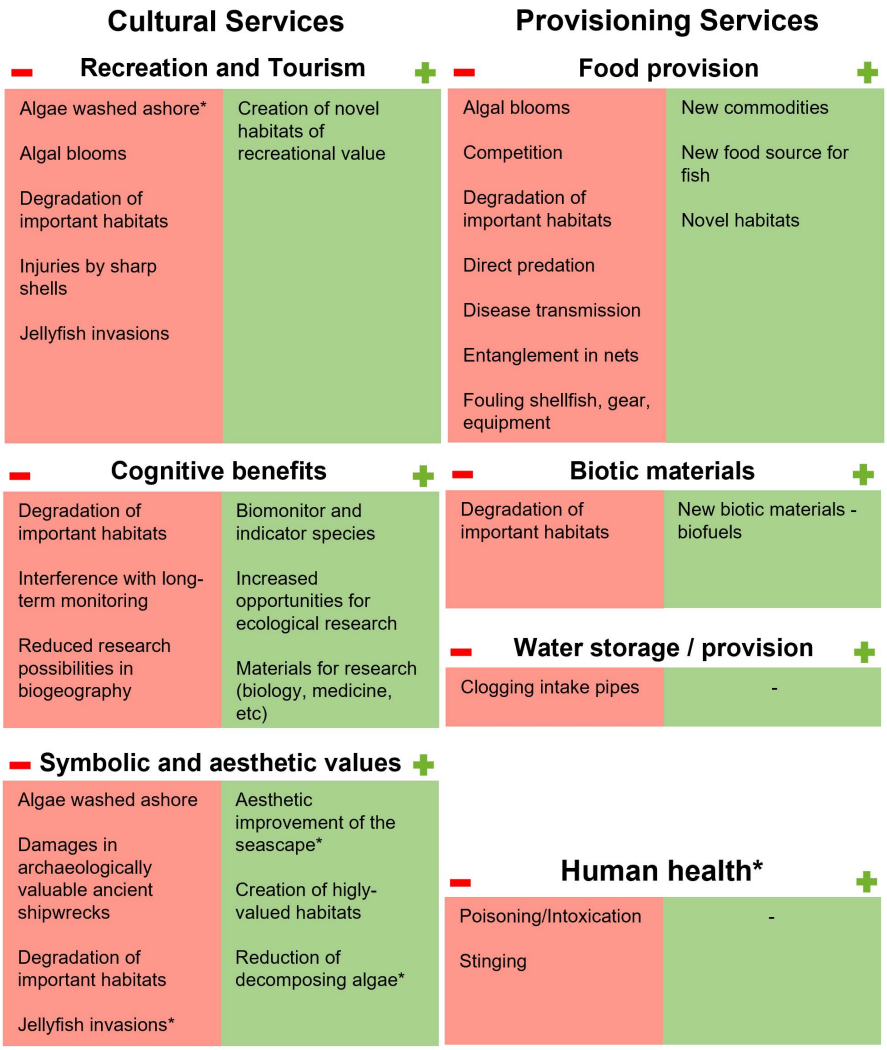


Figure 4. Main mechanisms through which marine alien species impact provisioning, cultural ecosystem services (*sensu* Liquete et al. 2013) and human health. Red background refers to negative impacts while green background refers to positive impacts. The classification of impacts on ecosystem services was based on Katsanevakis et al. (2014a), with the exception of categories marked with an asterisk (*) that are new.

To test the hypothesis that the magnitude of reported impacts on biodiversity increases with the residence time, i.e. the number of years passed since the first detection of the species in the Mediterranean Sea, we followed two different approaches. In the first approach, a one-way ANOVA was conducted with the maximum reported magnitude of impact on biodiversity for each species as the categorical factor and the residence time as the dependent variable. Levene's test was applied to test homogeneity of variances, and Tukey's honestly significant difference (HSD) procedure for multiple range tests. In the second approach, we created an impact score in which for each species all reports of impacts were summed up in a weighted sum with varying weights depending on the magnitude of impact: massive 4; major 3; moderate 2; minor 1; minimal 0. The relationship between the impact score and the residence time of each species was investigated with a linear regression approach. All analyses were conducted using Statgraphics Centurion XVI.

Table 1. Impact magnitude classification levels with criteria description (adapted from Blackburn et al. 2014, considering also Volery et al. 2020), referring to both negative and positive impacts.

Impact magnitude	Criteria description
Minimal	No effect on fitness of native species; negligible impact on native species due to competition, predation, parasitism, toxicity, bio-fouling, food provision or control of another invasive species; no effects on ecosystem processes and ecosystem functioning; no chemical, physical or structural impact on the ecosystem (not an ecosystem engineer).
Minor	Impact on individual of a native species due to competition, predation, parasitism, toxicity, bio-fouling, food provision, or control of another invasive species without substantial population changes; minor impact on ecosystem processes and ecosystem functioning with no related population changes; any environmental or habitat alterations in chemical, physical or structural characteristics do not result in population changes.
Moderate	Native species population changes due to competition, predation, parasitism, toxicity, bio-fouling, food provision or control of another invasive species but without changes in community composition; or impact on ecosystem processes and ecosystem functioning resulting in population declines/increases but no substantial change in species composition; or ecological engineering, resulting in population declines/increases but no substantial change in community composition.
Major	Changes in community composition through local or global extinction (negative) or re-establishment (positive) of at least one native species, because of competition, predation, parasitism, toxicity, bio-fouling, food provision or control of another invasive species; impact on ecosystem processes and ecosystem functioning resulting in species composition changes; or ecological engineering, resulting in change in community composition. Major magnitude applies when under the hypothetical scenario of the alien species extinction, the induced changes are considered as reversible within 10 years or within 3 generations of the extinct/re-established native taxon/ -a, whichever is longer.
Massive	Same conditions as in "major" magnitude, but changes are considered as irreversible under the hypothetical scenario of the alien species extinction, within 10 years or within 3 generations of the extinct/re-established native taxon/-a.

Results

Impact matrix

The 593 studies on the 103 alien and cryptogenic species resulted in 1,343 records of negative and positive impacts on biodiversity, ecosystem services, and human health (Table 3). A detailed description of impacts for each species is given in the online Supplementary material Appendix 1. Among the analysed taxa, Osteichthyes was the most numerous group (24 species), followed by Mollusca (17 species), and Arthropoda (Crustacea) (14 species), whereas 25 macroalgae were analysed, belonging to Rhodophyta (12 species), Chlorophyta (8 species), and Ochrophyta (5 species). Biodiversity was impacted by 70% of the studied species (72 taxa; Table 3), whereas the remaining ones (30%) showed no reported impacts on biodiversity. Only 3% of the studied species had only positive effects on biodiversity, whereas 27% had only negative ones. In most cases (40%) the studied species impacted biodiversity both negatively and positively.

Among the 72 species impacting biodiversity, 38 represented ecosystem engineers that caused alterations to the studied ecosystem as bioconstructors (structural engineers), regulators of light penetration (light engineers), modifiers of the chemical matrix of the environment (chemical engineers), and bioturbators (Table 3). Most ecosystem engineers were macroalgae (phyla Ochrophyta, Chlorophyta, and Rhodophyta) and Mollusca.

Table 2. The applied marine ecosystem services classification scheme, with a description of each service (*sensu* Liquete et al. 2013).

Ecosystem service	Category	Description
Food provision	Provisioning	Provision of biomass from the marine environment for human consumption. This includes all industrial, artisanal and recreational fishing activities and aquaculture.
Water storage and provision	Provisioning	Provision of water for human consumption and other uses. In the marine environment, these uses are mainly associated with coastal lakes, deltaic aquifers, desalination plants, industrial cooling processes, and coastal aquaculture in ponds and raceways.
Biotic materials and biofuels	Provisioning	Provision of biomass or biotic elements for non-food purposes, including medicinal (e.g. drugs, cosmetics), ornamental (e.g. corals, shells) and other commercial or industrial purposes, such as fishmeal, algal or plant fertilisers, and biomass to produce energy or biogas from decomposing material.
Water purification	Regulating and maintenance	Biochemical and physicochemical processes involved in the removal of wastes and pollutants from the aquatic environment, including treatment of human waste, dilution, sedimentation, trapping or sequestration (e.g. of pesticide residues or industrial pollution); bioremediation; oxygenation of "dead zones", filtration and absorption; remineralisation; and decomposition.
Air quality regulation	Regulating and maintenance	Regulation of air pollutant concentrations in the lower atmosphere.
Coastal protection	Regulating and maintenance	Natural protection of the coastal zone against inundation and erosion from waves, storms or sea level rise by biogenic and geologic structures that disrupt water movement and thus stabilise sediments or create protective buffer zones.
Climate regulation	Regulating and maintenance	The ocean acts as a sink for greenhouse and climate active gasses, as inorganic carbon is dissolved into the seawater and used by marine organisms, a percentage of which is sequestered; perennial large algae and higher plants can store carbon for longer periods.
Weather regulation	Regulating and maintenance	Influence on the local weather conditions, e.g. the influence of coastal vegetation and wetlands on air moisture and, eventually, on the saturation point and cloud formation.
Ocean nourishment	Regulating and maintenance	Natural cycling processes leading to the availability of nutrients in seawater for the production of organic matter.
Lifecycle maintenance	Regulating and maintenance	The biological and physical support to facilitate the healthy and diverse reproduction of species; this mainly refers to the maintenance of key habitats that act as nurseries, spawning areas or migratory routes.
Biological regulation	Regulating and maintenance	Biological control of pests. The control of pathogens especially in aquaculture installations, the role of cleaner fish in reefs, biological control on the spread of vector borne human diseases, and the control of invasive species.
Symbolic and aesthetic values	Cultural	This is about the exaltation of senses and emotions by seascapes, habitats or species, and values put on coastal natural and cultural sites, and on the existence and beauty of charismatic habitats and species such as corals or marine mammals.
Recreation and tourism	Cultural	Opportunities that the marine environment provides for relaxation and entertainment, including coastal activities such as bathing, sunbathing, snorkelling, SCUBA diving, and offshore activities such as sailing, recreational fishing, and whale watching.
Cognitive effects	Cultural	Inspiration for arts and applications (e.g. architectural designs inspired by marine shells, medical applications replicating marine organic compounds), material for research and education (e.g. as test organisms for biological experiments), information and awareness (e.g. respect for nature through the observation of marine wild life).

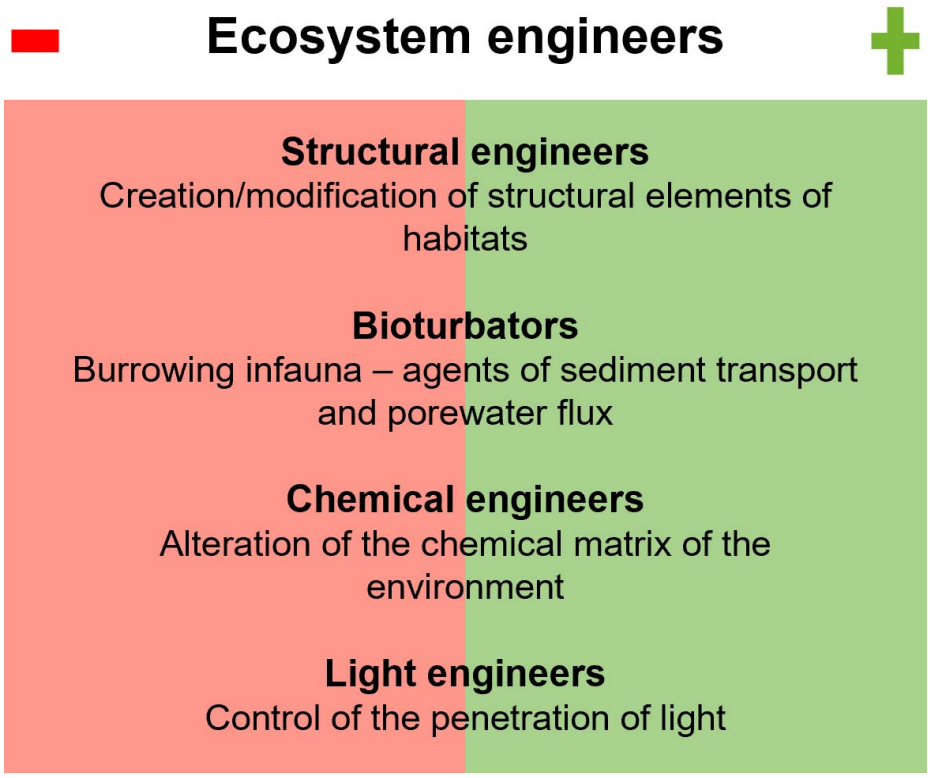


Figure 5. Ecosystem engineer types with impacts on biodiversity (both negative and positive).

Food provision (commercial and recreational fishing, aquaculture) was the most impacted ecosystem service, with 33 species causing negative impacts, 18 positive impacts, and 14 both (Table 3). Osteichthyes were the taxonomic group including the highest number of species with an impact on food provision (19 species). All impacts caused by macroalgae (in total 15 species) on this service were negative. The cultural ecosystem service of "cognitive effects" had the second-highest number of impactful species, with most of the studied taxa affecting this service positively, as they constituted model species for biomonitoring or *in vitro* research studies. Among regulating and maintenance services, "life-cycle maintenance" and "climate regulation" were affected by the highest number of species. Human health impacts were all negative, caused by 9 species.

Impacts on biodiversity

More negative than positive impacts on biodiversity were reported, with 468 records (78%) against 129 (22%) (Figure 6A). *Caulerpa cylindracea* was the invasive species for which most negative impacts on biodiversity were reported, with 53 cases. This chlorophyte of Australian origin thrives in a variety of habitats, depths and environmental conditions, and negatively affects species and communities in multiple ways (see Appendix 1). The species is widespread in the Mediterranean and so are its effects on biodiversity. *Womersleyella setacea* and *Lophocladia lallemandii* followed in terms of negative impact records. These invasive rhodophytes form dense

Table 3. Impact Matrix: Negative (red) and positive (green) impacts of marine alien and cryptogenic species on biodiversity and ecosystem services of the Mediterranean. Colour indicates strength of evidence (vivid colours for high strength of evidence, medium for medium strength, pale colours for low strength). For species without reported impacts or minimal impacts grey cells are depicted for biodiversity and blank cells for ecosystem services and human health. Type of evidence is indicated for each impact: Manipulative Experiments, E; Natural Experiments, N; Direct Observations of impact, O; Modelling, M; non-experimental-based Correlations, C; Expert Judgement, J. (Cr): Cryptogenic species.

	Impact on biodiversity			Impact on marine ecosystem services and human health														
				Provisioning			Regulating and maintenance								Cultural			Health
Alien Species	Minimal / No impact	Impact on species / communities	Ecosystem engineer	Food provision	Water Storage and provision	Biotic materials and biofuels	Water purification	Air quality regulation	Coastal protection	Climate regulation	Weather regulation	Ocean nourishment	Lifecycle maintenance	Biological regulation	Symbolic and aesthetic values	Recreation and tourism	Cognitive benefits	Human health
Cercozoa																		
Haplosporidium pinnae (Cr)		NOJ																
Foraminifera																		
Amphistegina lobifera		CJ J	O						J	J							NJ	
Ochrophyta																		
Chrysonephos lewisii		O	O												O	O		
Rugulopteryx okamurae		NOCJ	NO N	O					O				NO		O	O	O	
Sargassum muticum		J	OCJ O	O	J	J	J		J				J J		O	O	J EJ	
Stypopodium schimperi		OJ	OJ O									J			O	OJ	EJ	
Undaria pinnatifida		J	O O	O			J					J				O	EJ	
Chlorophyta																		
Caulerpa cylindracea		ENOMCJ	NOCJ ENOJ	J		J			EJ			J	ENOMJ EJ		J	J	J EOCJ	
Caulerpa taxifolia		ENOJ	ENOJ NO	OJ		J			J EJ				NJ		J	J	J J	
Caulerpa taxifolia var. *distichophylla*		EJ	N N	O									J					
Cladophora patentiramea															O	O		
Codium arabicum		J													O	O		
Codium fragile subsp. *fragile*		OJ O	OJ EO	O		J		J		J			J		O	O	J C	
Codium parvulum		J		O											O	O		
Halimeda incrassata		N	N N															
Rhodophyta																		
Acrothamnion preissii		ENOCJ	OJ O	O									J		J	J	J	
Agarophyton vermiculophyllum		CJ	NOJ NO	O		J							J		O O	O	J CJ	
Antithamnion nipponicum		J		O														
Asparagopsis armata		EJ O	OCJ OC	O								J			J	J	J EJ	
Asparagopsis taxiformis		EOCJ	N									J	J				EJ	
Bonnemaisonia hamifera																		
Galaxaura rugosa		J													O	O		
Ganonema farinosum (Cr)																		
Grateloupia turuturu		J	OJ O	O														
Lophocladia lallemandii		ENOCJ	NOCJ NO	J		J			J J			J	J		OJ	J	J	
Polysiphonia morrowii																		
Womersleyella setacea		ENOCJ	NOC OC	OJ		J	J		J J			J	ENOJ		J	J	J	
Tracheophyta																		
Halophila stipulacea		C O	O OC	J			J		J	NJ		J	J				C	
Porifera																		
Paraleucilla magna		EJ		O														
Cnidaria																		
Macrorhynchia philippina																		OJ
Oculina patagonica (Cr)		OCJ	O O	J		J							J		J	J	J E	
Rhopilema nomadica		OJ	E	O	O										O	OCJ	CJ	OJ
Ctenophora																		
Mnemiopsis leidyi		ENC J		O														

Table 3. (continued).

| | | |

Table 3. (continued).

Herklotsichthys punctatus					O															
Lagocephalus sceleratus		OMJ			OMJ															OJ
Nemipterus randalli		CJ			J	O													NC	
Parexocoetus mento																				
Parupeneus forsskali		C			C	O														
Pempheris rhomboidea		OMJ	J	J																
Plotosus lineatus		CJ			O															OJ
Pterois miles		O														J				OJ
Sargocentron rubrum		OC	J	J	O															
Saurida lessepsianus		MJ			J	O													N	
Scomberomorus commerson					O															
Siganus luridus		ENMCJ	MJ	J	J	J	O	J	J			J			EJ		J	J	J	OJ
Siganus rivulatus		ENMCJ	MJ	J	J	J	O	J	J			J			EJ		J	J	J	J
Sphyraena chrysotaenia		C				O														
Torquigener flavimaculosus																				J
Upeneus moluccensis		NC			C	O														
Upeneus pori		NC			C	O														

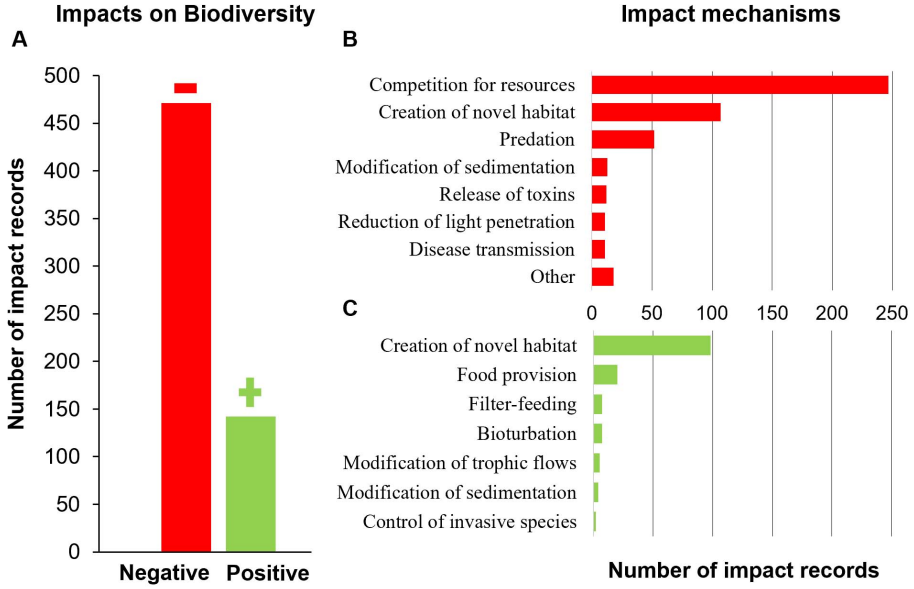


Figure 6. A) Number of impact records that resulted from the review analysis to impact biodiversity. Number of impact records by mechanism through which alien species impacted biodiversity B) negatively or/ and C) positively.

algal turfs that overgrow other species and alter ecologically important habitats, with negative implications in benthic communities. Although widespread in the Mediterranean, their effects were mainly reported from the western Mediterranean ecoregion. Apart from macroalgae, the mollusc *Brachidontes pharaonis* and the fishes *Siganus luridus* and *Siganus rivulatus* were the species with most negative impact records among the studied taxa. The Erythrean *B. pharaonis* is an old invader of the Mediterranean, with a wide range of distribution, but it did not exhibit an alarming invasive behaviour until the late 1990s. Subsequently, its populations exploded in many eastern Mediterranean localities, becoming dominant in shallow rocky reef platforms with extremely high densities, outcompeting native species and shaping community composition (see Appendix 1). The

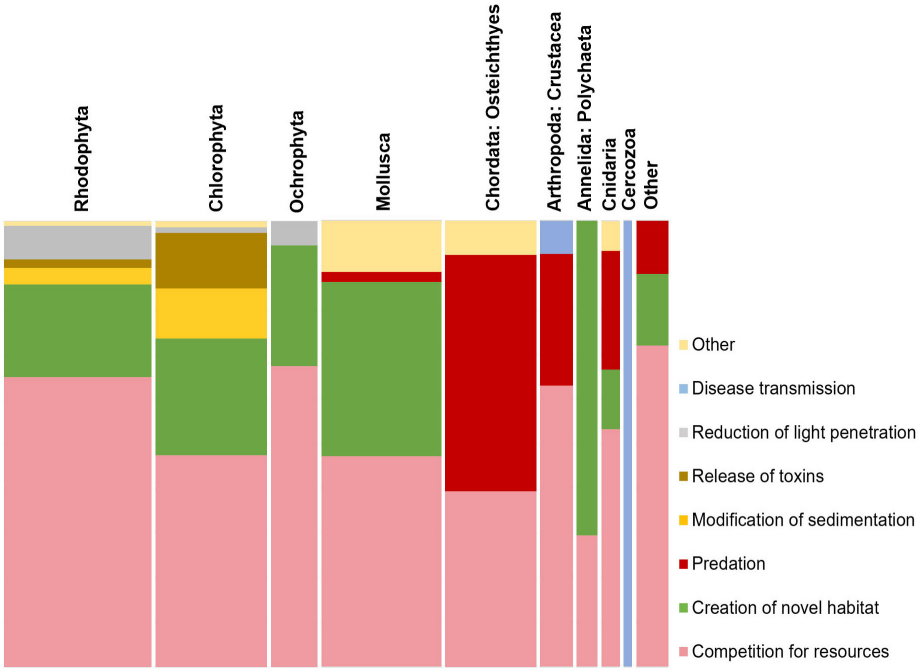


Figure 7. Mosaic chart of mechanisms of negative impacts on biodiversity for the studied different phyla.

Lessepsian invaders *Siganus* spp. dominate fish communities in many parts of the eastern Mediterranean and have caused detrimental losses on Mediterranean macroalgal communities through their herbivory (see Appendix 1 for more information).

Caulerpa cylindracea was also the species most reported for its positive impacts, with 12 records, followed by *B. pharaonis* and the serpulid *Ficopomatus enigmaticus*. Although the dense populations of *C. cylindracea* constitute a nuisance for the majority of native biota, it can also facilitate several other species, from seagrasses to invertebrates. *Brachidontes pharaonis* has acquired a functional role in Mediterranean ecosystems and contributes significantly as a structural ecosystem engineer, as a filter-feeder that reduces turbidity and increases light penetration, and as a food source for native biota. *Ficopomatus enigmaticus* is a reef-building structural engineer that provides novel habitat for many benthic taxa.

Negative impacts were caused by a variety of mechanisms (Figure 6B, C; Figure 7), significantly differing in frequency by taxonomic group (chi-square test; keeping the three most frequent mechanisms and grouping all others; keeping the six most frequent taxonomic groups and grouping all others; $p < 0.001$). Competition for resources was the most reported mechanism of negative impacts with almost 250 records, followed by the creation of novel habitat, and predation (Figure 6B). This was the case for most studied phyla except Chordata (Osteichthyes), Annelida (Polychaeta), and Cercozoa (Figure 7). Osteichthyes caused negative impacts mostly by preying on native biota. *Hydroides elegans* and *F. enigmaticus*, the two studied alien polychaetes, mainly affected other species through the creation of novel

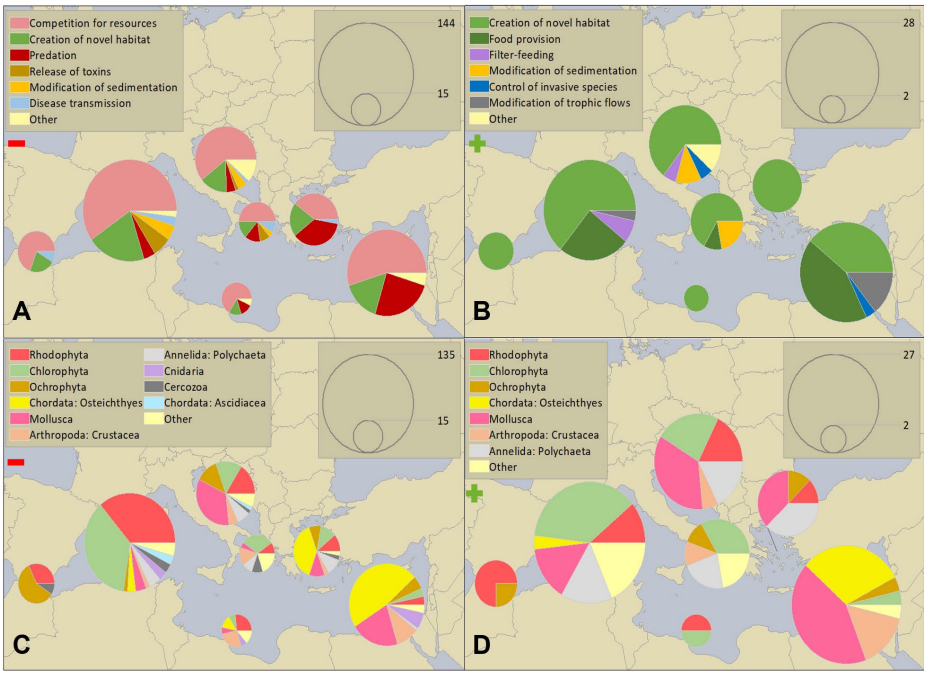


Figure 8. Geographical variation of the A) negative and B) positive mechanisms of impact on biodiversity by Mediterranean ecoregion and of analyzed alien phyla with C) negative and D) positive impacts on biodiversity per Mediterranean ecoregion. The size of the pie charts reflects the number of reported cases (the inset indicates the minimum and maximum sizes).

habitat. This was also an important mechanism of negative impacts for macroalgae such as *L. lallemandii*, *C. cylindracea*, *Caulerpa taxifolia* and molluscs such as *B. pharaonis*, and *Spondylus spinosus*. *Haplosporidium pinnae*, the sole representative of Cercozoa, has been associated with the disease that has caused the extinction of the endemic bivalve *Pinna nobilis* from almost the entire Mediterranean Sea, except for a small number of refugia. The creation of novel habitat was the most common mechanism of positive impacts on biodiversity accounting for 65% of the reported positive cases (Figure 6C). Species such as *F. enigmaticus*, *S. spinosus*, the bivalves of the genus *Magallana/Crassostrea* (see the notes in the Appendix 1 for the taxonomic status of the genus), and the rhodophyte *Asparagopsis armata* create novel habitats that support a variety of species.

Analysis of impacts by ecoregion revealed that interspecific competition is the most important mechanism generating negative impacts on biodiversity in all Mediterranean ecoregions (Figure 8A); nevertheless, the frequency of the various mechanisms significantly differed by ecoregion (chi-square test; keeping the three most frequent mechanisms—competition, creation of novel habitat, predation—and grouping all others; $p < 0.001$). The creation of novel habitat was the second most reported negative impact mechanism in western and central Mediterranean ecoregions. On the contrary, predation was the second most impactful mechanism in the eastern Mediterranean ecoregions (Figure 8A). The frequency of the mechanisms of reported positive impacts also differed by ecoregion (chi-square test; keeping the two most frequent mechanisms and grouping all others; excluding ecoregions

with < 5 records; p = 0.008). Structural ecosystem engineers that create novel habitats were the main contributors to positive impacts in all Mediterranean ecoregions, except for the Levantine Sea where positive impacts of food provision slightly exceeded the creation of novel habitat (Figure 8B). Food provision to native biodiversity was also important in the western Mediterranean and the Ionian Sea (Figure 8B).

There was significant variation in the taxonomic composition of the species that caused negative impacts on biodiversity among ecoregions (chi-square test; keeping the five most reported phyla and grouping all others; p < 0.001) (Figure 8C). In the western Mediterranean, the most reported negative impacts were caused by invasive Rhodophyta and Chlorophyta, whereas in the Levantine and the Aegean Sea by Osteichthyes, and in the Adriatic Sea by Mollusca (Figure 8C). *Caulerpa cylindracea*, *L. lallemandii*, *W. setacea*, *C. taxifolia*, and *Acrothamnion preissii* were among the chlorophytes and rhodophytes with negative effects in the western Mediterranean whereas, in the Levantine Sea, *B. pharaonis*, *S. luridus* and *S. rivulatus* were the species with the most recorded impacts. *Siganus luridus* was also the species that accounted for most of the recorded negative impacts in the Aegean Sea. Negative impacts caused by Crustacea had an important share of total impacts in the Tunisian plateau/Gulf of Sidra, the Levantine, and the Ionian Sea, but they had little relevance in the western Mediterranean and the Alboran Sea (Figure 8C). The Alboran Sea has been plagued by the negative impacts of the brown alga *Rugulopteryx okamurae*, a recent invader that has caused detrimental effects on local ecosystems (see Appendix 1 for more information).

There was also significant variation in the taxonomic composition of the species that caused positive impacts on biodiversity among ecoregions (chi-square test; keeping only the three ecoregions with the highest number of records and the four mostly reported phyla, grouping all others; p = 0.01). Macroalgae constituted the bulk of positive impact records for the western Mediterranean, the Alboran Sea, and the Tunisian plateau/Gulf of Sidra and had an important share in total reported positive impacts from the Adriatic and the Ionian Sea (Figure 8D). Mollusca ranked first in terms of reported positive impacts in the Levantine and the Adriatic Sea and had an important share in the western Mediterranean and the Aegean Sea. As creators of novel habitats, Polychaeta contributed to positive impacts in the Aegean, Ionian, Adriatic Sea, and western Mediterranean (Figure 8D). Furthermore, some Osteichthyes were reported to have positive impacts on biodiversity, because of their role in the novel trophic webs, but only in the Levantine Sea.

"Major" was the most reported impact magnitude category for both negative and positive impact records (Figure 9). Nevertheless, the frequency of impact magnitudes substantially differed between negative and positive impacts, with "major" impacts having a significantly higher frequency in

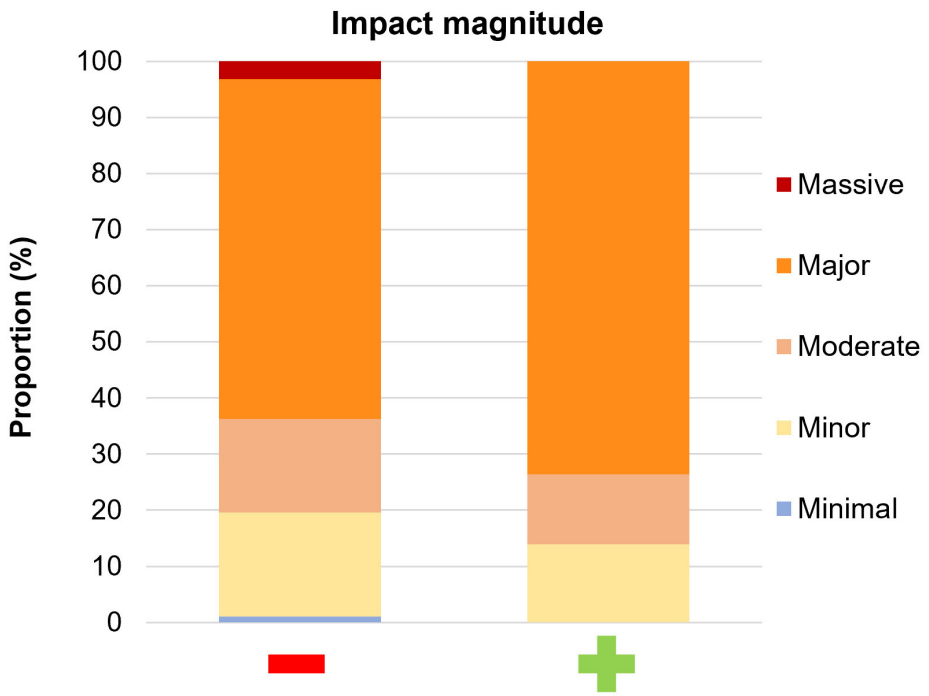


Figure 9. Proportion of impact magnitude categories of negative (left column) and positive (right column) impacts on biodiversity.

positive than negative impacts (chi-square test; excluding minimal and massive magnitude categories due to their low frequencies; $p = 0.011$). Overall, 61% of negative impacts and 74% of positive impacts were classified as major; no positive impacts of massive magnitude were reported. The frequency of the categories of magnitude of impact significantly differed among taxonomic groups (chi-square test; disregarding minimal and massive magnitude categories due to their low frequencies, combining phyla with a small number of records together; $p < 0.001$). Major negative impacts were the primary magnitude category recorded for Rhodophyta, Chlorophyta, Ochrophyta, Mollusca, Polychaeta, Cnidaria, Foraminifera, Ascidiacea, and Bryozoa (Figure 10A). Massive negative impacts were only recorded for Osteichthyes (*Siganus* spp.), Cercozoa (*H. pinnae*), and Ochrophyta (*R. okamurae*) (Figure 10A). Moderate and minor impacts were the most reported for Crustacea. Although the number of records of positive impacts was lower than that of negative impacts, they followed a similar pattern regarding impact magnitude (Figure 10B), with significant differences among taxonomic groups (chi-square test; combining phyla with a small number of records together; $p = 0.011$).

There was no evidence that the magnitude of impact increases with residence time. The average residence time of introduced species did not differ by the maximum reported magnitude of negative (ANOVA; $p = 0.947$) or positive (ANOVA; $p = 0.300$) impacts. The slope of the linear regression between the residence time of introduced species and the negative impact score did not differ significantly from zero ($p = 0.985$), and the intercept (i.e. the average score ± S.E.) was 11.3 ± 3.3 (Figure 11). The slope remained

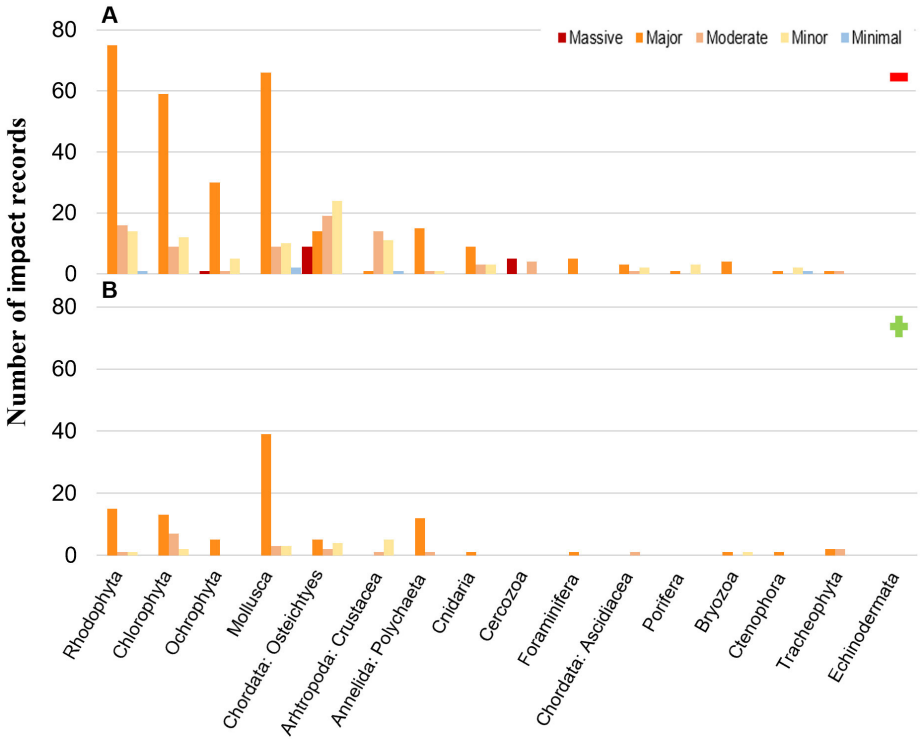


Figure 10. Impact magnitude of A) negative and B) positive impacts on biodiversity per phylum of alien species analysed..

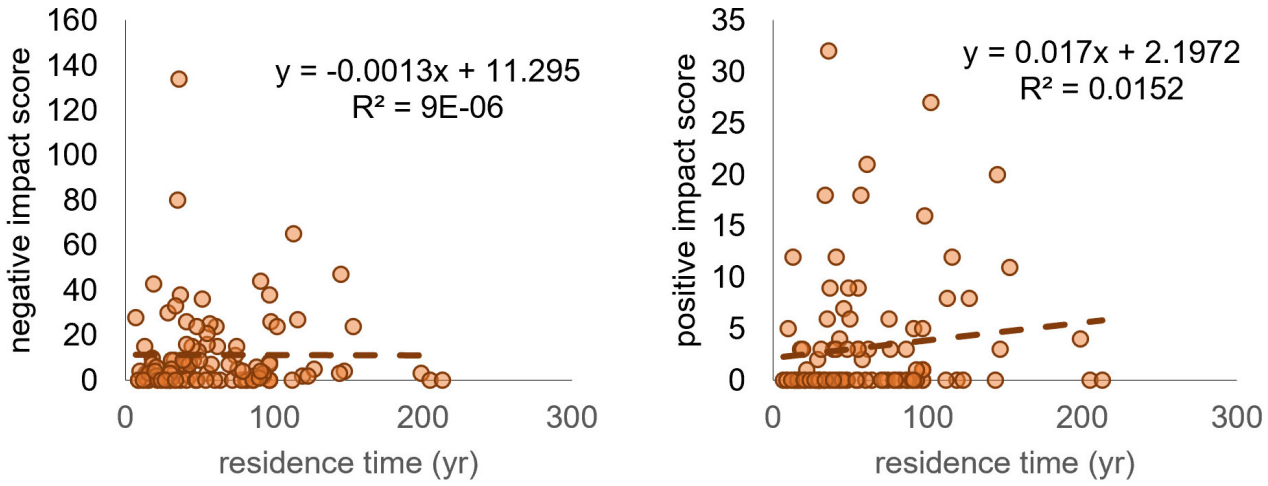


Figure 11. Regressions of negative (left) or positive (right) impact scores in relation to residence time (years since first detection) for each of the assessed species.

statistically not different from zero even when three influential points (with leverage values greater than five times that of an average data point) were removed ($p = 0.529$). Similarly, the slope of the linear regression between the residence time of introduced species and the positive impact score did not significantly differ from zero ($p = 0.215$), and the intercept (i.e. the average score ± S.E.) was 2.2 ± 1.0 (Figure 11). The slope remained statistically not different from zero even when three influential points (with leverage values greater than five times that of an average data point) were removed ($p = 0.057$).

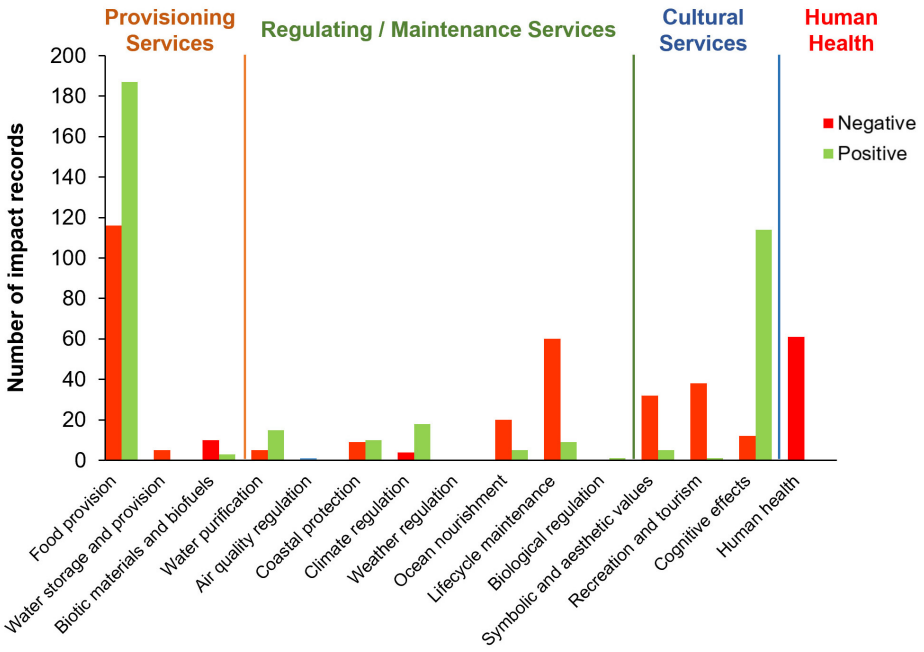


Figure 12. Overview of negative and positive impacts on ecosystem services and human health.

Impacts on ecosystem services

Overall, 685 negative and positive impact records were found to affect provisioning, regulating/maintenance, and cultural ecosystem services, with 312 negative and 373 positive records in total, whereas for human health 61 negative and no positive impacts were recorded. Most impact records on provisioning services were recorded for food provision, with 116 negative and 188 positive records (Figure 12). Negative impacts prevailed over positive for regulating/maintenance services. Still, for several regulating and maintenance services (climate regulation, water purification, coastal protection, and biological regulation) more positive than negative impacts were reported (Figure 12). Among regulating/maintenance services, lifecycle maintenance was the one with the highest number of recorded negative impacts. No impact records were found for weather regulation. For the cultural services "aesthetic values" and "recreation and tourism", 70 negative and only 6 positive impact records were reported. On the other hand, for "cognitive effects" records, positive impacts prevailed by 114 records against only 12 cases of negative impacts.

The frequency of the mechanisms of reported negative impacts on provisioning ecosystem services significantly differed by ecoregion (chi-square test; keeping the four most frequent mechanisms and excluding the Alboran Sea; $p < 0.001$). Fouling shellfish, gear, and equipment of aquaculture facilities was the primary mechanism of negative impacts on provisioning services in the Adriatic Sea, the Ionian Sea, and the western Mediterranean (Figure 13A). Entanglement in nets was the most important mechanism in the Levantine and the Alboran Sea, with a considerable contribution to negative impacts on provisioning services throughout the Mediterranean

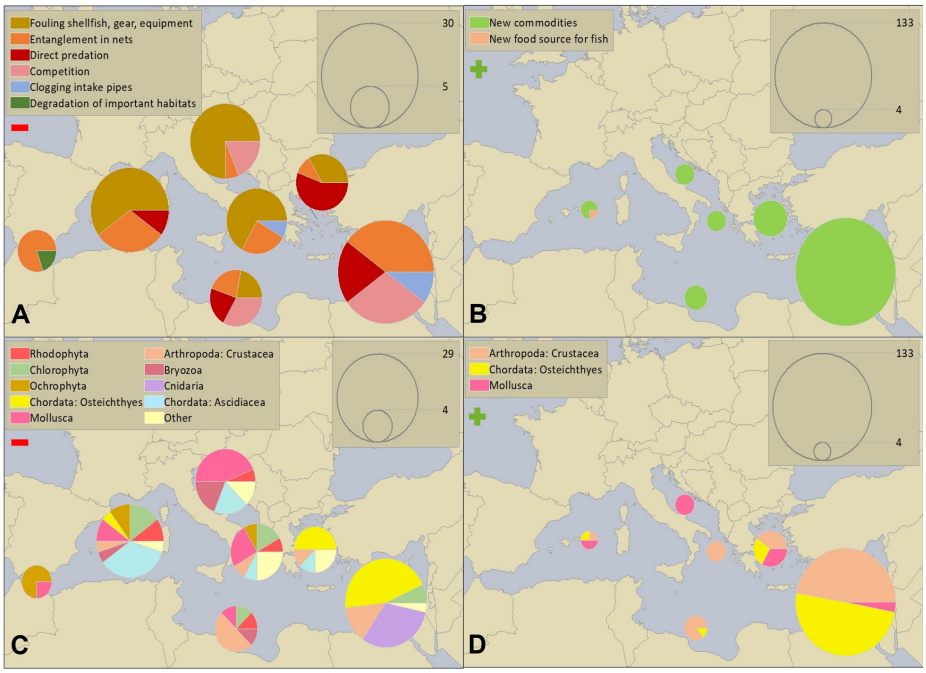


Figure 13. Geographical variation of the A) negative and B) positive mechanisms of impact on provisioning ecosystem services by Mediterranean ecoregion and of analyzed alien species phyla with C) negative and D) positive impacts on provisioning services per Mediterranean ecoregion. The size of the pie charts reflects the number of reported cases (the inset indicates the minimum and maximum sizes).

(Figure 13A). Predation was also a primary mechanism of negative impacts, especially in the eastern Mediterranean. From the analysis of positive impacts by ecoregion on provisioning services (Figure 13B), it became obvious that the Levantine Sea was the main beneficiary, due to new commodities for local fisheries. Most positive impacts were recorded in this ecoregion and significantly declined westwards (Figure 13B). Among all mechanisms positively impacting provisioning services across Mediterranean ecoregions, "new commodities" were by far the most important.

The taxonomic synthesis of the species that negatively impacted provisioning services differed significantly among ecoregions (chi-square test; keeping the four most frequent phyla and merging all the others; excluding the Alboran Sea; $p < 0.001$) (Figure 13C). Ascidians were the major group of negative impacts in the western Mediterranean, with an important contribution also in the Adriatic Sea (Figure 13C). This is due to species such as the alien ascidians *Styela plicata* and *Clavelina oblonga* that commonly foul farmed shellfish and aquaculture equipment. Molluscs (*Pinctada radiata*), bryozoans (*Tricellaria inopinata*), and sponges (*Paraleucilla magna*) also foul aquaculture facilities, introducing negative effects on production. Cnidaria and Osteichthyes were the main groups that impacted provisioning services in the Levantine Sea (Figure 13C). The invasive jellyfish *Rhopilema nomadica* formed massive swarms that became a nuisance for the local fisheries due to entanglement in nets and for water

supply for local power plants and desalination facilities due to blocking of intake pipes. The fish *Lagocephalus sceleratus* was also a major pest for fisheries in the Levantine and the Aegean Sea due to its predation on the catch and the damage caused to fishing gear. Alien crustacean species were also reported to negatively impact the provision of food across multiple ecoregions (Figure 13C). The alien crabs *Callinectes sapidus* and *Portunus segnis* interfered with local fisheries in multiple Mediterranean ecoregions by preying on the catches and by getting entangled in nets. Alien shrimps such as *Metapenaeus monoceros* and *Penaeus pulchricaudatus* have been associated with population declines of the commercially important native shrimp *Penaeus kerathurus* (see Appendix 1).

The main contributors of positive impacts on food provision were alien Osteichthyes and Crustacea, with positive impact records substantially increasing eastwards (Figure 13D). Several alien fish such as *Nemipterus randalli*, *Scomberomorus commerson*, *Sphyraena chrysotaenia*, *Saurida lessepsianus*, *Upeneus* spp., *Siganus* spp. and crustaceans such as *P. pulchricaudatus*, and *Metapenaeus* spp. are marketed in many Mediterranean countries. *Callinectes sapidus* is collected and sold in the northern Adriatic and Ebro Delta (Spain) where it is an appreciated shellfish. Mollusc species, such as those of the genus *Magallana/Crassostrea*, *Ruditapes philippinarum*, and *Conomurex persicus* have historically contributed to food provision as new commodities in various Mediterranean ecoregions.

Degradation of habitats was the primary mechanism of negative impacts on regulating services, mainly recorded in the western Mediterranean and affecting life-cycle maintenance (Figure 14A). *Posidonia oceanica* meadows and coralligenous communities are marine habitats with a fundamental role in the functioning of Mediterranean ecosystems and the conservation of marine life. Invasive Rhodophyta such as *W. setacea*, *A. preissii*, and *L. lallemandii* have the potential to degrade such ecosystems (Figure 14C) through the formation of dense algal turfs that epiphytise *Posidonia* meadows and homogenise the diversity and complexity of coralligenous communities, degrading their state and negatively affecting the life they support (see Appendix 1). Such habitats are also vulnerable to the invasion by *C. cylindracea* that negatively affects many keystone species. Furthermore, the recent Ochrophyta invader *R. okamurae* can displace native species, monopolise shallow communities, and even cause community shifts in coralligenous communities.

Positive mechanisms of impact on "regulating and maintenance" ecosystem services were much less reported (Figure 14B). Carbon sequestration overall accounted for most positive impacts either through the formation of shells or via primary production. Such positive contributions to climate change were attributed to Mollusca, Foraminifera, and Tracheophyta (Figure 14D). Shell-forming organisms such as the foraminiferan *Amphistegina*

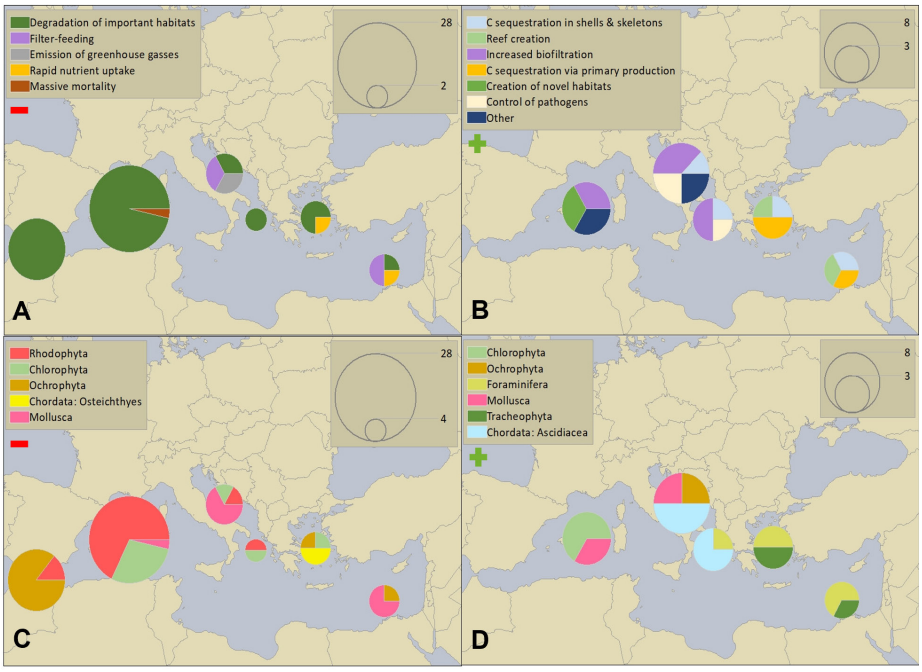


Figure 14. Geographical variation of the A) negative and B) positive mechanisms of impact on regulating and maintenance ecosystem services by Mediterranean ecoregion and of analyzed alien species phyla with C) negative and D) positive impacts on regulating and maintenance services per Mediterranean ecoregion. The size of the pie charts reflects the number of reported cases (the inset indicates the minimum and maximum sizes).

lobifera or the bivalves *R. philippinarum* and *Arcuatula senhousia* form dense aggregations that constitute banks of carbon storage in the marine environment, since their shells contain carbonate. Meadows of the alien seagrass *Halophila stipulacea* are also considered carbon sinks (see Appendix 1).

The Levantine Sea was the Mediterranean ecoregion with most studies of impacts on cultural ecosystem services (Figure 15A, B). The negative effects in the Levantine were primarily caused by Chlorophyta, Ochrophyta, and Rhodophyta (Figure 15C) through decomposing macroalgal material that washed ashore. Seaweed drifts of *Codium parvulum*, *Codium arabicum*, *Galaxaura rugosa*, and *Stypopodium schimperi* have regularly occurred in the eastern Mediterranean during recent decades, disturbing local activities and tourism and degrading the aesthetic value of the coast. Large and dense macroalgal thalli of *Sargassum muticum* and *Undaria pinnatifida* have sometimes become a nuisance in Adriatic lagoons, hindering navigation. In the Levantine Sea, *R. nomadica* massive swarms have also hindered tourism profits as they pose a threat to swimmers and deter tourists from visiting the coast.

On the other hand, alien species have offered materials for research on potential pharmaceutical products and biomonitoring services, which are the main positive impacts reported on cultural services (Figure 15B), with frequencies that were not found to differ significantly among ecoregions (chi-square test; excluding the Alboran Sea; $p = 0.136$). Many molluscs and

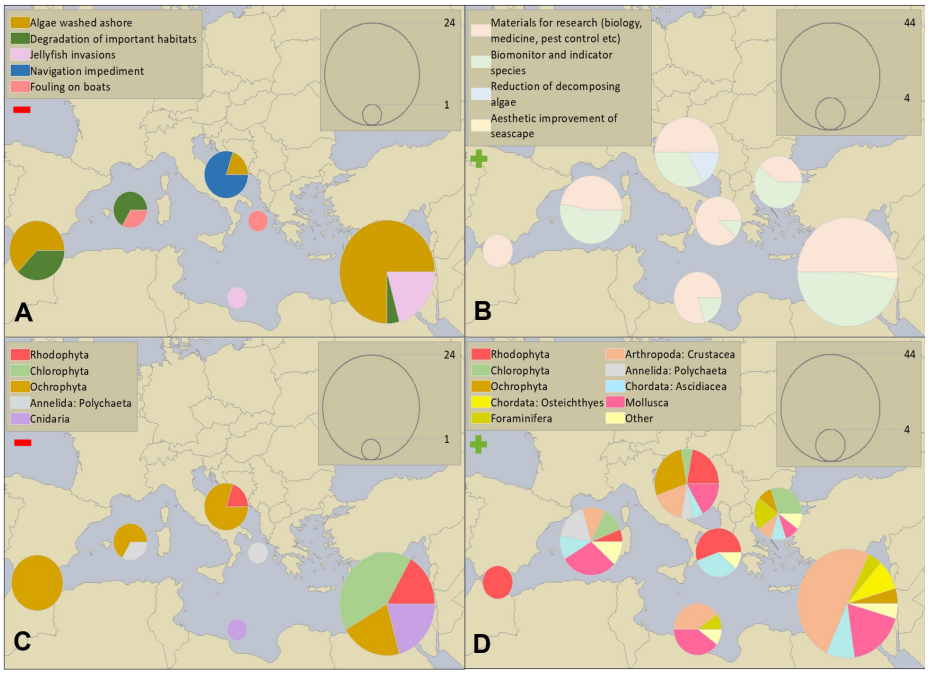


Figure 15. Geographical variation of the **A)** negative and **B)** positive mechanisms of impact on cultural ecosystem services by Mediterranean ecoregion and of analyzed alien species phyla with **C)** negative and **D)** positive impacts on cultural services per Mediterranean ecoregion. The size of the pie charts reflects the number of reported cases (the inset indicates the minimum and maximum sizes).

crustaceans such as *S. spinosus*, *P. radiata*, and *Penaeus semisulcatus*, and the foraminiferan *A. lobifera*, have been used effectively as biomonitoring species for marine pollution (Figure 15D; see Appendix 1).

Impacts on human health

Reported impacts on human health were only negative. The great majority of this evidence came from the Levantine Sea (Figure 16A) and was primarily related to stinging and poisoning/intoxication caused by only 9 species belonging to Osteichthyes, Cnidaria, and Echinodermata (Figure 16B), namely: *L. sceleratus*, *Torquigener flavimaculosus*, *Plotosus lineatus*, *P. miles*, *S. luridus*, *S. rivulatus*, *Macrorhynchia philippina*, *R. nomadica*, and *Diadema setosum*. Such unwanted accidents are sometimes described in the scientific literature. For example, in the eastern Mediterranean, severe intoxications and cases of death were attributed to the consumption of *L. sceleratus*, which contains in its tissues a paralytic neurotoxin called tetrodotoxin that can be lethal for humans. *Rhopilema nomadica* has caused a vast number of hospitalizations of swimmers and fishers in the Levantine Sea due to its painful stings. The long-spined sea urchin *D. setosum* poses a threat for swimmers in the eastern Mediterranean where it can be found at high densities in shallow waters, as its spines contain venom and may inflict painful stings.

Grouping of species according to the mechanisms of their impacts

Species with impacts on biodiversity, ecosystem services, and human health were grouped by hierarchical cluster analysis according to their

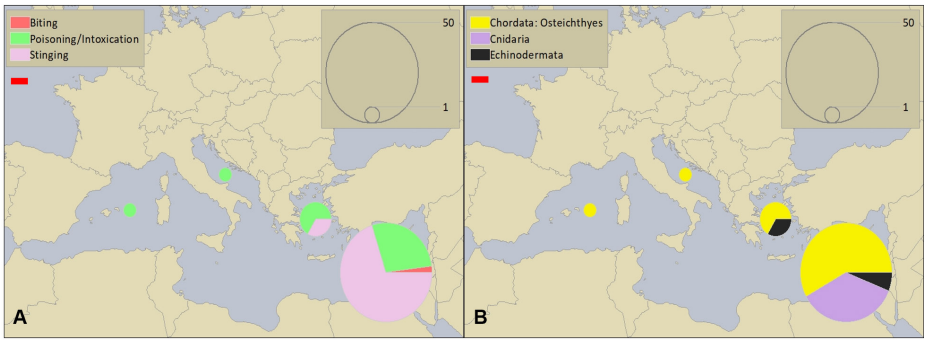


Figure 16. Geographical variation of **A)** mechanisms of negative impact and the responsible **B)** phyla causing the impacts on human health by Mediterranean ecoregion.

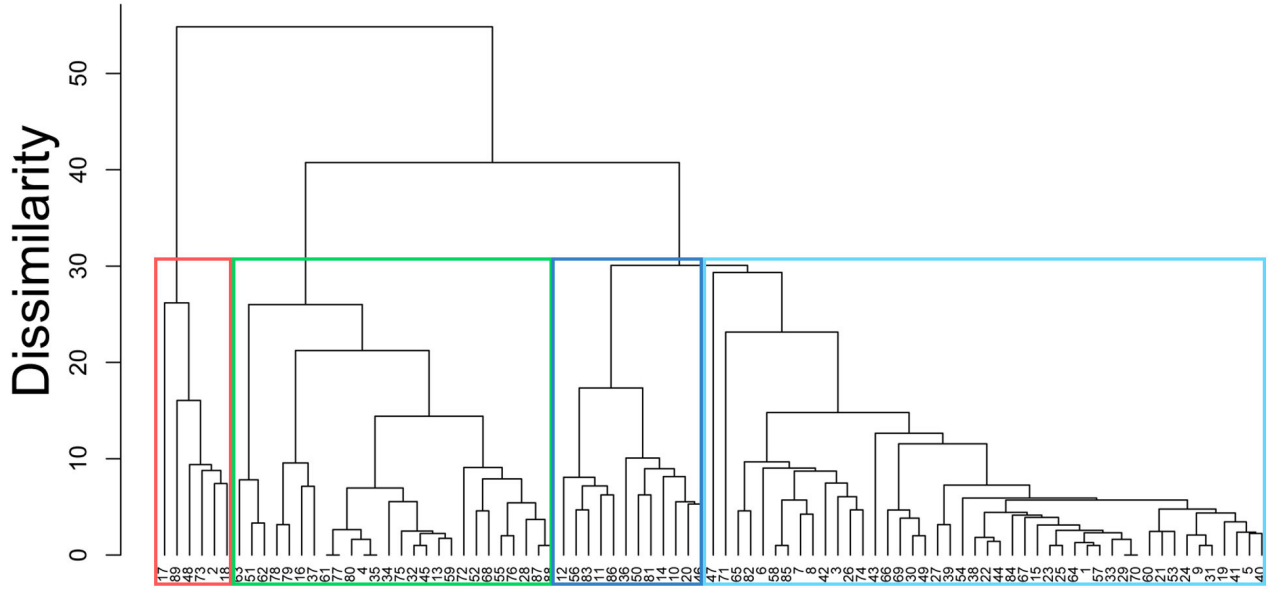


Figure 17. Hierarchical cluster dendrogram of alien and cryptogenic species (Cr: cryptogenic) based on the mechanisms of reported impacts on biodiversity, ecosystem services and human health. Coloured frames (red, green, blue, light blue) indicate the four major groups species of the dendrogram. Included species are numbered as follows: 1) *Acartia (Acanthacartia) tonsa* (Cr), 2) *Acrothamnion preissii*, 3) *Agarophyton vermiculophyllum*, 4) *Alepes djedaba*, 5) *Amathia verticillata* (Cr), 6) *Amphistegina lobifera*, 7) *Anadara kagoshimensis*, 8) *Anadara transversa*, 9) *Antithamnion nipponicum*, 10) *Arcuatula senhousia*, 11) *Asparagopsis armata* , 12) *Asparagopsis taxiformis*, 13) *Atherinomorus forskalii*, 14) *Brachidontes pharaonis*, 15) *Bursatella leachii* (Cr), 16) *Callinectes sapidus*, 17) *Caulerpa cylindracea*, 18) *Caulerpa taxifolia*, 19) *Caulerpa taxifolia* var. *distichophylla*, 20) *Chama pacifica*, 21) *Chrysonephos lewisii*, 22) *Ciona robusta*, 23) *Cladophora patentiramea*, 24) *Clavelina oblonga*, 25) *Codium arabicum*, 26) *Codium fragile* subsp. *fragile*, 27) *Codium parvulum*, 28) *Conomurex persicus*, 29) *Decapterus russelli*, 30) *Diadema setosum*, 31) *Didemnum vexillum*, 32) *Dussumieria elopsoides*, 33) *Dyspanopeus sayi*, 34) *Erugosquilla massavensis*, 35) *Etrumeus golanii*, 36) *Ficopomatus enigmaticus*, 37) *Fistularia commersonii*, 38) *Fulvia fragilis*, 39) *Galaxaura rugosa*, 40) *Grateloupia turuturu*, 41) *Halimeda incrassata*, 42) *Halophila stipulacea*, 43) *Haplosporidium pinnae* (Cr), 44) *Herdmania momus*, 45) *Herklotsichthys punctatus*, 46) *Hydroides elegans*, 47) *Lagocephalus sceleratus*, 48) *Lophocladia lallemandii*, 49) *Macrorhynchia philippina*, 50) *Magallana*/*Crassostrea* species, 51) *Metapenaeus monoceros*, 52) *Metapenaeus stebbingi*, 53) *Microcosmus squamiger*, 54) *Mnemiopsis leidyi*, 55) *Nemipterus randalli*, 56) *Oculina patagonica* (Cr), 57) *Paracerceis sculpta*, 58) *Paraleucilla magna*, 59) *Parupeneus forsskali*, 60) *Pempheris rhomboidea*, 61) *Penaeus aztecus*, 62) *Penaeus pulchricaudatus*, 63) *Penaeus semisulcatus*, 64) *Percnon gibbesi* (Cr), 65) *Pinctada radiata*, 66) *Plotosus lineatus*, 67) *Polyandrocarpa zorritensis*, 68) *Portunus segnis*, 69) *Pterois miles*, 70) *Rapana venosa*, 71) *Rhopilema nomadica*, 72) *Ruditapes philippinarum*, 73) *Rugulopteryx okamurae*, 74) *Sargassum muticum*, 75) *Sargocentron rubrum*, 76) *Saurida lessepsianus*, 77) *Scomberomorus commerson*, 78) *Siganus luridus*, 79) *Siganus rivulatus*, 80) *Sphyraena chrysotaenia*, 81) *Spondylus spinosus*, 82) *Styela plicata*, 83) *Stypopodium schimperi*, 84) *Torquigener flavimaculosus*, 85) *Tricellaria inopinata*, 86) *Undaria pinnatifida*, 87) *Upeneus moluccensis*, 88) *Upeneus pori*, 89) *Womersleyella setacea*.

similarity of mechanisms of reported impacts, resulting in 4 major groups (Figure 17).

The first cluster (red colour in Figure 17) included six alien macroalgae, namely *C. cylindracea*, *W. setacea*, *L. lallemandii*, *R. okamurae*, *A. preissii*, and *C. taxifolia*. A high number of negative impact records was reported for each of these species, with competition for resources being the most common mechanism of impact. A high number of impact records was also reported on ecosystem services through the mechanism of degradation of important habitats, with 84 negative cases on 8 different services. These species also constitute ecosystem engineers that mainly impacted other species negatively (34 records) rather than positively (21 records) through the creation of novel habitat.

The second cluster (green colour in Figure 17) was formed by 26 species that were grouped together primarily due to their positive impact on food provision, being new commodities. All these species, mainly crustaceans, fishes, and two molluscs, contributed to 91% of the overall positive impacts on food provision by new commodities. Among them, the alien shrimps *M. monoceros*, *P. pulchricaudatus*, and *P. semisulcatus* were the species with the highest number of positive reports as new commodities, but also some competitive negative impacts on native shrimp species and thus exhibited a high similarity. The alien fishes *N. randalli*, *Saurida lessepsianus*, *Upeneus* spp., the alien molluscs *C. persicus* and *R. philippinarum*, and the alien crab *P. segnis* formed a subgroup within this cluster following the same pattern of reported mechanisms of impact but with a lower frequency. Predation (including grazing) was also a mechanism of negative impact characteristic for some species of this cluster, such as the herbivorous fish *Siganus* spp., the omnivorous crab *C. sapidus*, and the piscivorous fish *F. commersonii.*

The third major cluster (blue colour in Figure 17) included alien molluscs such as *B. pharaonis*, *Chama pacifica*, and *Magallana/Crassostrea* species, the alien polychaetes *F. enigmaticus* and *H. elegans*, the alien macroalgae *Asparagopsis* spp. and *U. pinnatifida*, and the cryptogenic hexacoral *Oculina patagonica*. A high number of impacts on biodiversity was recorded for these species, mainly through the mechanisms of competition and the creation of novel habitat (both negative and positive for the latter) as structural ecosystem engineers.

The final cluster (light blue colour) was delineated by 45 species with 394 impact records. Thirty-six species of this cluster had less than 10 records each. Competition for resources was the most common mechanism of impact with 59 records, caused by 33 of the 46 species of the cluster. Fouling species with negative impacts on aquaculture followed as the second most common mechanism. Such species with both competition and fouling impacts were the ascidians *Styela plicata*, *Clavelina oblonga*, and *Didemnum vexillum*, the bivalve *P. radiata*, the sponge *P. magna*, and the bryozoan *T. inopinata.* Most species with negative impacts on human health were also included in this cluster. *Diadema setosum*, *M. philippina*, *P. lineatus*, and *P. miles* were grouped together with high similarity as stinging species.

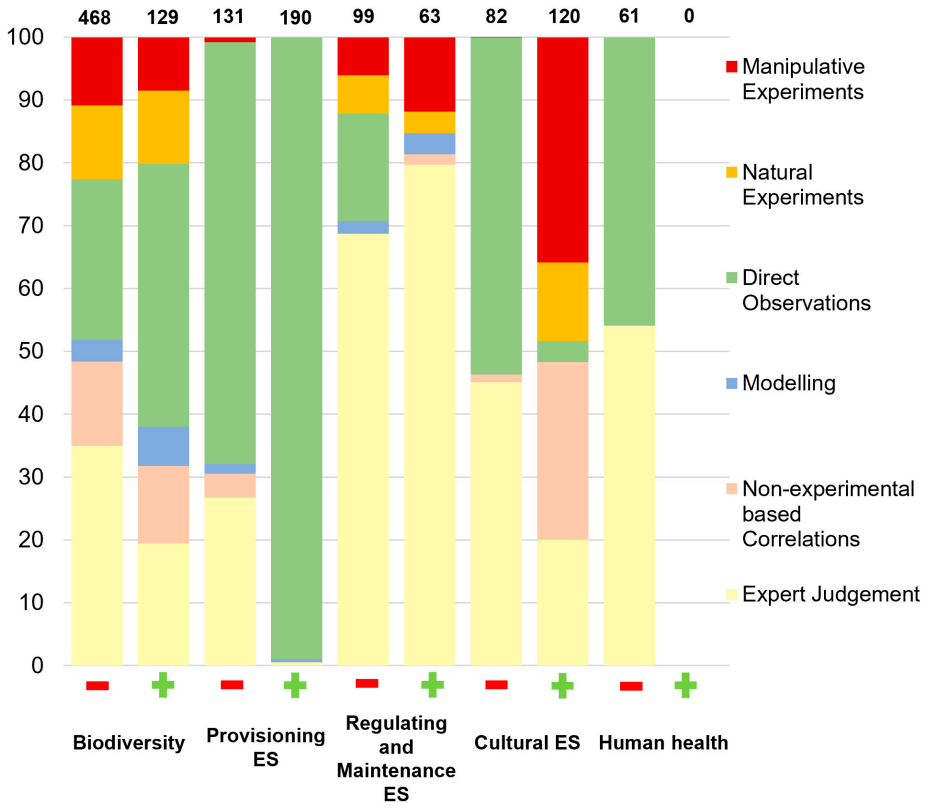


Figure 18. Type of evidence of the analysed impact records on biodiversity, ecosystem services and human health. The numbers on top of the bars indicate the sample size (number of reported cases) for each category.

Type of evidence

Only 16% of impact records were experimental (9% were based on manipulative and 7% on natural experiments; Figure 18). Moreover, many of the experimental studies were *in vitro* experiments on alien species extracts and compounds. Most of the taxa studied by experimental studies were Chlorophyta and Rhodophyta. Overall, direct observation was the most common type of evidence accounting for 40% of all records. Reported impacts on provisioning ecosystem services were almost exclusively based on direct observations (Figure 18). Fouling on aquaculture facilities, entanglement in nets, and new commodities in the fisheries and fish markets are undoubtedly direct impacts and as such were classified as direct observations. For biodiversity records, direct observations referred to the creation of novel habitat, apparent competitive interactions such as overgrowth of sessile organisms, predation impacts derived from stomach content analysis, and massive mortalities. Expert judgement and non-experimentally based correlations accounted for 32% and 9% of impact records, respectively (Figure 18), the former being dominant for "regulating and maintenance" ecosystem services. Modelling overall accounted for only 2% of the records.

The western Mediterranean and the Alboran Sea exhibited the highest percentages of experimental studies assessing negative impacts on biodiversity,

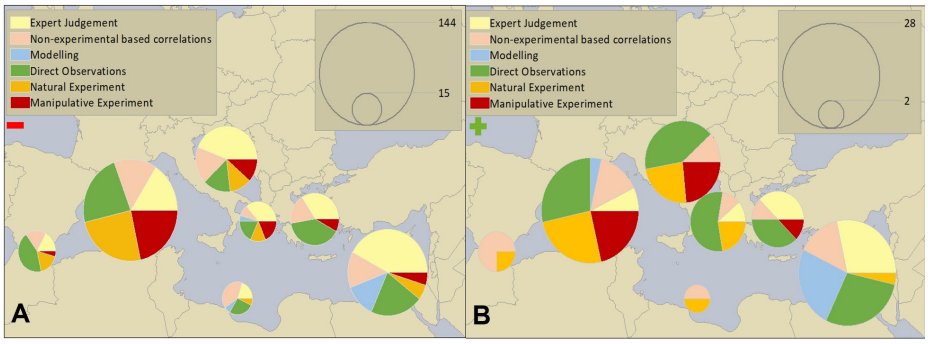


Figure 19. Geographical variation of type of evidence for negative (A) and (B) positive impacts on biodiversity across Mediterranean ecoregions.

followed by the Adriatic and the Ionian Sea (Figure 19A). Much less experimental studies were recorded in the Aegean and the Levantine Sea. Instead, expert judgement was the main type of evidence in these ecoregions, as well as in the Adriatic and the Ionian Sea. The western Mediterranean and the Adriatic Sea were the ecoregions with the highest proportion of experimental studies for positive impacts on biodiversity (Figure 19B). Most impact reporting through modelling studies for both negative and positive impacts was from the Levantine Sea (Figure 19A, B).

Inventory of high impact species in the Mediterranean Sea

An inventory of impactful species, based on both negative and positive reported impacts on biodiversity, ecosystem services and human health, is proposed in Table 4 and includes 88 species. Of the 103 assessed species, 15 were excluded from this inventory due to the complete absence of impact records or the reporting of only minor impacts. For three included species there was only weak evidence for their impact, based on expert judgement. Based on their negative impacts score on biodiversity, a list of the ten worst invasive species was compiled (Table 5). *Caulerpa cylindracea* ranked first, followed by *W. setacea* and *L. lallemandii*. Macroalgae dominated in the list of the ten worst invasives (6 species), followed by fishes and bivalve molluscs (2 species each).

Discussion

The number of reported negative impact records on biodiversity was approximately four times higher than the number of positive ones. Analysing the mechanisms of these effects, it was revealed that many alien species strongly compete for space and resources with native biota (e.g., Turon et al. 2007; Fanelli et al. 2015; Manconi et al. 2020) whereas others act as ecosystem engineers and alter the structure of habitats causing major negative effects on the local communities (e.g., Rilov et al. 2004; Bedini et al. 2014). Furthermore, intense feeding activities of invasive species can cause the decline of native populations (e.g., Kampouris et al. 2019), with alien grazers even being able to cause massive negative impacts in eastern

Table 4. Proposed inventory of alien and cryptogenic marine species with reported moderate to high impacts on biodiversity or ecosystem services or human health. Species whose impact was only reported by expert judgement are marked in light yellow (weak evidence); Cr: For cryptogenic species.

Cercozoa	**Tracheohyta**	**Annelida: Polychaeta**	**Chordata: Osteichthyes**
Haplosporidium pinnae (Cr)	*Halophila stipulacea*	*Ficopomatus enigmaticus*	*Alepes djedaba*
Foraminifera	**Porifera**	*Hydroides elegans*	*Atherinomorus forskalii*
Amphistegina lobifera	*Paraleucilla magna*	**Arthropoda: Crustacea**	*Decapterus russelli*
Ochrophyta	**Cnidaria**	*Acartia (Acanthacartia) tonsa* (Cr)	*Dussumieria elopsoides*
Chrysonephos lewisii	*Macrorhynchia philippina*	*Callinectes sapidus*	*Etrumeus golanii*
Rugulopteryx okamurae	*Oculina patagonica* (Cr)	*Dyspanopeus sayi*	*Fistularia commersonii*
Sargassum muticum	*Rhopilema nomadica*	*Erugosquilla massavensis*	*Herklotsichthys punctatus*
Stypopodium schimperi	**Ctenophora**	*Metapenaeus monoceros*	*Lagocephalus sceleratus*
Undaria pinnatifida	*Mnemiopsis leidyi*	*Metapenaeus stebbingi*	*Nemipterus randalli*
Chlorophyta	**Bryozoa**	*Paracerceis sculpta*	*Parupeneus forsskali*
Caulerpa cylindracea	*Amathia verticillata* (Cr)	*Penaeus aztecus*	*Pempheris rhomboidea*
Caulerpa taxifolia	*Tricellaria inopinata*	*Penaeus pulchricaudatus*	*Plotosus lineatus*
Caulerpa taxifolia var. *distichophylla*	**Mollusca**	*Penaeus semisulcatus*	*Pterois miles*
Cladophora patentiramea	*Anadara kagoshimensis*	*Portunus segnis*	*Sargocentron rubrum*
Codium arabicum	*Anadara transversa*	**Echinodermata**	*Saurida lessepsianus*
Codium fragile subsp. *fragile*	*Arcuatula senhousia*	*Diadema setosum*	*Scomberomorus commerson*
Codium parvulum	*Brachidontes pharaonis*	**Chordata: Ascidiacea**	*Siganus luridus*
Halimeda incrassata	*Bursatella leachii* (Cr)	*Ciona robusta*	*Siganus rivulatus*
Rhodophyta	*Chama pacifica*	*Clavelina oblonga*	*Sphyraena chrysotaenia*
Acrothamnion preissii	*Conomurex persicus*	*Didemnum vexillum*	*Torquigener flavimaculosus*
Agarophyton vermiculophyllum	*Fulvia fragilis*	*Herdmania momus*	*Upeneus moluccensis*
Antithamnion nipponicum	*Magallana/Crassostrea* species	*Microcosmus squamiger*	*Upeneus pori*
Asparagopsis armata	*Pinctada radiata*	*Polyandrocarpa zorritensis*	
Asparagopsis taxiformis	*Rapana venosa*	*Styela plicata*	
Galaxaura rugosa	*Ruditapes philippinarum*		
Grateloupia turuturu	*Spondylus spinosus*		
Lophocladia lallemandii			
Womersleyella setacea			

Table 5. The ten worst invasive species, based on their negative impact score (accounting only for impacts on biodiversity). This ranking does not account for the spatial extent of impacts but is based on a sum of all reported impacts in the literature, weighted by their magnitudes.

Species	Negative Impacts Score
Caulerpa cylindracea	134
Womersleyella setacea	80
Lophocladia lallemandii	65
Brachidontes pharaonis	47
Siganus luridus	44
Rugulopteryx okamurae	43
Caulerpa taxifolia	38
Siganus rivulatus	38
Acrothamnion preissii	36
Spondylus spinosus	33

Mediterranean ecoregions by depleting rocky reef algal biomass (e.g., Sala et al. 2011). At the same time, some alien species create novel habitats that offer shelter to many other native organisms (e.g., Di Martino et al. 2007; Munari et al. 2015), constitute new food sources for native predators (e.g., Giacoletti et al. 2016; Tiralongo et al. 2021), and contribute to other ecological functions of the recipient ecosystem (e.g., Sarà et al. 2021).

It is noteworthy that a higher number of positive than negative impacts were recorded affecting the flow of ecosystem services. Food provision

appears as the most affected ecosystem service by both positive and negative impacts. Invasive fish have significantly increased their numbers in the last thirty years, representing today more than half of the total abundance and biomass of the Levantine fish (Katsanevakis et al. 2018). Simultaneously, severe population declines in some native fish populations occurred (Edelist et al. 2013). All surveys that indicated a competitive effect of alien species on commercial native species stocks were supported by weak or modest strength of evidence. There is no strong evidence supporting the hypothesis of native species population declines exclusively or largely due to competition with alien species. On the other hand, research has demonstrated that many species have declined in the Levantine Sea due to climate change, as the new temperature regime is beyond their thermal niche (Rilov 2016). Climate change is an important stressor for native biota and has negatively affected the Mediterranean Sea (Marbà et al. 2015; Rilov 2016; Albano et al. 2021). In the western Mediterranean, shallow waters have been warming for more than a century with more abrupt positive trends during the recent decades that have resulted in local sea surface temperature increases that even exceed 1 °C (Lejeusne et al. 2010) and deleterious marine heatwaves (Garrabou et al. 2009, 2019, 2022). The eastern basin was shown to be warming faster (Pisano et al. 2020; Novi et al. 2021), with surface water temperature even exceeding a 3 °C increase during the period 1978–2014 in the southeastern regions (Ozer et al. 2017). Climate change has played a crucial role in the alteration of eastern Mediterranean ecosystems and the collapse of several species (Rilov 2016; Albano et al. 2021), but these dramatic changes are better explained as a result of the combined effects of climate change and biological invasions (Marras et al. 2015; Azzurro et al. 2019; Yeruham et al. 2020). Indeed, multiple stressors often act in synergy, leading to multiplicative effects (Korpinen et al. 2019; Gissi et al. 2021).

A progressive transition towards a more thermophilic biota is reported for the global fishery catch for most marine ecosystems (Cheung et al. 2013), and also in the Mediterranean Sea (Tsikliras and Stergiou 2014), where warm adapted invaders of Indo-Pacific origin are already replacing native biota (Stergiou et al. 2016 and references therein; Katsanevakis et al. 2018; Albano et al. 2021). Yet, to date many alien species contribute to food provision as new commodities (Katsanevakis et al. 2018), especially in the eastern Mediterranean where alien fishes and crustaceans are more abundant in comparison to the western basin (Katsanevakis et al. 2014b). Levantine fisheries have even begun to shift their target from deeper to shallower waters where they can catch larger quantities of thermophilic alien species (van Rijn et al. 2020).

Contrary to the general idea that invading alien species are inherently "bad", a view that is often dependent on social perceptions (Katsanevakis et al. 2014a), the positive effects of tropical invaders are worth exploring in

detail, especially in the current climate change context. In the Levantine Sea, the ecological space made available by the shift of temperate species towards higher latitudes and greater depths cannot be covered by neonatives (*sensu* Essl et al. 2019) from southern regions, as this is a land-locked basin. In that sense, it can be argued that thermophilic Lessepsian immigrants entering the Mediterranean through the Suez Canal may contribute to limiting the loss of ecosystem functions and services. Restoring the Levantine Sea ecosystems to their previous state before climate change and massive biological invasions is unrealistic. Except for targeted management actions for specific species (e.g. *P. miles* and *L. sceleratus*), marine managers in the region need to be adaptive and realistic, understanding and accepting the role of alien species in the novel marine ecosystems.

Regarding the impacts of invasive species on human health, we observed that these are mostly limited to the eastern basin. Among the nine species, only *L. sceleratus* was found to have an impact in locations west of the Aegean Sea, and the species has already reached the westernmost end of the Mediterranean (Azzurro et al. 2020). The actual number of negative impact cases on human health is probably underestimated because many non-life-threatening episodes do not require hospitalisation and are treated by first aid. Such cases are most often not officially reported (Bédry et al. 2021), especially not by scientific literature. Bédry et al. (2021) proposed a series of actions to manage the effects of marine biological invasions on human health: i) to reinforce public awareness of the potential dangers that specific alien species may pose to human health, ii) to train and prepare professional medical personnel on the physiological effects of toxic alien species, iii) to establish a regional warning and monitoring system. In this review, we did not record positive impacts of alien or cryptogenic species on human health but future research on alien species is expected to disclose their potential as providers of biomolecules, to be used by the pharmaceutical industry (e.g. Genovese et al. 2009; Minicante et al. 2016; Dhahri et al. 2020). However, the discovery of new potentially active molecules is a well-worn argument very often put forward to minimise the problem of species introductions (a "chestnut" in journalistic terms), but its validity has only rarely, if ever, been demonstrated and evaluated. Marine species capable of producing active metabolites are well known around the world and invasions are not necessary to initiate research and exploitation. The industrial exploitation of such molecules often requires either aquaculture production or chemical synthesis. So far, to the best of our knowledge, there are no examples of industrial exploitation of Mediterranean invaders for active molecules.

Biological invasions remain one of the most catastrophic threats to global biodiversity, but the complexity of their impacts along with their ecological, and socio-economic dimensions are worth exploring in detail and at different scales. Some scientists consider that the origin of a species

does not make it *de facto* responsible for negative consequences (Davis et al. 2011) since native species also possess the ecological ability to affect ecosystems and cause deleterious impacts under certain conditions. For example, the coastal rocky reefs of the eastern Mediterranean are overgrazed by the invasive rabbitfishes *Siganus luridus* and *S. rivulatus* (Sala et al. 2011; Giakoumi 2014; Vergés et al. 2014; Yeruham et al. 2020) but under certain conditions, similar effects can be provoked by native grazers (Hereu 2006; Vergés et al. 2009; Bonaviri et al. 2011; Gianni et al. 2017; Tsirintanis et al. 2018; Papadakis et al. 2021), often due to cascading effects caused by the loss of overfished native predators (Sala et al. 1998). It should also be highlighted that some of the high-impact species of the current proposed inventory are cryptogenic, meaning that their origin cannot be completely ascertained. Non-factual perception of alien species as invasive (i.e. negatively impacting ecosystems and human well-being) neglects a holistic approach to impact assessment and can lead to bias (Goodenough 2010; Katsanevakis et al. 2014a). Commonly the same species have both negative and positive impacts on biodiversity, and the overall balance is hard to assess. For example, the possible facilitation of the restoration of a degraded ecosystem by an invasive alien species like the facilitation of seagrass seedlings by *C. cylindracea* in degraded meadows (Ceccherelli and Campo 2002; Pereda-Briones et al. 2018) deserves further consideration and confirmation by long-term studies evaluating the survival rate of germlings in dense *C. cylindracea* meadows. This brings up ecological, cultural, and socio-economic considerations that complicate decision making in invasive species management, as changes in host communities are not always perceived as harmful (Bonanno 2016), and management decisions need to account for conflicts and trade-offs (Mason et al. 2017).

In this study, we found a clear geographic differentiation in the distribution of reported impacts. For example, predation as a mechanism of impact was more important in the Levantine Sea than in the rest of the basin. This is following the higher richness and abundance of invasive fishes that characterise the eastern sectors of the Mediterranean, being introduced from the Red Sea through the Suez Canal and favoured by the higher temperatures of the eastern Mediterranean (Katsanevakis et al. 2014b). The great taxonomic differences of alien species among ecoregions (Zenetos et al. 2012; Katsanevakis et al. 2014b), as well as the significant differences in impacts among taxonomic groups, revealed in this study, partly explain the variation detected among Mediterranean ecoregions.

A global effect of alien species invasions is biotic homogenization, the process of native biodiversity impoverishment happening simultaneously with a proliferation of alien species that results in the expansion of homogeneity in terms of genetic, taxonomic and functional diversity with unclear biodiversity distinctions (Olden et al. 2004 and references therein). Signs of biotic homogenization are evident in the marine ecosystems of the

Mediterranean Sea, as the establishment and advancement of biological invasions in the basin have occurred alongside native biota impoverishment and losses (Galil 2007 and references therein). In many cases, an impoverished homogeneous state has been spread within the Mediterranean basin, through the spread and dominance of some alien structural ecosystem engineers (Navarro-Barranco et al. 2018; Morri et al. 2019). The increasing rate of biological invasions in the Mediterranean and the continuing seawater warming led to the replacement of endemic populations by mostly thermophilic Lessepsian species. Hence, the "Mediterranean character" of the marine biota progressively declines, contributing to the breakdown of the regional distinctiveness of the Mediterranean Sea (Ben Rais Lasram and Mouillot 2009).

In the current literature review, most studies on impacts on biodiversity were based on medium and low strength of evidence. In agreement with Katsanevakis et al. (2014a), the proportion of reported impacts with high strength of evidence (i.e. manipulative and natural experiments) was low. These studies were conducted in 13 out of the 22 Mediterranean countries, with most cases (84%) reported from Italy, Spain, and France (Figure 20A). The latter are the Mediterranean countries with the higher budget for research and development (UNESCO 2021) (Figure 20B), reflecting the connection between research robustness, number of experimental studies, and investment in research and development. Indeed, several studies relate scientific output to national spending on research and development, the number of universities in a country, GDP, and English proficiency (Man et al. 2004; Meo et al. 2013; Jamjoom and Jamjoom 2016; Mueller 2016).

Another possible reason for the higher inferential strength of impact assessment studies in the western Mediterranean countries could be related to the taxonomic distribution of alien species within the Mediterranean. There is a higher species richness of alien macroalgae in the western Mediterranean in comparison to the eastern basin, and the opposite pattern for alien fish species, which have primarily invaded the eastern Mediterranean (Katsanevakis et al. 2014b). Our analysis revealed that the vast majority (90%, n = 76) of experimental impact cases on biodiversity reported from the western Mediterranean and the Alboran Sea assess impacts caused by alien macroalgae, whereas no experimental study investigates impacts caused by alien fish. At the same time, experimental impact records are significantly lower in numbers in the Levantine and the Aegean Sea and mainly refer to alien fish effects (71%; n = 14). Macroalgae are sessile organisms, easier to be controlled in confined experimental treatments, in contrast to mobile organisms such as fish. There is already a high level of difficulty in performing underwater experiments to investigate ecological interactions due to the various factors that affect a diver's awareness such as visibility and temperature (O'Brien and Caramanna 2017). In addition, species mobility may interfere with the success of an

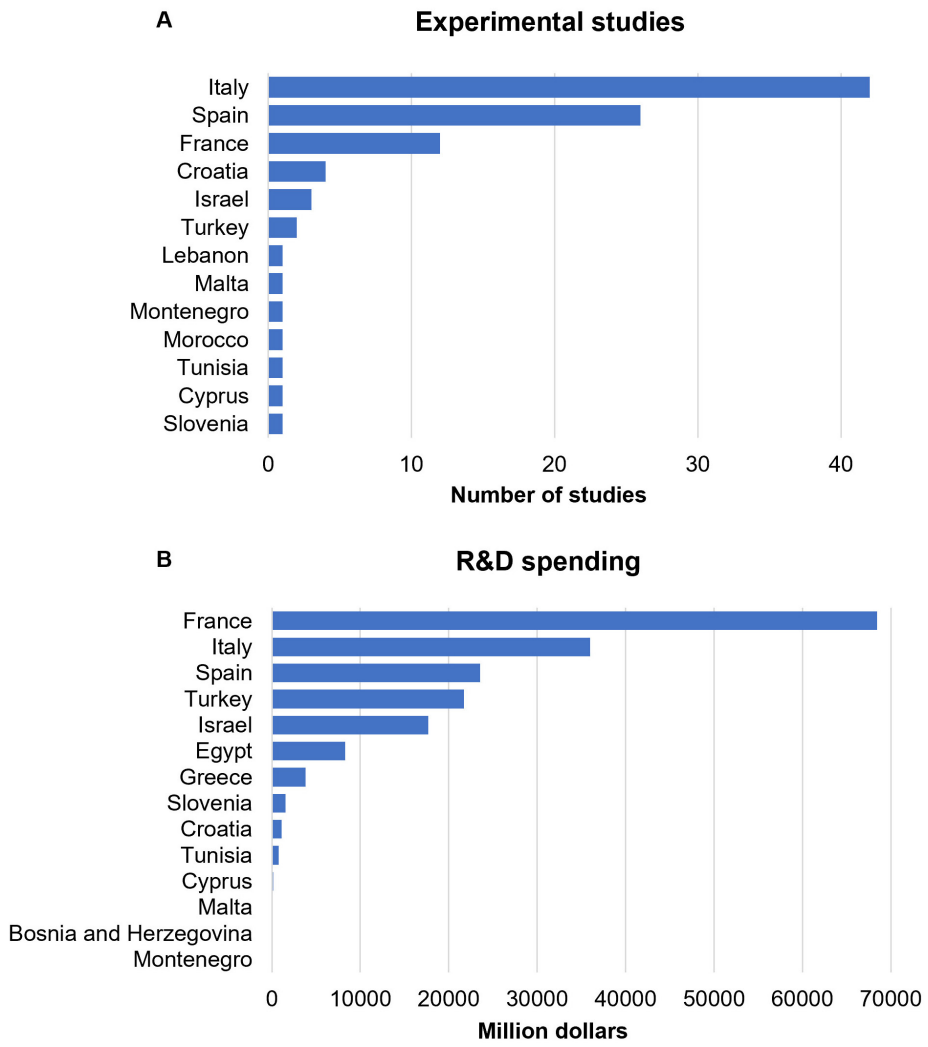


Figure 20. A) Number of reported experimental studies included in this review assessing impacts on biodiversity, per Mediterranean country, B) Total intramural expenditure on Research and Development (R&D), performed by some Mediterranean countries during 2018, expressed in Purchasing Power Parity dollars (UNESCO 2021).

applied underwater experiment and this fact can explain why experimental research on alien species is more limited in the eastern Mediterranean, dominated by mobile species invasions. Similar results were reported by Kytinou et al. (2020), who reviewed methodological approaches globally that analyse coastal shelf food webs, and concluded that only 14% of the reviewed studies conducted manipulative or natural experiments, and most of the studies focused on benthic species and much less on fish. Also, Thomsen et al. (2014) reviewed aquatic alien species' experimental impact assessment surveys within forty years (1972–2012) and found only one alien marine fish species studied by experiments among more than a hundred different species. The species mobility hypothesis is further supported by the fact that in the Levantine and the Aegean Sea most of the impacts were reported by experimental studies on the herbivorous fishes *Siganus* spp. with assessments based on the effects on macroalgal communities, i.e. the sessile food of siganids.

Furthermore, there are several additional confounding factors that distort the actual impact patterns, such as paucity of data (Ojaveer et al. 2015), taxonomic impediment (Engel et al. 2021), challenges for assessing and quantifying the actual impact of particular alien taxa (Carlton 2002; Simberloff 2011; Davidson and Hewitt 2014; Strayer et al. 2017), and weak inferential strength of evidence (Katsanevakis et al. 2014a). Another aspect to consider is that the current analysis examines impacts caused by each alien species separately. But species do interact, and their cumulative impacts are not necessarily additive but can be multiplicative or mitigative (Katsanevakis et al. 2016), also often interacting with other local or global stressors such as climate change (Gissi et al. 2021). Hence, impacts by alien species reported in a specific location are not necessarily representative of the entire ecoregion. As a consequence, spatial patterns herein reported should be interpreted with caution, as highlighted in other studies reporting spatial patterns in biological invasions (e.g. Pyšek et al. 2008; Stranga and Katsanevakis 2021).

In addition, the methodological approach of the current impact assessment framework is performed without chronological restrictions and depicts the effects of alien and cryptogenic species on biodiversity, ecosystem services and human health from the moment of the first impact report of each targeted species until 2021. The temporal variation of impacts was not taken into account. Still, invasive alien species can regress after an invasion phase, following a so-called "boom and bust" invasion pattern, as has been reported for *Caulerpa cylindracea*, *C. taxifolia*, *L. lallemandii* and *S. schimperi* (Iveša et al. 2006; Montefalcone et al. 2015; Dimitriadis et al. 2021; Santamaría 2021). Unfortunately, the literature of marine invasions sorely lacks scientific articles showing the evolution of invaded sites over several decades (Strayer et al. 2017; Ojaveer et al. 2018). The reason may be due to the functioning of scientific research, i.e. the short duration of doctoral thesis projects, short-term funding, the need to publish quickly, the lack of interest of scientific journals and reviewers in what seems routine monitoring, and probably also the fact that spectacular bad news is easier to publish than good news. Hence, it is possible that some of the published impacts later declined in magnitude, due to the "boom-and-bust" dynamics of biological invasions. This stresses the need for repetitive assessments and regular re-evaluation of the impacts of alien species.

We have provided a list of the "ten worst invasive species" in the Mediterranean, based on reported impacts. Similar lists have been compiled in the past (e.g. see Streftaris and Zenetos 2006; Katsanevakis et al. 2016) based on different approaches and metrics. Depending on the criteria applied for impact assessment, different schemes can lead to strikingly different outcomes (González-Moreno et al. 2019). Hence, any such ranking of invasive species should be perceived under the limitations and assumptions of the analysis that produced it. For example, the present

study did not account for the spatial distribution of impactful species and the geographical extent of reported impacts, which for some species can be quite small (i.e. high impact but in a restricted area). Nevertheless, it is remarkable that our inventory of the ten worst invasive species is quite similar to the respective ranking in Katsanevakis et al. (2016) [their indicator D3], produced by a quite different approach, i.e. the sum of cumulative impact scores of the species on marine habitats based on a conservative additive model (CIMPAL) across all 10 × 10 km cells that cover the entire Mediterranean Sea. Eight of the ten top species are shared by the two rankings.

We recorded a variety of impacts on biodiversity, ecosystem services and human health caused by alien and cryptogenic species. Without forgetting that all introduced species represent a disturbance to nature by modifying native ecosystems (Ricciardi et al. 2013), management choices need to be based on robust evidence. This remains a primary need in the process of evaluating the effects of alien species in ecosystems. The way forward to interpret biological invasions and prioritise management actions is to incorporate holistic approaches to alien species impact assessments, accounting for both positive and negative impacts and socio-ecological tradeoffs, and increase the strength of evidence through the implementation of more experimental studies.

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Authors' contribution

KTs: research conceptualization, design and methodology, review and data collection, data analysis, writing the first draft of the manuscript; SK: research conceptualization, design and methodology, data analysis, supervision, editing and writing; all authors: validating data, contribution with additional data and taxonomic expertise, interpretation, editing and writing.

References

Albano PG, Steger J, Bošnjak M, Dunne B, Guifarro Z, Turapova E, Hua Q, Kaufman DS, Rilov G, Zuschin M (2021) Native biodiversity collapse in the eastern Mediterranean. *Proceedings of the Royal Society B* 288: 20202469, https://doi.org/10.1098/rspb.2020.2469

Apostolaki ET, Vizzini S, Santinelli V, Kaberi H, Andolina C, Papathanassiou E (2019) Exotic *Halophila stipulacea* is an introduced carbon sink for the Eastern Mediterranean Sea. *Scientific Reports* 9: 9643, https://doi.org/10.1038/s41598-019-45046-w

Azzurro E, Sbragaglia V, Cerri J, Bariche M, Bolognini L, Ben Souissi J, Busoni G, Coco S, Chryssanthi A, Fanelli E, Ghanem R, Garrabou J, Gianni F, Grati F, Kolitari J, Letterio G, Lipej L, Mazzoldi C, Milone N, Pannacciulli F, Pešić A, Samuel-Rhoads Y, Saponari L, Tomanic J, Topçu NE, Vargiu G, Moschella P (2019) Climate change, biological invasions, and the shifting distribution of Mediterranean fishes: A large-scale survey based on local ecological knowledge. *Global Change Biology* 25: 2779–2792, https://doi.org/10.1111/gcb.14670

Azzurro E, Bariche M, Cerri J, Garrabou J (2020) The long reach of the Suez Canal: *Lagocephalus sceleratus* (Gmelin, 1789) an unwanted Indo-Pacific pest at the Atlantic gates. *BioInvasions Records* 9: 204–208, https://doi.org/10.3391/bir.2020.9.2.05

Bacher S, Blackburn TM, Essl F, Jeschke JM, Genovesi P, Heikkilä J, Jones G, Keller R, Kenis M, Kueffer C, Martinou AF, Nentwig W, Pergl J, Pyšek P, Rabitsch W, Richardson DM, Roy HE, Saul WC, Scalera R, Vilà M, Wilson JRU, Kumschick S (2018) Socio-economic impact classification of alien taxa (SEICAT). *Methods in Ecology and Evolution* 9: 159–168, https://doi.org/10.1111/2041-210X.12844

Bedini R, Bedini M, Bonechi L, Piazzi L (2014) Effects of non-native turf-forming Rhodophyta on mobile macro-invertebrate assemblages in the north-western Mediterranean Sea. *Marine Biology Research* 11: 430–437, https://doi.org/10.1080/17451000.2014.952310

Bédry R, de Haro L, Bentur Y, Senechal N, Galil BS (2021) Toxicological risks on the human health of populations living around the Mediterranean Sea linked to the invasion of non-indigenous marine species from the Red Sea: A review. *Toxicon* 191: 69–82, https://doi.org/10.1016/j.toxicon.2020.12.012

Bellard C, Cassey P, Blackburn TM (2016) Alien species as a driver of recent extinctions. *Biology Letters* 12: 20150623, https://doi.org/10.1098/rsbl.2015.0623

Ben Rais Lasram F, Mouillot D (2009) Increasing southern invasion enhances congruence between endemic and exotic Mediterranean fish fauna. *Biological Invasions* 11: 697–711, https://doi.org/10.1007/s10530-008-9284-4

Berke SK (2010) Functional groups of ecosystem engineers: a proposed classification with comments on current issues. *Integrative and Comparative Biology* 50: 147–157, https://doi.org/10.1093/icb/icq077

Blackburn TM, Pyšek P, Bacher S, Carlton JT, Duncan RP, Jarošík V, Wilson JR, Richardson DM (2011) A proposed unified framework for biological invasions. *Trends in Ecology and Evolution* 26: 333–339, https://doi.org/10.1016/j.tree.2011.03.023

Blackburn TM, Essl F, Evans T, Hulme PE, Jeschke JM, Kühn I, Kumschick S, Marková Z, Mrugała A, Nentwig W, Pergl J, Pyšek P, Rabitsch W, Ricciardi A, Richardson DM, Sendek A, Vilà M, Wilson JRU, Winter M, Genovesi P, Bacher S (2014) A Unified Classification of Alien Species Based on the Magnitude of their Environmental Impacts. *PLoS Biology* 12: e1001850, https://doi.org/10.1371/journal.pbio.1001850

Bonanno G (2016) Alien species: to remove or not to remove? That is the question. *Environmental Science & Policy* 59: 67–73, https://doi.org/10.1016/j.envsci.2016.02.011

Bonaviri C, Vega FernándezT, Fanelli G, Badalamenti F, Gianguzza P (2011) Leading role of the sea urchin *Arbacia lixula* in maintaining the barren state in southwestern Mediterranean. *Marine Biology* 158: 2505–2513, https://doi.org/10.1007/s00227-011-1751-2

Carlton JT (2002) Bioinvasion Ecology: Assessing Invasion Impact and Scale. In: Leppäkoski E, Gollasch S, Olenin S, (eds), Invasive Aquatic Species of Europe. Distribution, Impacts and Management. Kluwer Academic Publishers, Dordrecht, pp 7–19, https://doi.org/10.1007/978-94-015-9956-6_2

Castro-Díez P, Vaz AS, Silva JS, van Loo M, Alonso Á, Aponte C, Bayón Á, Bellingham PJ, Chiuffo MC, DiManno N, Julian K, Kandert S, La Porta N, Marchante H, Maule HG, Mayfield MM, Metcalfe D, Monteverdi MC, Núñez MA, Ostertag R, Parker IM, Peltzer DA, Potgieter LJ, Raymundo M, Rayome D, Reisman-Berman O, Richardson DM, Roos RE, Saldaña A, Shackleton RT, Torres A, Trudgen M, Urban J, Vicente JR, Vilà M, Ylioja T, Zenni RD, Godoy O (2019) Global effects of non-native tree species on multiple ecosystem services. *Biological Reviews* 94: 1477–1501, https://doi.org/10.1111/brv.12511

Ceccherelli G, Campo D (2002) Different effects of *Caulerpa racemosa* on two co-occurring seagrasses in the Mediterranean. *Botanica Marina* 45: 71–76, https://doi.org/10.1515/BOT.2002.009

Cheung WW, Watson R, Pauly D (2013) Signature of ocean warming in global fisheries catch. *Nature* 497: 365–368, https://doi.org/10.1038/nature12156

Clavero M, Brotons L, Pons P, Sol D (2009) Prominent role of invasive species in avian biodiversity loss. *Biological Conservation* 142: 2043–2049, https://doi.org/10.1016/j.biocon.2009.03.034

Coll M, Piroddi C, Steenbeek J, Kaschner K, Ben Rias Lasram F, Aguzzi J, Ballesteros E, Bianchi CN, Corbera J, Dailianis T, Danovaro R, Estrada M, Froglia C, Galil BS, Gasol JM, Gertwagen R, Gil J, Guilhaumon F, Kesner-Reyes K, Kitsos M, Koukouras A, Lampadariou N, Laxamana E, López-Fé de la Cuadra CM, Lotze HK, Martin D, Mouillot D, Oro D, Raicevich S, Rius Barile J, Saiz-Salinas JI, San Vicente C, Somot S, Templado J, Turon X, Vafidis D, Villanueva R, Voultsiadou E (2010) The Biodiversity of the

Mediterranean Sea: estimates, patterns, and threats. *PLoS ONE* 5: e11842, https://doi.org/10.1371/journal.pone.0011842

Costello MJ, Dekeyzer D, Galil BS, Hutchings P, Katsanevakis S, Pagad S, Robinson TB, Turon X, Vandepitte L, Vanhoorne B, Verfaille K, Willan RC, Rius M (2021) Introducing the World Register of Introduced Marine Species (WRiMS). *Management of Biological Invasions* 12: 792–811, https://doi.org/10.3391/mbi.2021.12.4.02

Davidson AD, Hewitt CL (2014) How often are invasion-induced ecological impacts missed? *Biological Invasions* 16: 1165–1173, https://doi.org/10.1007/s10530-013-0570-4

Davis MA, Chew MK, Hobbs RJ, Lugo AE, Ewel JJ, Vermeij GJ, Brown JH, Rosenzweig ML, Gardener MR, Carroll SP, Thompson K, Pickett A, Stromberg JC, Del Tredici P, Suding KN, Ehrenfeld JG, Grime JP, Mascaro J, Briggs JC (2011) Don't judge species on their origins. *Nature* 474: 153–154, https://doi.org/10.1038/474153a

Dhahri M, Sioud S, Dridi R, Hassine M, Boughattas NA, Almulhim F, Al Talla Z, Jaremko M, Emwas AH (2020) Extraction, Characterization, and Anticoagulant Activity of a Sulfated Polysaccharide from *Bursatella leachii* Viscera. *ACS Omega* 5: 14786–14795, https://doi.org/10.1021/acsomega.0c01724

Diagne C, Leroy B, Vaissière AC, Gozlan RE, Roiz D, Jarić I, Salles JM, Bradshaw CJ, Courchamp F (2021) High and rising economic costs of biological invasions worldwide. *Nature* 592: 571–576, https://doi.org/10.1038/s41586-021-03405-6

Di Martino V, Stancanelli B, Molinari A (2007) Fish community associated with *Halophila stipulacea* meadow in the Mediterranean Sea. *Cybium* 31: 451–458, https://doi.org/10.26028/cybium/2007-314-006

Dimitriadis C, Galanidi M, Zenetos A, Corsini-Foka M, Giovos I, Karachle PK, Fournari-Konstantinidou I, Kytinou E, Issaris Y, Azzurro E, Castriota L, Falautano M, Kalimeris A, Katsanevakis S (2020) Updating the occurrences of *Pterois miles* in the Mediterranean Sea, with considerations on thermal boundaries and future range expansion. *Mediterranean Marine Science* 21: 62–69, https://doi.org/10.12681/mms.21845

Dimitriadis C, Fournari-Konstantinidou I, Sourbès L, Koutsoubas D, Katsanevakis S (2021) Long term interactions of native and invasive species in a marine protected area suggest complex cascading effects challenging conservation outcomes. *Diversity* 13: 71, https://doi.org/10.3390/d13020071

Doherty TS, Glen AS, Nimmo DG, Ritchie EG, Dickman CR (2016) Invasive predators and global biodiversity loss. *Proceedings of the National Academy of Sciences* 113: 11261–11265, https://doi.org/10.1073/pnas.1602480113

Edelist D, Rilov G, Golani D, Carlton JT, Spanier E (2013) Restructuring the sea: profound shifts in the world's most invaded marine ecosystem. *Diversity and Distributions* 19: 69–77, https://doi.org/10.1111/ddi.12002

Ehrenfeld JG (2010) Ecosystem consequences of biological invasions. *Annual Review of Ecology, Evolution and Systematics* 41: 59–80, https://doi.org/10.1146/annurev-ecolsys-102209-144650

Engel MS, Ceríaco LMP, Daniel GM, Dellapé PM, Löbl I, Marinov M, Reis RE, Young MT, Dubois A, Agarwal I, Lehmann P, Alvarado M, Alvarez N, Andreone F, Araujo-Vieira K, Ascher JS, Baêta D, Baldo D, Bandeira SA, Barden P, Barrasso DA, Bendifallah L, Bockmann FA, Böhme W, Borkent A, Brandão CRF, Busack SD, Bybee SM, Channing A, Chatzimanolis S, Christenhusz MJM, Crisci JV, D'elía G, Da Costa LM, Davis SR, De Lucena CAS, Deuve T, Fernandes SE, Faivovich J, Farooq H, Ferguson AW, Gippoliti S, Gonçalves FMP, Gonzalez VH, Greenbaum E, Hinojosa-Díaz IA, Ineich I, Jiang J, Kahono S, Kury AB, Lucinda PHF, Lynch JD, Malécot V, Marques MP, Marris JWM, Mckellar RC, Mendes LF, Nihei SS, Nishikawa K, Ohler A, Orrico VGD, Ota H, Paiva J, Parrinha D, Pauwels OSG, Pereyra MO, Pestana LB, Pinheiro PDP, Prendini L, Prokop J, Rasmussen C, Rödel MO, Rodrigues MT, Rodríguez SM, Salatnaya H, Sampaio I, Sánchez-García A, Shebl MA, Santos BS, Solórzano-Kraemer MM, Sousa ACA, Stoev P, Teta P, Trape JF, Van-Dúnem Dos Santos C, Vasudevan K, Vink CJ, Vogel G, Wagner P, Wappler T, Ware JL, Wedmann S, Zacharie CK (2021) The taxonomic impediment: a shortage of taxonomists, not the lack of technical approaches. *Zoological Journal of the Linnean Society* 193: 381–387, https://doi.org/10.1093/zoolinnean/zlab072

Essl F, Dullinger S, Genovesi P, Hulme PE, Jeschke JM, Katsanevakis S, Kühn I, Lenzner B, Pauchard A, Pyšek P, Rabitsch W, Richardson DM, Seebens H, van Kleunen M, van der Puttten WH, Vilà M, Bacher S (2019) A conceptual framework for range-expanding species that track human-induced environmental change. *BioScience* 69: 908–919, https://doi.org/10.1093/biosci/biz101

Evers CR, Wardropper CB, Branoff B, Granek EF, Hirsch SL, Link TE, Olivero-Lora S, Wilson C (2018) The Ecosystem Services and Biodiversity of Novel Ecosystems: A Literature Review. *Global Ecology and Conservation* 13: e00362, https://doi.org/10.1016/j.gecco.2017.e00362

Fanelli E, Azzurro E, Bariche M, Cartes JE, Maynou F (2015) Depicting the novel Eastern Mediterranean food web: a stable isotopes study following Lessepsian fish invasion. *Biological Invasions* 17: 2163–2178, https://doi.org/10.1007/s10530-015-0868-5

Galanidi M, Zenetos A, Bacher S (2018) Assessing the socio- economic impacts of priority marine invasive fishes in the Mediterranean with the newly proposed SEICAT methodology. *Mediterranean Marine Science* 19: 107–123, https://doi.org/10.12681/mms.15940

Galil BS (2007) Loss or gain? Invasive aliens and biodiversity in the Mediterranean Sea. *Marine Pollution Bulletin* 55: 314–322, https://doi.org/10.1016/j.marpolbul.2006.11.008

Galil B (2018) Poisonous and venomous: marine alien species in the Mediterranean Sea and human health. In: Mazza G, Tricarico E (eds), CABI Invasive Series 10: Invasive Species and Human Health. CABI International, Walingford, United Kingdom, pp 1–15, https://doi.org/10.1079/9781786390981.0001

Galil BS, Marchini A, Occhipinti-Ambrogi A (2016) East is east and West is west? Management of marine bioinvasions in the Mediterranean Sea. *Estuarine, Coastal and Shelf Science* 201: 7–16, https://doi.org/10.1016/j.ecss.2015.12.021

García-Gómez JC, Sempere-Valverde J, González AR, Martínez-Chacón M, Olaya-Ponzone L, Sánchez-Moyano E, Ostalé-Valriberas E, Megina C (2020) From exotic to invasive in record time: The extreme impact of *Rugulopteryx okamurae* (Dictyotales, Ochrophyta) in the strait of Gibraltar. *Science of The Total Environment* 704: 135408, https://doi.org/10.1016/j.scitotenv.2019.135408

Garrabou J, Coma R, Bensoussan N, Bally M, Chevaldonné P, Cigliano M, Diaz D, Harmelin JG, Gambi MC, Kersting DK, Ledoux JB, Lejeusne C, Linares C, Marschal C, Pérez T, Ribes M, Romano JC, Serrano E, Teixido N, Torrents O, Zabala M, Zuberer F, Cerrano C (2009) Mass mortality in Northwestern Mediterranean rocky benthic communities: effects of the 2003 heat wave. *Global Change Biology* 15: 1090–1103, https://doi.org/10.1111/j.1365-2486.2008.01823.x

Garrabou J, Gómez-Gras D, Ledoux JB, Linares C, Bensoussan N, López-Sendino P, Bazairi H, Espinosa F, Ramdani M, Grimes S, Benabdi M, Souissi JB, Soufi E, Khamassi F, Ghanem R, Ocaña O, Ramos-Esplà A, Izquierdo A, Anton I, Rubio-Portillo E, Barbera C, Cebrian E, Marbà N, Hendriks IE, Duarte CM, Deudero S, Díaz D, Vázquez-Luis M, Alvarez E, Hereu B, Kersting DK, Gori A, Viladrich N, Sartoretto S, Pairaud I, Ruitton S, Pergent G, Pergent-Martini C, Rouanet E, Teixidó N, Gattuso JP, Fraschetti S, Rivetti I, Azzurro E, Cerrano C, Ponti M, Turicchia E, Bavestrello G, Cattaneo-Vietti R, Bo M, Bertolino M, Montefalcone M, Chimienti G, Grech D, Rilov G, Tuney Kizilkaya IT, Kizilkaya Z, Eda Topçu N, Gerovasileiou V, Sini M, Bakran-Petricioli T, Kipson S, Harmelin JG (2019) Collaborative database to track mass mortality events in the Mediterranean Sea. *Frontiers in Marine Science* 6: 707, https://doi.org/10.3389/fmars.2019.00707

Garrabou J, Gómez-Gras D, Medrano A, Cerrano C, Ponti M, Schlegel R, Bensoussan N, Turicchia E, Sini M, Gerovasileiou V, Teixido N, Mirasole A, Tamburello L, Cebrian E, Rilov G, Ledoux JB, Ben Souissi J, Khamassi F, Ghanem R, Benabdi M, Grimes S, Ocaña O, Bazairi H, Hereu B, Linares C, Kersting DK, Rovira G, Ortega J, Casals D, Pagès-Escolà M, Margarit N, Capdevila P, Verdura J, Ramos A, Izquierdo A, Barbera C, Rubio-Portillo E, Anton I, López-Sendino P, Díaz D, Vázquez-Luis M, Duarte C, Marbà N, Aspillaga E, Espinosa F, Grech D, Guala I, Azzurro E, Farina S, Gambi MC, Chimienti G, Montefalcone M, Azzola A, Pulido Mantas T, Fraschetti S, Ceccherelli G, Kipson S, Bakran-Petricioli T, Petricioli D, Jimenez C, Katsanevakis S, Tuney Kizilkaya I, Kizilkaya Z, Sartoretto S, Rouanet E, Ruitton S, Comeau S, Gattuso JP, Harmelin JG (2022) Marine heatwaves drive recurrent mass mortalities in the Mediterranean Sea. *Global Change Biology* (*in press*)

Genovese G, Tedone L, Hamann MT, Morabito M (2009) The Mediterranean red alga *Asparagopsis*: A Source of Compounds against *Leishmania*. *Marine Drugs* 7: 361–366, https://doi.org/10.3390/md7030361

Giacoletti A, Rinaldi A, Mercurio M, Mirto S, Sarà G (2016) Local consumers are the first line to control biological invasions: a case of study with the whelk *Stramonita haemastoma* (Gastropoda: Muricidae). *Hydrobiologia* 772: 117–129, https://doi.org/10.1007/s10750-016-2645-6

Giakoumi S (2014) Distribution patterns of the invasive herbivore *Siganus luridus* (Rüppell, 1829) and its relation to native benthic communities in the central Aegean Sea, Northeastern Mediterranean. *Marine Ecology* 35: 96–105, https://doi.org/10.1111/maec.12059

Gianni F, Bartolini F, Pey A, Laurent M, Martins GM, Airoldi L, Mangialajo L (2017) Threats to large brown algal forests in temperate seas: the overlooked role of native herbivorous fish. *Scientific Reports* 7: 6012, https://doi.org/10.1038/s41598-017-06394-7

Gissi E, Manea E, Mazaris AD, Fraschetti S, Almpanidou V, Bevilacqua S, Coll M, Guarnieri G, Lloret-Lloret E, Pascual M, Petza D, Rilov G, Schonwald M, Stelzenmüller V, Katsanevakis S (2021) A review of the combined effects of climate change and other human stressors on the marine environment. *Science of the Total Environment* 755: 142564, https://doi.org/10.1016/j.scitotenv.2020.142564

Gómez F (2008) Phytoplankton invasions: Comments on the validity of categorizing the non-indigenous dinoflagellates and diatoms in European Seas. *Marine Pollution Bulletin* 56: 620–628, https://doi.org/10.1016/j.marpolbul.2007.12.014

Gómez F (2019) Comments on the non-indigenous microalgae in the European seas. *Marine Pollution Bulletin* 148: 1–2, https://doi.org/10.1016/j.marpolbul.2019.07.048

González-Moreno P, Lazzaro L, Vilà M, Preda C, Adriaens T, Bacher S, Brundu G, Copp GH, Essl F, García-Berthou E, Katsanevakis S, Lucy F, Nentwig W, Roy H, Srėbalienė G, Talgø V, Vanderhoeven S, Andjelković A, Arbačiauskas K, Auger-Rozenberg MA, Bae MJ, Bariche M, Boets P, Boieiro M, Borges P, Canning-Clode J, Cardigos F, Chartosia N, Cottier-Cook EJ, Crocetta F, D'hondt B, Foggi B, Follak S, Gallardo B, Gammelmo Ø, Giakoumi S, Giuliani C, Guillaume F, Jeschke J, Jover M, Juárez-Escario A, Kalogirou S, Kočić A, Kytinou E, Laverty C, Lozano V, Maceda-Veiga A, Marchante E, Marchante H, Martinou AF, Meyer S, Minchin D, Montero-Castaño A, Morais MC, Morales-Rodriguez C, Muhthassim N, Zoltan Arpad N, Ogris N, Onen H, Pergl J, Puntila R, Rabitsch W, Ramburn TT, Rego C, Reichenbach F, Romeralo C, Saul WC, Schrader G, Jelaska LŠ, Sheehan R, Simonović P, Skolka M, Soares AO, Sundheim L, Tarkan AS, Tomov R, Tricarico E, Tsiamis K, Uludağ A, van Valkenburg J, Verreycken H, Vettraino AM, Vilar L, Wiig Ø, Witzell J, Zanetta A, Kenis M (2019) Consistency of impact assessment protocols for non-native species. *Neobiota* 44: 1–25, https://doi.org/10.3897/neobiota.44.31650

Goodenough AE (2010) Are the ecological impacts of alien species misrepresented? A review of the "native good, alien bad" philosophy. *Community Ecology* 11: 13–21, https://doi.org/10.1556/ComEc.11.2010.1.3

Harper GA, Bunbury N (2015) Invasive rats on tropical islands: their population biology and impacts on native species. *Global Ecology and Conservation* 3: 607–627, https://doi.org/10.1016/j.gecco.2015.02.010

Hereu B (2006) Depletion of palatable algae by sea urchins and fishes in a Mediterranean subtidal community. *Marine Ecology Progress Series* 313: 95–103, https://doi.org/10.3354/meps313095

Hobbs RJ, Higgs E, Harris JA (2009) Novel ecosystems: implications for conservation and restoration. *Trends in Ecology & Evolution* 24: 599–605, https://doi.org/10.1016/j.tree.2009.05.012

Howard BR, Francis FT, Côté IM, Therriault TW (2019) Habitat alteration by invasive European green crab (*Carcinus maenas*) causes eelgrass loss in British Columbia, Canada. *Biological Invasions* 21: 3607–3618, https://doi.org/10.1007/s10530-019-02072-z

Hulme PE (2014) Invasive species challenge the global response to emerging diseases. *Trends in Parasitology* 30: 267–270, https://doi.org/10.1016/j.pt.2014.03.005

Iveša L, Jaklin A, Devescovi M (2006) Vegetation patterns and spontaneous regression of *Caulerpa taxifolia* (Vahl) C. Agardh in Malinska (Northern Adriatic, Croatia). *Aquatic Botany* 85: 324–330, https://doi.org/10.1016/j.aquabot.2006.06.009

Jamjoom BA, Jamjoom AB (2016) Impact of country-specific characteristics on scientific productivity in clinical neurology research. *eNeurologicalSci* 4: 1–3, https://doi.org/10.1016/j.ensci.2016.03.002

Kampouris TE, Porter JS, Sanderson WG (2019) *Callinectes sapidus* Rathbun, 1896 (Brachyura: Portunidae): An assessment on its diet and foraging behaviour, Thermaikos Gulf, NW Aegean Sea, Greece: Evidence for ecological and economic impacts. *Crustacean Research* 48: 23–37, https://doi.org/10.18353/crustacea.48.0_23

Karachle PK, Corsini-Foka M, Crocetta F, Dulčić J, Dzhembekova N, Galanidi M, Ivanova P, Shenkar N, Skolka M, Stefanova E, Stefanova K, Surugiu V, Uysal I, Verlaque M, Zenetos A (2017) Setting-up a billboard of marine invasive species in the ESENIAS area: current situation and future expectancies. *Acta Adriatica* 58: 429–458, https://doi.org/10.32582/aa.58.3.4

Katsanevakis S, Bogucarskis K, Gatto F, Vandekerkhove J, Deriu I, Cardoso AC (2012) Building the European Alien Species Information Network (EASIN): a novel approach for the exploration of distributed alien species data. *BioInvasions Records* 1: 235–245, https://doi.org/10.3391/bir.2012.1.4.01

Katsanevakis S, Wallentinus I, Zenetos A, Leppäkoski E, Çinar ME, Oztürk B, Grabowski M, Golani D, Cardoso AC (2014a) Impacts of invasive alien marine species on ecosystem services and biodiversity: a pan-European review. *Aquatic Invasions* 9: 391–423, https://doi.org/10.3391/ai.2014.9.4.01

Katsanevakis S, Coll M, Piroddi C, Steenbeek J, Ben Rais Lasram F, Zenetos A, Cardoso AC (2014b). Invading the Mediterranean Sea: biodiversity patterns shaped by human activities. *Frontiers in Marine Science* 1: 32, https://doi.org/10.3389/fmars.2014.00032

Katsanevakis S, Tempera F, Teixeira H (2016) Mapping the impact of alien species on marine ecosystems: the Mediterranean Sea case study. *Diversity and Distributions* 22: 694–707, https://doi.org/10.1111/ddi.12429

Katsanevakis S, Rilov G, Edelist D (2018) Impacts of marine invasive alien species on European fisheries and aquaculture - plague or boon? In: Briand F (ed), CIESM Monograph 50 - Engaging marine scientists and fishers to share knowledge and perceptions - early lessons. CIESM Publisher, Monaco and Paris, pp 125–132

Katsanevakis S, Coll M, Fraschetti S, Giakoumi S, Goldsborough D, Mačić V, Mackelworth P, Rilov G, Stelzenmüller V, Albano PG, Bates AE, Bevilacqua S, Gissi E, Hermoso V, Mazaris AD, Pita C, Rossi V, Teff-Seker Y, Yates K (2020a) Twelve Recommendations for Advancing Marine Conservation in European and Contiguous Seas. *Frontiers in Marine Science* 7: 565968, https://doi.org/10.3389/fmars.2020.565968

Katsanevakis S, Tsirintanis K, Sini M, Gerovasileiou V, Koukourouvli N (2020b) Aliens in the Aegean - A sea under siege (ALAS). *Research Ideas and Outcomes* 6: e53057, https://doi.org/10.3897/rio.6.e53057

Kideys AE (2002) Fall and rise of the Black Sea ecosystem. *Science* 297: 1482–1484, https://doi.org/10.1126/science.1073002

Korpinen S, Klančnik K, Peterlin M, Nurmi M, Laamanen L, Zupančič G, Popit A, Murray C, Harvey T, Andersen JH, Zenetos A, Stein U, Tunesi L, Abhold K, Piet G, Kallenbach E, Agnesi S, Bolman B, Vaughan D, Reker J, Royo Gelabert E (2019) Multiple pressures and their combined effects in Europe's seas. ETC/ICM Technical Report 4/2019: European Topic Centre on Inland, Coastal and Marine waters, 164 pp, https://www.eionet.europa.eu/etcs/etc-icm/products/etc-icm-report-4-2019-multiple-pressures-and-their-combined-effects-in-europes-seas

Kumschick S, Bacher S, Dawson W, Heikkilä J, Sendek A, Pluess T, Robinson TB, Kühn I (2012) A conceptual framework for prioritization of invasive alien species for management according to their impact. *NeoBiota* 15: 69–100, https://doi.org/10.3897/neobiota.15.3323

Kumschick S, Bacher S, Evans T, Markova Z, Pergl J, Pyšek P, Vaes-Petignat S, van der Veer G, Vilà M, Nentwig W (2015) Comparing impacts of alien plants and animals in Europe using a standard scoring system. *Journal of Applied Ecology* 52: 552–561, https://doi.org/10.1111/1365-2664.12427

Kytinou E, Sini M, Issaris Y, Katsanevakis S (2020) Global systematic review of methodological approaches to analyze coastal shelf food webs. *Frontiers in Marine Science* 7: 636, https://doi.org/10.3389/fmars.2020.00636

Lejeusne C, Chevaldonné P, Pergent-Martini C, Boudouresque CF, Pérez T (2010) Climate change effects on a miniature ocean: the highly diverse, highly impacted Mediterranean Sea. *Trends in Ecology & Evolution* 25: 250–260, https://doi.org/10.1016/j.tree.2009.10.009

Liquete C, Piroddi C, Drakou EG, Gurney L, Katsanevakis S, Charef A, Egoh B (2013) Current status and future prospects for the assessment of marine and coastal ecosystem services: a systematic review. *PLoS ONE* 8: e67737, https://doi.org/10.1371/journal.pone.0067737

Mačić V, Albano PG, Almpanidou V, Claudet J, Corrales X, Essl F, Evagelopoulos A, Giovos I, Jimenez C, Kark S, Marković O, Mazaris AD, Ólafsdóttir GÁ, Panayotova M, Petović S, Rabitsch W, Ramdani M, Rilov G, Tricarico E, Vega Fernández T, Sini M, Trygonis V, Katsanevakis S (2018) Biological Invasions in Conservation Planning: A Global Systematic Review. *Frontiers in Marine Science* 5: 178, https://doi.org/10.3389/fmars.2018.00178

Man JP, Weinkauf JG, Tsang M, Sin JHDD (2004) Why do some countries publish more than others? An international comparison of research funding, English proficiency and publication output in highly ranked general medical journals. *European Journal of Epidemiology* 19: 811–817, https://doi.org/10.1023/B:EJEP.0000036571.00320.b8

Manconi R, Padiglia A, Padedda BM, Pronzato R (2020) Invasive green algae in a western Mediterranean Marine Protected Area: interaction of photophilous sponges with *Caulerpa cylindracea*. *Journal of the Marine Biological Association of the United Kingdom* 100: 361–373, https://doi.org/10.1017/S0025315420000193

Marbà N, Jordà G, Agusti S, Girard C, Duarte CM (2015) Footprints of climate change on Mediterranean Sea biota. *Frontiers in Marine Science* 2: 56, https://doi.org/10.3389/fmars.2015.00056

Marras S, Cucco A, Antognarelli F, Azzurro E, Milazzo M, Bariche M, Butenschön M, Kay S, Di Bitetto M, Quattrocchi G, Sinerchia M, Domenici P (2015) Predicting future thermal habitat suitability of competing native and invasive fish species: from metabolic scope to oceanographic modelling. *Conservation Physiology* 3: 1–14, https://doi.org/10.1093/conphys/cou059

Mason NWH, Palmer DJ, Vetrova V, Brabyn L, Paul T, Willemse P, Peltzer DA (2017) Accentuating the positive while eliminating the negative of alien tree invasions: a multiple ecosystem services approach to prioritising control efforts. *Biological Invasions* 19: 1181–1195, https://doi.org/10.1007/s10530-016-1307-y

Meo SA, Al Masri AA, Usmani AM, Memon AN, Zaidi SZ (2013) Impact of GDP, spending on R&D, number of universities and scientific journals on research publications among Asian countries. *PLoS ONE* 8: e66449, https://doi.org/10.1371/journal.pone.0066449

Minicante SA, Michelet S, Bruno F, Castelli G, Vitale F, Sfriso A, Morabito M, Genovese G (2016) Bioactivity of phycocolloids against the mediterranean protozoan *Leishmania infantum*: An inceptive study. *Sustainability* 8: 1131, https://doi.org/10.3390/su8111131

Montefalcone M, Morri C, Parravicini V, Bianchi CN (2015) A tale of two invaders: divergent spreading kinetics of the alien green algae *Caulerpa taxifolia* and *Caulerpa cylindracea*. *Biological Invasions* 17: 2717–2728, https://doi.org/10.1007/s10530-015-0908-1

Morri C, Montefalcone M, Gatti G, Vassallo P, Paoli C, Bianchi CN (2019) An alien invader is the cause of homogenization in the recipient ecosystem: a simulation-like approach. *Diversity* 11: 146, https://doi.org/10.3390/d11090146

Mueller CE (2016) Accurate forecast of countries' research output by macro-level indicators. *Scientometrics* 109: 1307–1328, https://doi.org/10.1007/s11192-016-2084-1

Munari C, Bocchi N, Mistri M (2015) Epifauna associated to the introduced *Gracilaria vermiculophylla* (Rhodophyta; Florideophyceae: Gracilariales) and comparison with the

native *Ulva rigida* (Chlorophyta; Ulvophyceae: Ulvales) in an Adriatic lagoon. *Italian Journal of Zoology* 82: 436–445, https://doi.org/10.1080/11250003.2015.1020349
Navarro-Barranco C, Florido M, Ros M, González-Romero P, Guerra-García JM (2018) Impoverished mobile epifaunal assemblages associated with the invasive macroalga *Asparagopsis taxiformis* in the Mediterranean Sea. *Marine Environmental Research* 141: 44–52, https://doi.org/10.1016/j.marenvres.2018.07.016
Nentwig W, Bacher S, Pyšek P, Vilà M, Kumschick S (2016) The generic impact scoring system (GISS): a standardized tool to quantify the impacts of alien species. *Environmental Monitoring and Assessment* 188: 315, https://doi.org/10.1007/s10661-016-5321-4
Novi L, Bracco A, Falasca F (2021) Uncovering marine connectivity through sea surface temperature. *Scientific Reports* 11: 8839, https://doi.org/10.1038/s41598-021-87711-z
O'Brien E, Caramanna G (2017) Human Factor in Scientific Diving: an Experimental Approach. AAUS Diving For Science Symposium, Thunder Bay National Marine Sanctuary, Alpena, MI, USA, 11 pp
Ojaveer H, Galil BS, Campbell ML, Carlton JT, Canning-Clode J, Cook EJ, Davidson AD, Hewitt CL, Jelmert A, Marchini A, McKenzie CH, Minchin D, Occhipinti-Ambrogi A, Olenin S, Ruiz G (2015) Classification of Non-Indigenous Species Based on Their Impacts: Considerations for Application in Marine Management. *PLoS Biology* 13: e1002130, https://doi.org/10.1371/journal.pbio.1002130
Ojaveer H, Galil BS, Carlton JT, Alleway H, Goulletquer P, Lehtiniemi M, Marchini A, Miller W, Occhipinti-Ambrogi A, Peharda M, Ruiz GM, Williams SL, Zaiko A (2018) Historical baselines in marine bioinvasions: Implications for policy and management. *PLoS ONE* 13: e0202383, https://doi.org/10.1371/journal.pone.0202383
Olden JD, Poff NL, Douglas MR, Douglas ME, Fausch KD (2004) Ecological and evolutionary consequences of biotic homogenization. *Trends in Ecology and Evolution* 19: 18–24, https://doi.org/10.1016/j.tree.2003.09.010
Otero M, Cebrian E, Francour P, Galil B, Savini D (2013) Monitoring marine invasive species in Mediterranean Marine Protected Areas (MPAs): a strategy and practical guide for managers. Medpan North project. IUCN, Malaga, Spain, 136 pp
Ozer T, Gertman I, Kress N, Silverman J, Herut B (2017) Interannual thermohaline (1979-2014) and nutrient (2002-2014) dynamics in the Levantine surface and intermediate water masses, SE Mediterranean Sea. *Global and Planetary Change* 151: 60–67, https://doi.org/10.1016/j.gloplacha.2016.04.001
Papadakis O, Tsirintanis K, Lioupa V, Katsanevakis S (2021) The neglected role of omnivore fish in the overgrazing of Mediterranean rocky reefs. *Marine Ecology Progress Series* 673: 107–116, https://doi.org/10.3354/meps13810
Parker IM, Simberloff D, Lonsdale WM, Goodell K, Wonham M, Kareiva PM, Williamson MH, Von Holle B, Moyle PB, Byers JE, Goldwasser L (1999) Impact: toward a framework for understanding the ecological effects of invaders. *Biological Invasions* 1: 3–19, https://doi.org/10.1023/A:1010034312781
Pereda-Briones L, Tomas F, Terrados J (2018) Field transplantation of seagrass (*Posidonia oceanica*) seedlings: Effects of invasive algae and nutrients. *Marine Pollution Bulletin* 134: 160–165, https://doi.org/10.1016/j.marpolbul.2017.09.034
Peyton J, Martinou AF, Pescott OL, Demetriou M, Adriaens T, Arianoutsou M, Bazos I, Bean WC, Booy O, Botham M, Britton RJ, Cervia JL, Charilaou P, Chartosia N, Dean JH, Delipetrou P, Dimitriou CA, Dörflinger, G, Fawcett J, Fyttis G, Galanidis A, Galil B, Hadjikyriakou T, Hadjistylli M, Ieronymidou C, Jimenez C, Karachle P, Kassinis N, Kerametsidis G, Kirschel GNA, Kleitou P, Kleitou D, Manolaki P, Michailidis N, Owen Mountford J, Nikolaou C, Papatheodoulou A, Payiatas G, Ribeiro F, Rorke LS, Samouel Y, Savvides P, Schafer MS, Serhan Tarkan A, Silva-Rocha I, Top N, Tricarico E, Turvey K, Tziortzis I, Tzirkalli E, Verreycken H, Winfield JI, Zenetos A, Roy EH (2019) Horizon scanning for invasive alien species with the potential to threaten biodiversity and human health on a Mediterranean island. *Biological Invasions* 21: 2107–2125, https://doi.org/10.1007/s10530-019-01961-7
Pisano A, Marullo S, Artale V, Falcini F, Yang C, Leonelli FE, Santoleri R, Buongiorno Nardelli B (2020) New Evidence of Mediterranean Climate Change and Variability from Sea Surface Temperature Observations. *Remote Sensing* 12: 132, https://doi.org/10.3390/rs12010132
Pranovi F, Franceschini G, Casale M, Zucchetta M, Torricelli P, Giovanardi O (2006) An ecological imbalance induced by a non-native species: the Manila clam in the Venice Lagoon. *Biological Invasions* 8: 595–609, https://doi.org/10.1007/s10530-005-1602-5
Pyšek P, Richardson DM, Pergl J, Jarošík V, Siztová Z, Weber E (2008) Geographical and taxonomic biases in invasion ecology. *Trends in Ecology & Evolution* 23: 237–244, https://doi.org/10.1016/j.tree.2008.02.002
Pyšek P, Hulme PE, Simberloff D, Bacher S, Blackburn TM, Carlton JT, Dawson W, Essl F, Foxcroft LC, Genovesi P, Jeschke JM, Kühn I, Liebhold AM, Mandrak NE, Meyerson LA, Pauchard A, Pergl J, Roy HE, Seebens H, van Kleunen M, Vilà M, Wingfield MJ,

Richardson DM (2020) Scientists' warning on invasive alien species. *Biological Reviews* 95: 1511–1534, https://doi.org/10.1111/brv.12627

Ricciardi A (2007) Are modern biological invasions an unprecedented form of global change? *Conservation Biology* 21: 329–336, https://doi.org/10.1111/j.1523-1739.2006.00615.x

Ricciardi A, Hoopes MF, Marchetti MP, Lockwood JL (2013) Progress toward understanding the ecological impacts of nonnative species. *Ecological Monographs* 83: 263–282, https://doi.org/10.1890/13-0183.1

Rilov G (2016) Multi-species collapses at the warm edge of a warming sea. *Scientific Reports* 6: 36897, https://doi.org/10.1038/srep36897

Rilov G, Benayahu Y, Gasith A (2004) Prolonged lag in population outbreak of an invasive mussel: a shifting-habitat model. *Biological Invasions* 6: 347–364, https://doi.org/10.1023/B:BINV.0000034614.07427.96

Sala E, Boudouresque CF, Harmelin-Vivien M (1998) Fishing, trophic cascades and the structure of algal assemblages: evaluation of an old but untested paradigm. *Oikos* 82: 425–439, https://doi.org/10.2307/3546364

Sala E, Kizilkaya Z, Yildirim D, Ballesteros E (2011) Alien marine fishes deplete algal biomass in the eastern Mediterranean. *PLoS ONE* 6: e17356, https://doi.org/10.1371/journal.pone.0017356

Santamaría J (2021) Unraveling the success of invaders: Biotic and abiotic factors determining the invasibility of Mediterranean benthic assemblages by *Caulerpa cylindracea*. PhD thesis, University of Girona, Girona, Spain, 201 pp

Sarà G, Giommi C, Giacoletti A, Conti E, Mulder C, Mangano MC (2021) Multiple climate-driven cascading ecosystem effects after the loss of a foundation species. *Science of The Total Environment* 770: 144749, https://doi.org/10.1016/j.scitotenv.2020.144749

Schaffner F, Medlock JM, Van Bortel AW (2013) Public health significance of invasive mosquitoes in Europe. *Clinical Microbiology and Infection* 19: 685–692, https://doi.org/10.1111/1469-0691.12189

Schlaepfer MA, Sax DF, Olden JD (2011) The potential conservation value of non-native species. *Conservation Biology* 25: 428–437, https://doi.org/10.1111/j.1523-1739.2010.01646.x

Seebens H, Blackburn TM, Dyer EE, Genovesi P, Hulme PE, Jeschke JM, Pagad S, Pyšek P, Winter M, Arianoutsou M, Bacher S, Blasius B, Brundu G, Capinha C, Celesti-Grapow L, Dawson W, Dullinger S, Fuentes N, Jäger H, Kartesz J, Kenis M, Kreft H, Kühn I, Lenzner B, Liebhold A, Mosena A, Moser D, Nishino M, Pearman D, Pergl J, Rabitsch W, Rojas-Sandoval J, Roques A, Rorke S, Rossinelli S, Roy HE, Scalera R, Schindler S, Štajerová K, Tokarska-Guzik B, van Kleunen M, Walker K, Weigelt P, Yamanaka T, Essl F (2017) No saturation in the accumulation of alien species worldwide. *Nature Communications* 8: 14435, https://doi.org/10.1038/ncomms14435

Sfriso A, Buosi A, Wolf MA, Sfriso AA (2020) Invasion of alien macroalgae in the Venice Lagoon, a pest or a resource? *Aquatic Invasions* 15: 245–270, https://doi.org/10.3391/ai.2020.15.2.03

Shackleton RT, Shackleton CM, Kull CA (2019) The role of invasive alien species in shaping local livelihoods and human well-being: A review. *Journal of Environmental Management* 229: 145–157, https://doi.org/10.1016/j.jenvman.2018.05.007

Simberloff D (2011) How common are invasion-induced ecosystem impacts? *Biological Invasions* 13: 1255–1268, https://doi.org/10.1007/s10530-011-9956-3

Simberloff D, Martin JL, Genovesi P, Maris V, Wardle DA, Aronson J, Courchamp F, Galil B, García-Berthou E, Pascal M, Pyšek P, Sousa R, Tabacchi E, Vilà M (2013) Impacts of biological invasions: what's what and the way forward. *Trends in Ecology & Evolution* 28: 58–66, https://doi.org/10.1016/j.tree.2012.07.013

Spalding MD, Fox HE, Allen GR, Davidson N, Ferdaña ZA, Finlayson M, Halpern BS, Jorge MA, Lombana A, Lourie SA, Martin KD, McManus E, Molnar J, Recchia CA, Robertson J (2007) Marine ecoregions of the world: A bioregionalization of coastal and shelf areas. *BioScience* 57: 573–583, https://doi.org/10.1641/B570707

Stergiou KI, Somarakis S, Triantafyllou G, Tsiaras KP, Giannoulaki M, Petihakis G, Machias A, Tsikliras AC (2016) Trends in productivity and biomass yields in the Mediterranean Sea Large Marine Ecosystem during climate change. *Environmental Development* 17: 57–74, https://doi.org/10.1016/j.envdev.2015.09.001

Stranga Y, Katsanevakis S (2021) Eight years of BioInvasions Records: patterns and trends in alien and cryptogenic species records. *Management of Biological Invasions* 12: 221–239, https://doi.org/10.3391/mbi.2021.12.2.01

Strayer DL, D'Antonio CM, Essl F, Fowler MS, Geist J, Hilt S, Jarić I, Jöhnk K, Jones CG, Lambin X, Latzka AW, Pergl J, Pysek P., Robertson P, von Schmalensee M, Stefansson RA, Wright J, Jeschke JM (2017) Boom-bust dynamics in biological invasions: towards an improved application of the concept. *Ecology Letters* 20: 1337–1350, https://doi.org/10.1111/ele.12822

Streftaris N, Zenetos A (2006) Alien Marine Species in the Mediterranean - the 100 'Worst Invasives' and their Impact. *Mediterranean Marine Science* 7: 87–118, https://doi.org/10.12681/mms.180

Thomsen MS, Wernberg T, Olden JD, Byers JE, Bruno JF, Silliman BR, Schiel DR (2014) Forty years of experiments on aquatic invasive species: are study biases limiting our understanding of impacts? *NeoBiota* 22: 1–22, https://doi.org/10.3897/neobiota.22.6224

Tiralongo F, Messina G, Lombardo BM (2021) Invasive Species Control: Predation on the Alien Crab *Percnon gibbesi* (H. Milne Edwards, 1853) (Malacostraca: Percnidae) by the Rock Goby, *Gobius paganellus* Linnaeus, 1758 (Actinopterygii: Gobiidae). *Journal of Marine Science and Engineering* 9: 393, https://doi.org/10.3390/jmse9040393

Tsiamis K, Azzurro E, Bariche M, Çinar ME, Crocetta F, De Clerck O, Galil B, Gomez F, Hoffman R, Jensen K, Kamburska L, Langeneck J, Langer M, Levitt-Barmats Y, Lezzi M, Marchini A, Occhipinti-Ambrogi A, Ojaveer H, Piraino S, Shenkar N, Yankova M, Zenetos A, Žuljević A, Cardoso AC (2020) Prioritizing marine invasive alien species in the EU through Horizon Scanning. *Aquatic Conservation: Marine and Freshwater Ecosystems* 30: 794–845, https://doi.org/10.1002/aqc.3267

Tsiamis K, Palialexis A, Connor D, Antoniadis S, Bartilotti C, Bartolo G.A, Berggreen UC, Boschetti S, Buschbaum C, Canning-Clode J, Carbonell A, Castriota L, Corbeau C, Costa A, Cvitković I, Despalatović M, Dragičević B, Dulčić J, Fortič A, Francé J, Gittenberger A, Gizzi F, Gollasch S, Gruszka P, Hegarty M, Hema T, Jensen K, Josephides M, Kabuta S, Kerckhof F, Kovtun-Kante A, Krakau M, Kraśniewski W, Lackschewitz D, Lehtiniemi M, Lieberum C, Linnamägi M, Lipej L, Livi S, Lundgreen K, Magliozzi C, Massé C, Mavrič B, Michailidis N, Moncheva S, Mozetič P, Naddafi R, Ninčević Gladan Z, Ojaveer H, Olenin S, Orlando-Bonaca M, Ouerghi A, Parente M, Pavlova P, Peterlin M, Pitacco V, Png-Gonzalez L, Rousou M, Sala-Pérez M, Serrano A, Skorupski J, Smolders S, Srebaliene G, Stæhr PA, Stefanova K, Strake S, Tabarcea C, Todorova V, Trkov D, Tuaty-Guerra M, Vidjak O, Zenetos A, Žuljević A, Cardoso AC (2021) Marine Strategy Framework Directive - Descriptor 2, Non-Indigenous Species, Delivering solid recommendations for setting threshold values for non-indigenous species pressure on European seas, EUR 30640EN, Publications Office of the European Union, Luxembourg, https://doi.org/10.2760/035071

Tsikliras AC, Stergiou KI (2014) The mean temperature of the catch increases quickly in the Mediterranean Sea. *Marine Ecology Progress Series* 515: 281–284, https://doi.org/10.3354/meps11005

Tsirintanis K, Sini M, Doumas O, Trygonis V, Katsanevakis S (2018) Assessment of grazing effects on phytobenthic community structure at shallow rocky reefs: An experimental field study in the North Aegean Sea. *Journal of Experimental Marine Biology and Ecology* 503: 31–40, https://doi.org/10.1016/j.jembe.2018.01.008

Turon X, Nishikawa T, Rius M (2007) Spread of *Microcosmus squamiger* (Ascidiacea: Pyuridae) in the Mediterranean Sea and adjacent waters. *Journal of Experimental Marine Biology and Ecology* 342: 185–188, https://doi.org/10.1016/j.jembe.2006.10.040

UNESCO (2021) UNESCO Institute for Statistics (UIS). Research and development spending. http://uis.unesco.org/apps/visualisations/research-and-development-spending/ (accessed 1 November 2021)

van Rijn I, Kiflawi M, Belmaker J (2020) Alien species stabilize local fisheries catch in a highly invaded ecosystem. *Canadian Journal of Fisheries and Aquatic Sciences* 77: 752–761, https://doi.org/10.1139/cjfas-2019-0065

Vergés A, Alcoverro T, Ballesteros E (2009) Role of fish herbivory in structuring the vertical distribution of canopy algae *Cystoseira* spp. in the Mediterranean Sea. *Marine Ecology Progress Series* 375: 1–11, https://doi.org/10.3354/meps07778

Vergés A, Tomas F, Cebrian E, Ballesteros E, Kizilkaya Z, Dendrinos P, Karamanlidis AA, Spiegel D, Sala E (2014) Tropical rabbitfish and the deforestation of a warming temperate sea. *Journal of Ecology* 102: 1518–1527, https://doi.org/10.1111/1365-2745.12324

Vilà M, Hulme PE (eds) (2017) Impact of biological invasions on ecosystem services. Invading Nature - Springer Series in Invasion Ecology, volume 12. Springer International Publishing, Berlin, 354 pp, https://doi.org/10.1007/978-3-319-45121-3

Vilà M, Basnou C, Pyšek P, Josefsson M, Genovesi P, Gollasch S, Nentwig W, Olenin S, Roques A, Roy D, Hulme PE and DAISIE partners (2010) How well do we understand the impacts of alien species on ecosystem services? A pan-European, cross-taxa assessment. *Frontiers in Ecology and the Environment* 8: 135–144, https://doi.org/10.1890/080083

Vilà M, Espinar JL, Hejda M, Hulme PE, Jarošík V, Maron JL, Pergl J, Schaffner U, Sun Y, Pyšek P (2011) Ecological impacts of invasive alien plants: a meta-analysis of their effects on species, communities and ecosystems. *Ecology Letters* 14: 702–708, https://doi.org/10.1111/j.1461-0248.2011.01628.x

Vimercati G, Kumschick S, Probert AF, Volery L, Bacher S (2020) The importance of assessing positive and beneficial impacts of alien species. *NeoBiota* 62: 525–545, https://doi.org/10.3897/neobiota.62.52793

Vitousek PM, D'Antonio CM, Loope LL, Westbrooks R (1996) Biological invasions as global environmental change. *American Scientist* 84: 468–478

Volery L, Blackburn TM, Bertolino S, Evans T, Genovesi P, Kumschick S, Roy HE, Smith KG, Bacher S (2020) Improving the Environmental Impact Classification for Alien Taxa (EICAT): a summary of revisions to the framework and guidelines. In: Wilson JR, Bacher S,

Daehler CC, Groom QJ, Kumschick S, Lockwood JL, Robinson TB, Zengeya TA, Richardson DM (eds), Frameworks used in Invasion Science. *NeoBiota* 62: 547–567, https://doi.org/10.3897/neobiota.62.52723

Wallentinus I, Nyberg CD (2007) Introduced marine organisms as habitat modifiers. *Marine Pollution Bulletin* 55: 323–332, https://doi.org/10.1016/j.marpolbul.2006.11.010

WoRMS Editorial Board (2021) World Register of Marine Species. https://www.marinespecies.org (accessed 25 October 2021)

Yeruham E, Rilov G, Shpigel M, Abelson A (2015) Collapse of the echinoid *Paracentrotus lividus* populations in the Eastern Mediterranean - result of climate change? *Scientific Reports* 5: 13479, https://doi.org/10.1038/srep13479

Yeruham E, Shpigel M, Abelson A, Rilov G (2020) Ocean warming and tropical invaders erode the performance of a key herbivore. *Ecology* 101: e02925, https://doi.org/10.1002/ecy.2925

Zenetos A, Galanidi M (2020) Mediterranean non indigenous species at the start of the 2020s: recent changes. *Marine Biodiversity Records* 13: 10, https://doi.org/10.1186/s41200-020-00191-4

Zenetos A, Gofas S, Verlaque M, Çinar ME, García Raso JE, Bianchi CN, Morri C, Azzurro E, Bilecenoglu M, Froglia C, Siokou I, Violanti D, Sfriso A, San Martín G, Giangrande A, Katagan T, Ballesteros E, Ramos-Espla A, Mastrototaro F, Ocana O, Zingone A, Gambi MC, Streftaris N (2010) Alien species in the Mediterranean Sea by 2010. A contribution to the application of European Union's Marine strategy framework directive (MSFD). Part I. Spatial distribution. *Mediterranean Marine Science* 11: 381–493, https://doi.org/10.12681/mms.87

Zenetos A, Gofas S, Morri C, Rosso A, Violanti D, García Raso JE, Çinar ME, Almogi Labin A, Ates AS, Azzuro E, Ballesteros E, Bianchi CN, Bilecenoglu M, Gambi MC, Giangrande A, Gravili C, Hyams-Kaphzan O, Karachle V, Katsanevakis S, Lipej L, Mastrototaro F, Mineur F, Pancucci-Papadopoulou MA, Ramos Esplá A, Salas C, San Martín G, Sfriso A, Streftaris N, Verlaque M (2012) Alien species in the Mediterranean Sea by 2012. A contribution to the application of European Union's Marine Strategy Framework Directive (MSFD). Part 2. Introduction trends and pathways. *Mediterranean Marine Science* 13: 328–352, https://doi.org/10.12681/mms.327

Zenetos A, Çinar ME, Crocetta F, Golani D, Rosso A, Servello G, Shenkar N, Turon X, Verlaque M (2017) Uncertainties and validation of alien species catalogues: The Mediterranean as an example. *Estuarine, Coastal and Shelf Science* 191: 171–187, https://doi.org/10.1016/j.ecss.2017.03.031

Zenetos A, Corsini-Foka M, Crocetta F, Gerovasileiou V, Karachle V, Simboura M, Tsiamis K, Pancucci-Papadopoulou M (2018) Deep cleaning of alien and cryptogenic species records in the Greek Seas (2018 update). *Management of Biological Invasions* 9: 209–226, https://doi.org/10.3391/mbi.2018.9.3.04

Zenetos A, Albano PG, López Garcia E, Stern N, Tsiamis K, Galanidi M (2022) Established non-indigenous species increased by 40% in 11 years in the Mediterranean Sea. *Mediterranean Marine Science* 23: 196–212, https://doi.org/10.12681/mms.29106

Supplementary material

The following supplementary material is available for this article:

Appendix 1. Species-specific review of the impacts of alien and cryptogenic species on biodiversity, ecosystem services and human health in the Mediterranean Sea, and other related information.

This material is available as part of online article from:
http://www.reabic.net/aquaticinvasions/2022/Supplements/AI_2022_Tsirintanis_etal_Appendix.pdf