

# Economic costs of invasive alien species in the Mediterranean basin

Melina Kourantidou<sup>1,2\*</sup>, Ross N. Cuthbert<sup>3,4\*</sup>, Phillip J. Haubrock<sup>5,6\*</sup>, Ana Novoa<sup>7\*</sup>, Nigel G. Taylor<sup>8\*</sup>, Boris Leroy<sup>9</sup>, César Capinha<sup>10</sup>, David Renault<sup>11,12</sup>, Elena Angulo<sup>13</sup>, Christophe Diagne<sup>13</sup>, Franck Courchamp<sup>13</sup>

**1** Woods Hole Oceanographic Institution, Marine Policy Center, Woods Hole, MA 02543, USA **2** Institute of Marine Biological Resources and Inland Waters, Hellenic Center for Marine Research, Athens 164 52, Greece **3** GEOMAR Helmholtz-Zentrum für Ozeanforschung Kiel, 24105, Kiel, Germany **4** School of Biological Sciences, Queen's University Belfast, Belfast BT9 5DL, Northern Ireland, UK **5** Senckenberg Research Institute and Natural History Museum Frankfurt, Department of River Ecology and Conservation, Gelnhausen 63571, Germany **6** University of South Bohemia in České Budějovice, Faculty of Fisheries and Protection of Waters, South Bohemian Research Center of Aquaculture and Biodiversity of Hydrocenoses, Zátiší 728/II, 389 25, Vodňany, Czech Republic **7** Department of Invasion Ecology, Institute of Botany, Czech Academy of Sciences, CZ-252 43, Průhonice, Czech Republic **8** Tour du Valat, Research Institute for the Conservation of Mediterranean Wetlands, 13200, Arles, France **9** Unité Biologie des Organismes et Ecosystèmes Aquatiques (BOREA UMR 7208), Muséum National d'Histoire Naturelle, Sorbonne Universités, Université de Caen Normandie, Université des Antilles, CNRS, IRD, Paris, France **10** Centro de Estudos Geográficos, Instituto de Geografia e Ordenamento do Território – 26 IGOT, Universidade de Lisboa, Lisboa, Portugal **11** University of Rennes, CNRS, ECOBIO [(Ecosystèmes, biodiversité, évolution)] – UMR 6553, F 35000, Rennes, France **12** Institut Universitaire de France, 1 Rue Descartes, 75231 Paris cedex 05, France **13** Université Paris-Saclay, CNRS, AgroParisTech, Ecologie Systématique Evolution, 91405, Orsay, France

Corresponding author: Melina Kourantidou (mkour@dal.ca)

---

Academic editor: E. García-Berthou | Received 30 September 2020 | Accepted 11 December 2020 | Published 29 July 2021

---

**Citation:** Kourantidou M, Cuthbert RN, Haubrock PJ, Novoa A, Taylor NG, Leroy B, Capinha C, Renault D, Angulo E, Diagne C, Courchamp F (2021) Economic costs of invasive alien species in the Mediterranean basin. In: Zenni RD, McDermott S, García-Berthou E, Essl F (Eds) The economic costs of biological invasions around the world. NeoBiota 67: 427–458. <https://doi.org/10.3897/neobiota.67.58926>

---

## Abstract

Invasive alien species (IAS) negatively impact the environment and undermine human well-being, often resulting in considerable economic costs. The Mediterranean basin is a culturally, socially and economically diverse region, harbouring many IAS that threaten economic and societal integrity in multiple ways. This paper is the first attempt to collectively quantify the reported economic costs of IAS in the Medi-

---

\* Contributed equally as the first authors.

terranean basin, across a range of taxonomic, temporal and spatial descriptors. We identify correlates of costs from invasion damages and management expenditures among key socioeconomic variables, and determine network structures that link countries and invasive taxonomic groups. The total reported invasion costs in the Mediterranean basin amounted to \$27.3 billion, or \$3.6 billion when only realised costs were considered, and were found to have occurred over the last three decades. Our understanding of costs of invasions in the Mediterranean was largely limited to a few, primarily western European countries and to terrestrial ecosystems, despite the known presence of numerous high-impact aquatic invasive taxa. The vast majority of costs were attributed to damages or losses from invasions (\$25.2 billion) and were mostly driven by France, Spain and to a lesser extent Italy and Libya, with significantly fewer costs attributed to management expenditure (\$1.7 billion). Overall, invasion costs increased through time, with average annual costs between 1990 and 2017 estimated at \$975.5 million. The lack of information from a large proportion of Mediterranean countries, reflected in the spatial and taxonomic connectivity analysis and the relationship of costs with socioeconomic variables, highlights the limits of the available data and the research effort needed to improve a collective understanding of the different facets of the costs of biological invasions. Our analysis of the reported costs associated with invasions in the Mediterranean sheds light on key knowledge gaps and provides a baseline for a Mediterranean-centric approach towards building policies and designing coordinated responses. In turn, these could help reach socially desirable outcomes and efficient use of resources invested in invasive species research and management.

### **Abstract in French**

**Coûts économiques des espèces exotiques envahissantes dans le bassin méditerranéen.** Les espèces exotiques envahissantes (EEE) impactent négativement l'environnement et le bien-être humain, et résultent souvent en des coûts économiques considérables. Le bassin méditerranéen est une région culturellement, socialement et économiquement variée; elle abrite de nombreuses EEE qui menacent son intégrité économique et sociétale de multiples façons. Cet article constitue la première tentative de quantification collective des coûts économiques associés aux EEE dans le bassin méditerranéen au travers de divers descripteurs taxonomiques, temporels et spatiaux. Nous identifions les corrélations des coûts dûs aux dégâts des EEE et aux dépenses induites par leur gestion avec des variables socio-économiques clés, et nous déterminons les structures des réseaux qui lient les pays et les différents groupes taxonomiques envahissants. Le montant total du coût des invasions dans le bassin méditerranéen s'élève à \$27,3 milliards, et \$3,6 milliards si seuls les coûts réalisés sont pris en compte au cours des trois dernières décennies. Notre compréhension du coût des invasions biologiques en Méditerranée est largement réduite aux données concernant quelques pays, essentiellement d'Europe de l'Ouest, et aux écosystèmes terrestres, malgré la présence avérée de nombreux organismes aquatiques envahissants à fort impact. La grande majorité des coûts reportés correspondent à des dégâts ou des pertes (\$25,2 milliards) et concerne essentiellement la France, l'Espagne et, dans une moindre mesure, l'Italie et la Libye, avec significativement moins de coûts correspondant à des dépenses de gestion (\$1,7 milliard). De façon générale, les coûts liés aux invasions augmentent avec le temps, avec un coût annuel moyen entre 1990 et 2017 estimé à \$975,5 millions. Le manque d'information pour une grande part des pays méditerranéen, qui se reflète dans l'analyse de connectivité spatiale et taxonomique et les relations entre les coûts et les variables socio-économiques, met en évidence les limites des données disponibles, ainsi que l'effort de recherche qui est nécessaire pour une compréhension plus globale des différentes facettes des coûts des invasions biologiques. Notre analyse des coûts reportés pour la région méditerranéenne met en lumière les principales lacunes de connaissance et pose les bases d'une approche Méditerranée-centrée visant la mise en place de politiques et le design de réponses coordonnées. En retour, celles-ci pourront aider à atteindre une utilisation efficace et socialement acceptable des ressources investies dans la recherche sur les espèces envahissantes et dans leur gestion.

### Abstract in Spanish

**Costos económicos de las especies exóticas invasoras en la cuenca mediterránea.** Las especies exóticas invasoras (EEI) tienen un impacto negativo en el medio ambiente y perjudican el bienestar humano, lo que a menudo genera costos económicos considerables. La cuenca del Mediterráneo es una región cultural, social y económicamente diversa, que alberga un gran número de especies exóticas invasoras que amenazan la integridad económica y social de múltiples maneras. Este artículo es el primer intento de cuantificar colectivamente los costos económicos reportados de las EEI en la cuenca del Mediterráneo, a través de una variedad de descriptores taxonómicos, temporales y espaciales. Identificamos las correlaciones de los costos causados por los daños de las EEI y los gastos relacionados con su gestión con una serie de variables socioeconómicas clave y determinamos las estructuras de red que vinculan a los países de la cuenca Mediterránea y los grupos taxonómicos invasores. Los costos totales de invasión reportados en la cuenca del Mediterráneo ascendieron a \$27.3 mil millones, o \$3.6 mil millones cuando solamente se consideraron los costos realizados, los cuales ocurrieron durante las últimas tres décadas. Nuestro conocimiento de los costos de las invasiones en el Mediterráneo se limitó en gran medida a unos pocos países, principalmente de Europa occidental, y a ecosistemas terrestres, a pesar de la presencia conocida de numerosos taxones invasores acuáticos de alto impacto. La gran mayoría de los costos se atribuyeron a daños o pérdidas por invasiones (\$25.2 mil millones) y fueron impulsados principalmente por Francia, España y, en menor medida, Italia y Libia, con costos significativamente menores atribuidos a los gastos de gestión (\$1.7 mil millones). En general, los costos aumentaron con el tiempo, con costos anuales promedio entre 1990 y 2017 estimados en \$975.5 millones. La falta de información de costos en una gran proporción de países mediterráneos, reflejada en el análisis de conectividad espacial y taxonómica y la relación de los costes con las variables socioeconómicas, pone de manifiesto los límites de los datos disponibles y el esfuerzo investigador necesario para mejorar la comprensión colectiva de las diferentes facetas de los costos de las invasiones biológicas. Nuestro análisis de los costes reportados asociados con las invasiones en el Mediterráneo pone de relieve las actuales lagunas de conocimiento y proporciona una línea de base para un enfoque centrado en el Mediterráneo hacia la creación de políticas y el diseño de respuestas coordinadas. A su vez, este estudio podría ayudar a alcanzar resultados socialmente deseables y un uso eficiente de los recursos invertidos en la investigación y el manejo de EEI en la cuenca del Mediterráneo.

### Abstract in Italian

**Costi economici delle specie aliene invasive nel bacino del Mediterraneo.** Le specie aliene invasive (SAI) impattano negativamente l'ambiente e minacciano il benessere umano, spesso con conseguenti costi economici. Il bacino Mediterraneo è una regione culturalmente, socialmente ed economicamente diversa, ospitando molte SAI che minacciano l'integrità economica e sociale in molti modi. Questo articolo è il primo tentativo di quantificare collettivamente i costi economici riportati per le SAI nel bacino Mediteraneo, con un uno spettro di descrittori tassonomici, temporali e spaziali. Identifichiamo i correlati dei costi dai danni delle invasioni e le spese di gestione tra le variabili socioeconomiche chiave, e determiniamo strutture a rete che collegano Paesi e gruppi tassonomici invasivi. I costi totali delle invasioni riportati nel bacino Mediterraneo ammontano a \$27,3 miliardi, o \$3,6 miliardi se si considerano solo i costi realizzati, e si sono verificati nel corso degli ultimi tre decenni. La nostra comprensione dei costi delle invasioni nel Mediterraneo era ampiamente limitata a pochi Paesi Europei, soprattutto quelli occidentali, e agli ecosistemi terrestri, nonostante la nota presenza di numerosi taxa acquatici invasivi di alto impatto. La grande maggioranza dei costi delle invasioni sono stati attribuiti a danni o perdite (\$25,2 miliardi) e sono stati principalmente determinati dalla Francia, dalla Spagna e, in misura minore, dall'Italia e dalla Libia, con costi significativamente minori attribuiti alle spese di gestione (\$1,7 miliardi). In generale, i costi delle invasioni sono aumentati nel tempo, con un costo annuale medio tra il 1990 e il 2017 stimato a \$975,5 miliardi. La mancanza di informazioni da una larga proporzione di Paesi del Mediterraneo, riflessa nell'analisi di connettività spaziale e

tassonomica e nella relazione tra i costi e le variabili socioeconomiche, sottolinea i limiti dei dati disponibili e delle ricerche necessarie per migliorare la conoscenza collettiva dei diversi aspetti dei costi delle invasioni biologiche. La nostra analisi dei costi riportati associate alle invasioni nel Mediterraneo fa luce sulle lacune chiave nella conoscenza e fornisce una base per un approccio Mediterraneo-centrico verso la formulazione di politiche e di risposte coordinate. A sua volta, queste potrebbero aiutare a raggiungere risultati socialmente desiderabili e un uso efficiente delle risorse investite nella ricerca e nella gestione delle specie invasive.

### **Abstract in Greek**

**Οικονομικά κόστη εισβολικών ειδών στην λεκάνη της Μεσογείου.** Τα εισβολικά είδη επηρεάζουν αρνητικά το περιβάλλον και υποβαθμίζουν την ανθρώπινη ευημερία, κάτι που συχνά καταλήγει σε σημαντικά οικονομικά κόστη. Η λεκάνη της Μεσογείου είναι μια πολιτιστικά, κοινωνικά και οικονομικά ποικιλόμορφη περιοχή που φιλοξενεί πολλά εισβολικά είδη τα οποία απειλούν την οικονομική και κοινωνική συνοχή με διάφορους τρόπους. Η εργασία αυτή είναι μια πρώτη προσπάθεια να ποσοτικοποιήσει συνολικά τα οικονομικά κόστη εισβολικών ειδών που έχουν αναφερθεί για την λεκάνη της Μεσογείου με τη χρήση ενός εύρους ταξινομικών, χρονικών και χωρικών περιγραφών. Προσδιορίζουμε συσχετίσεις του κόστους από τις ζημιές και διαχείριση των εισβολικών ειδών με βασικές κοινωνικό-οικονομικές μεταβλητές, καθώς επίσης και τις δομές του δικτύου που συνδέουν τις χώρες με τις εισβολικές ταξινομικές ομάδες. Το συνολικά κόστη από εισβολές στην λεκάνη της Μεσογείου εκτιμήθηκαν σε \$27,3 δις, ή \$3,6 δις λαμβάνοντας υπόψη μόνο τα πραγματικά/υλοποιηθέντα κόστη, και έλαβαν χώρα στη διάρκεια των τριών τελευταίων δεκαετιών. Η γνώση μας για τα κόστη των εισβολικών ειδών στην Μεσόγειο περιορίστηκε σε μεγάλο βαθμό σε λίγες, κυρίως δυτικό-Ευρωπαϊκές χώρες και σε χερσαία οικοσυστήματα, παρά το ότι γνωρίζουμε για την παρουσία πολλών εισβολικών ειδών σε υδατινά οικοσυστήματα με σημαντικές επιπτώσεις. Η συντριπτική πλειοψηφία του κόστους αποδόθηκε σε ζημιές ή απώλειες από εισβολές (\$25,2 δις) και κυρίως από την Γαλλία, Ισπανία και σε μικρότερο βαθμό από την Ιταλία και την Λιβύη, ενώ σημαντικά λιγότερα κόστη αποδόθηκαν στη διαχείριση (\$1,7 δις). Συνολικά, τα κόστη των εισβολικών ειδών αυξήθηκαν στην διάρκεια του χρόνου με το μέσο ετήσιο κόστος μεταξύ του 1990 και 2017 να εκτιμάται στα \$975,5 εκατομμύρια. Η έλλειψη πληροφορίας από μεγάλη μερίδα Μεσογειακών χωρών, που αντικατοπτρίζεται στην χωρική και ταξινομική ανάλυση συσχέτισης και στην σχέση μεταξύ του κόστους και κοινωνικό-οικονομικών μεταβλητών, αναδεικνύει τους περιορισμούς που θέτουν τα διαθέσιμα δεδομένα και την ανάγκη για έρευνα, για μια καλύτερη συλλογική κατανόηση των διαφορετικών πτυχών του κόστους των βιολογικών εισβολών. Η ανάλυσή μας για τα καταγεγραμμένα κόστη εισβολικών ειδών στη Μεσόγειο φέρνει στο φως σημαντικά κενά γνώσης και προσέφερει την βάση για μια προσέγγιση με επίκεντρο την Μεσόγειο, για τον σχεδιασμό συντονισμένων δράσεων και την δημιουργία πολιτικών. Με τη σειρά τους αυτές μπορούν να βοηθήσουν στην επίτευξη επιθυμητών αποτελεσμάτων και αποδοτικής χρήσης των πόρων που επενδύονται στην έρευνα και διαχείριση εισβολικών ειδών.

### **Abstract in German**

**Kosten invasive Arten Kosten invasiver gebietsfremder Arten im Mittelmeerraum.** Invasive gebietsfremde Arten wirken sich negativ auf die Umwelt aus und beeinträchtigen das Wohlbefinden des Menschen, was häufig zu erheblichen wirtschaftlichen Kosten führt. Das Mittelmeerbecken ist eine kulturell, sozial und wirtschaftlich vielfältige Region mit vielen gebietsfremden Arten, die die wirtschaftliche und gesellschaftliche Integrität auf vielfältige Weise gefährden. Dieses Arbeit ist der erste Versuch, die gemeldeten wirtschaftlichen Kosten dieser Arten im Mittelmeerraum über eine Reihe taxonomischer, zeitlicher und räumlicher Deskriptoren hinweg kollektiv zu quantifizieren. Wir identifizieren Korrelationen von Kosten biologischer Invasionen und Verwaltungsausgaben unter den wichtigsten sozioökonomischen Variablen und bestimmen Netzwerkstrukturen, die Länder und invasive taxonomische Gruppen verbinden. Die gesamten gemeldeten Kosten im Mittelmeerraum beliefen sich auf \$27,3 Mrd. oder \$3,6 Mrd., wenn nur realisierte Kosten berücksichtigt wurden, und wurden in den letzten drei Jahrzehnten festgestellt. Unser Verständnis der Kosten biologischer Invasionen im Mittelmeerraum war trotz des bekannten Vorhanden-

seins zahlreicher hoch-invasiver aquatischer invasiver Taxa weitgehend auf einige wenige, hauptsächlich westeuropäische Länder und terrestrische Ökosysteme beschränkt. Die überwiegende Mehrheit der Kosten entfiel auf Schäden oder Verluste an Ressourcen durch Invasionen (\$25,2 Mrd.) und wurde hauptsächlich von Frankreich, Spanien und in geringerem Maße von Italien und Libyen getragen, wobei die Verwaltungsausgaben (\$1,7 Mrd.) erheblich geringer waren. Insgesamt stiegen diese Kosten im Laufe der Zeit, wobei die durchschnittlichen jährlichen Kosten zwischen 1990 und 2017 auf \$975,5 Mio. geschätzt wurden. Der Mangel an Informationen aus einem großen Teil der Mittelmeerlande, der sich in der räumlichen und taxonomischen Konnektivitätsanalyse und dem Verhältnis der Kosten zu sozioökonomischen Variablen widerspiegelt, zeigt die Grenzen der verfügbaren Daten und den Forschungsaufwand auf, der erforderlich ist, um ein kollektives Verständnis der verschiedenen Facetten der Kosten für biologische Invasionen zu verbessern. Unsere Analyse der gemeldeten Kosten im Zusammenhang mit Invasionen im Mittelmeerraum beleuchtet wichtige Wissenslücken und bietet eine Grundlage für einen auf den Mittelmeerraum ausgerichteten Ansatz zur Erstellung von Strategien und zur Gestaltung koordinierter Reaktionen. Dies könnte wiederum dazu beitragen, sozial wünschenswerte Ergebnisse zu erzielen und die Ressourcen die in die Forschung an invasiven Arten und deren Bewirtschaftung investiert werden, effizient zu nutzen.

### **Abstract in Croatian**

**Ekonomski troškovi invazivnih stranih vrsta u mediteranskom bazenu.** Invazivne strane vrste negativno utječu na okoliš i sabotiraju dobrobit ljudi, što često rezultira značajnim ekonomskim troškovima. Mediteranski bazen je kulturno, socijalno i ekonomski raznolika regija u kojoj se nalaze mnoge invazivne strane vrste koje na više načina ugrožavaju njezin ekonomski i društveni integritet. Ovaj rad je prvi pokušaj kolektivnog kvantificiranja prijavljenih ekonomskih troškova invazivnih stranih vrsta u mediteranskom bazenu, kroz niz taksonomske, vremenske i prostornih deskriptori. Utvrđili smo korelati troškova od štete prouzročene invazivnim stranim vrstama i izdataka za upravljanje među ključnih socioekonomskih varijabli, i utvrđili mrežne strukture koje povezuju države i invazivne taksonomske skupine. Ukupni prijavljeni troškovi invazije u mediteranskom bazenu iznosili su 27,3 milijarde dolara, odnosno 3,6 milijardi dolara kada su se uzimali u obzir samo ostvareni troškovi, a koji su zabilježeni u posljednja tri desetljeća. Naše razumijevanje troškova invazije na Sredozemlju uglavnom je bilo ograničeno na nekoliko, prvenstveno zapadnoeuropskih zemalja i kopnene ekosustave, unatoč poznatoj prisutnosti brojnih vodenih invazivnih svojstava s prepoznatim velikim utjecajem. Velika većina troškova pripisana je šteti ili gubicima od strane invazija (25,2 milijarde dolara), uglavnom predvođenim od strane Francuske i Španjolske te u manjoj mjeri Italije i Libije, uz znatno manje troškova pripisanih izdacima za upravljanje (1,7 milijardi dolara). Sveukupni troškovi invazije s vremenom su se povećavali, a prosječni godišnji troškovi između 1990. i 2017. procjenjuju se na 975,5 milijuna dolara. Nedostatak informacija iz velikog dijela mediteranskih zemalja, koji se ogleda u analizi prostorne i taksonomske povezanosti te odnosu troškova sa socioekonomskim varijablama, ukazuje na ograničenost dostupnih podataka i istraživačkog napora potrebnim za poboljšanje kolektivnog razumijevanja različitih aspekata troškova bioloških invazija. Naša analiza prijavljenih troškova povezanih s invazijama na Mediteranu ukazuje na ključne nedostatke u znanju i daje osnovu za mediteranski usmjeren pristup izgradnji politika i osmišljavanju koordiniranih odgovora. Takav pristup bi zauzvrat mogao pomoći u postizanju društveno poželjnih rezultata i učinkovitom korištenju resursa uloženih u istraživanje i upravljanje invazivnim stranim vrstama.

### **Abstract in Arabic**

التكليف الاقتصادي لأنواع الغريبة الغازية في حوض البحر الأبيض المتوسط.

تؤثر "الأنواع الغربية الغازية" سلباً على البيئة ورفاهية الإنسان، وغالباً ما تؤدي إلى تكاليف اقتصادية مهمة. من جهتها، تعتبر منطقة حوض البحر الأبيض المتوسط مجالاً متعدداً ثقافياً واجتماعياً واقتصادياً،

مما جعل منها موطننا للعديد من "الأنواع الغازية" التي تهدد سلامتها الاقتصادية والاجتماعية بطرق شتى. تشكل الدراسة التي بين أيدينا محاولة أولية لتقدير جماعي للتکاليف الاقتصادية المرتبطة بـ"الأنواع الغازية" في حوض البحر الأبيض المتوسط، وذلك من خلال وصفات تصنیفیة وزمینیة ومکانیة مختلفة. كما نحدد ارتباطات التکاليف الاقتصادية التي سببها أضرار "الأنواع الغازية" وتکاليف تسییرها مع المتغيرات الاجتماعية والاقتصادية الرئيسية، ونحدد كذلك بینة الشبکات التي تربط البلدان والمجموعات التصنیفیة الغازية المختلفة. وحسب هذه الدراسة، بلغ إجمالي تکاليف "الأنواع الغازية" في حوض البحر الأبيض المتوسط 27.3 مليار دولار، و3.6 مليار دولار إذا تمأخذ التکاليف المحققة فقط بین الاعتبار على مدى العقود الثلاثة الماضية.

إن فهمنا لتکلفة الغزو البيولوچي في حوض البحر الأبيض المتوسط اقتصر إلى حد كبير على البيانات المتعلقة بعدد قليل من البلدان، خاصة من أوروبا الغربية، وبعض النظم الإيكولوجية القاربة، على الرغم من الوجود المؤكّد للعديد من الكائنات المائية الغازية ذات التأثير الكبير. إن الغالبية العظمى من التکاليف المبلغ عنها تتعلق بالأضرار أو الخسائر (25.2 مليار دولار) وتهتم بشكل رئيسي فرنسا وإسبانيا ودرجة أقل إيطاليا ولیبيا، مع تکاليف أقل بكثير تخص نفقات التسییر الإداري (1.7 مليار دولار). بشكل عام، تزداد التکاليف المرتبطة بالغزو البيولوچي بمروز الوقت وذلك بمتوسط تکلفة سنوية تقدر بـ 975.5 مليون دولار بين عامي 1990 و2017. إن نقص المعلومات في جزء كبير من دول البحر الأبيض المتوسط، الشيء الذي ينعكس من خلال تحليل الرابط المکانی والتصنیفی والعلاقات بين التکاليف والمتغيرات الاجتماعية والاقتصادية. يسلط الضوء على حدود البيانات المتاحة، وكذلك جهود البحث الضرورية من أجل فهم أكثر شمولاً للحوافن المختلفة لتکاليف الغزو البيولوچي.

لقد سلط تحليلنا للتکاليف المرتبطة بمنطقة البحر الأبيض المتوسط الضوء على الفجوات المعرفية الرئيسية ووضع الأساس لمقارنة "متوسطية" تهدف إلى وضع سياسات ملائمة وتصاميم تدخلات متناسبة، مما يمكن أن يؤمن استخدام فعال ومقبول اجتماعياً للموارد المستثمرة في الأبحاث حول الأنواع الغازية وكيفية إدارتها.

## Keywords

geographic connectivity, InvaCost, monetary impacts, non-indigenous species, resource losses, socioeconomic dimensions

## Introduction

The ongoing spread of invasive alien species (IAS) is a key driver of biodiversity and ecosystem degradation that continues to adversely affect human and social well-being at local, national and global scales (Pyšek et al. 2020; Secretariat of the Convention on Biological Diversity 2020). With increasingly globalised trade and transport networks, there is no sign of abatement in invasion rates worldwide (Seebens et al. 2017), owing to high propagule and colonisation pressures sustained from increasingly interconnected biogeographic regions (Seebens et al. 2018). Despite the relatively well-characterised ecological impacts of several IAS among ecosystem types and geographic regions (Dick et al. 2017; Crystal-Ornelas and Lockwood 2020), a paucity in estimation of economic costs, along with a poor understanding of socioeconomic impacts, limits monetary investments in management (Courchamp et al. 2017). In turn, this also hampers rationale for timely management of IAS at national or regional scales. That is despite the well-known and accepted fact that investments in prevention are far more economically efficient than longer-term control protocols (Leung et al. 2002).

Large-scale efforts to quantify invasion costs have primarily focused on a single country (e.g. the U.S.; Pimentel et al. 2000, 2005 or Australia; Hoffmann and Broadhurst 2016), taxonomic group (e.g., insects; Bradshaw et al. 2016) or economic sector (e.g., agriculture; Paini et al. 2016). Whilst these studies have promoted attention towards burgeoning economic costs of invasions, a lack of understanding of these costs at smaller spatial scales, across countries, species or sectors, presently impairs regional-scale interventions, and particularly for regions that are interconnected biogeographically. Moreover, extrapolations in previous estimations of IAS costs have prompted debate on their relevance and reliability (Cuthbert et al. 2020). For interconnected countries with borders lacking natural or anthropogenic barriers for species' movement, a unified approach to IAS management may be most efficient: investments from one country could offset future costs in another, given the ease at which invaders can spread. However, the factors driving invasion success are also often highly context-dependent, and can vary depending on many parameters, such as taxa, introduction pathways, spread mechanisms, characteristics and vulnerability of recipient ecosystems (Novoa et al. 2020). Factors that mediate the economic impacts of IAS have yet to be considered in monetary quantifications to better inform decision-making and management.

The Mediterranean basin is a major biogeographic unit, whether defined by its shared climate or marine resources, its distinct biome (Dinerstein et al. 2017), or as one of the world's most diverse biodiversity hotspots (CEPF 2020). Spanning three continents, countries within the Mediterranean basin are highly connected through terrestrial and aquatic routes and often share similar pathways and ecosystem characteristics (e.g. Katsanevakis et al. 2013). This interconnectedness calls for coordinated responses and management actions (Traveset et al. 2008; Tempesti et al. 2020). For example, in the Mediterranean Sea, the opening of the Suez Canal in 1869 facilitated the widespread introduction of numerous alien marine taxa. The speed of invasion and range of Lessepsian IAS have been increasing ever since, owing to a number of factors such as currents, climate change, removal of high and low-salinity barriers, overexploitation of native fish, etc (Lasram et al. 2008, 2010; Raitsos et al. 2010; Edelist et al. 2011, 2013; Vergés et al. 2014). Indeed, for marine taxa, recorded species introductions into the Mediterranean Sea significantly exceed the numbers of species introductions in other European seas, with the eastern Mediterranean possibly the most heavily impacted (Edelist et al. 2013; Galil et al. 2014).

Aside from the marine realm, terrestrial and freshwater ecosystems also share similar invasion patterns across countries of the Mediterranean basin, such as similar species traits of successful invaders or habitat vulnerability (e.g., Arianoutsou et al. 2013), and deserve attention given the diversity and impacts of invasions there (Clavero et al. 2010).

The millenary history of trade and travel, and multiple other anthropogenic disturbances in the region, has led to a biogeographically diverse set of invaders (Arianoutsou et al. 2013). These IAS have strong socioeconomic and geographical imprints which are particularly high in both the mainland and islands of the basin (Groves and di Castri 1991; Vilà and Pujadas 2001; Pyšek and Richardson 2010). Notably, the Mediterranean-type climate imposes stringent regulatory effects over the invasion potential of many species, hindering the establishment of species requiring colder or wetter con-

ditions, and leading to the development of circum-Mediterranean or quasi-circum-Mediterranean ranges for well-adapted ones. Among the latter are many highly damaging species, such as the Asian tiger mosquito (*Aedes albopictus*) (Gasperi et al. 2012), the red swamp crayfish (*Procambarus clarkii*) (Gherardi and Acquistapace 2007), or the palm moth (*Paysandisia archon*) (Muñoz-Adalia and Colinas 2020). Despite efforts to understand economic dimensions for some of the most prominent IAS in this region along with their impact on human well-being, integrated analyses encompassing impacts and costs at the scale of the Mediterranean basin are still largely missing.

Recognising this gap and the often-expected connectivity of invasions across ecosystems in the region, a useful approach for prioritising the allocation of resources aimed at IAS management is to identify which species pose the greatest economic risks and build collaborative strategies for their management. Additionally, lessons gained from the successes and failures of managing a species in one country can guide managers in others. Indeed, regional approaches are recognised to be essential in sustainable and efficient prevention against IAS (Faulkner et al. 2020). Identifying in which habitat types costs are reported, which socioeconomic sectors are affected, and how costs accrue over time further informs targeted management interventions. However, at present, economic impacts attributable to IAS are not centrally examined, categorised or systematically reported within the Mediterranean basin, impeding effective ecosystem management responses, and reducing efficiencies of investments. The Mediterranean region is also a cradle of civilisations that encompasses a wide range of environmental, socioeconomic and cultural elements. Well-being, social and economic development are highly dependent on natural resources and a vulnerable environment that, similar to the rest of the world, is at risk from biological invasions.

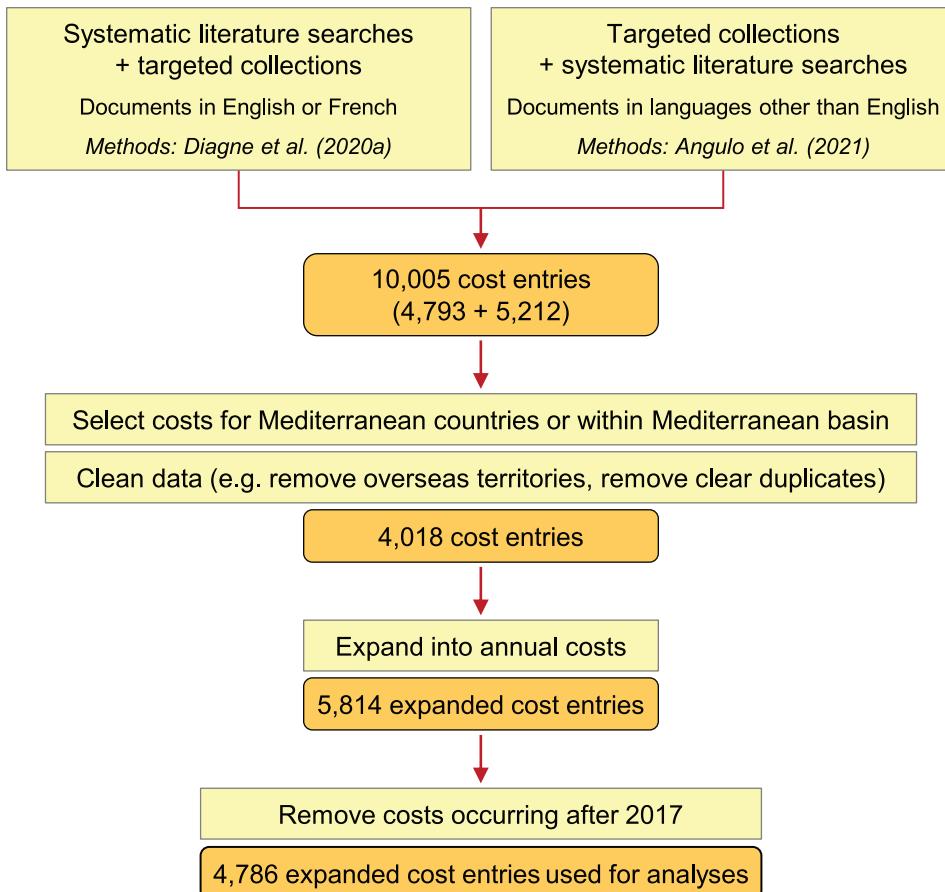
The present study thus builds on the InvaCost initiative (Diagne et al. 2020a, c) to present the first large scale analysis of invasion costs in the Mediterranean basin. We examine how costs in this region are distributed over time and across countries, habitat types, taxonomic groups and economic sectors. We also estimate the influence of socioeconomic drivers (e.g., trade, tourism, research) on the reporting of IAS costs. Moreover, countries with the highest economic costs are identified, as well as similarities and differences in their cost characteristics and network structures that indicate countries impacted by similar taxa.

## Materials and methods

### Data collection and extraction

For the purposes of quantifying the costs associated with IAS in the Mediterranean basin, we combined information from databases linked to the InvaCost project, the first global effort to systematically compile and synthesise the monetary costs of invasive species (Diagne et al. 2020a) (Fig. 1).

InvaCost is a living database, meant to be updated on an ongoing basis by authors and future users (Diagne et al. 2020a). We used the cost entries available at



**Figure 1.** Process of compiling data sources for a database of invasion costs for the Mediterranean.

the time of writing (November, 2020; 4,793 entries, Ballesteros-Mejia et al. 2020; Diagne et al. 2020b), which were the result of both systematic and targeted searches, conducted through standardised English-language search strings in Web of Science, Google Scholar and Google. Targeted searches allowed opportunistic addition of supplementary cost entries, in both English and French. These searches were conducted in a number of different ways which span from examining the content of relevant web pages to contacting national and international experts for obtaining published or unpublished documents. Further methodological details regarding the search strategies, search terms used, material included, the screening process and the inclusion criteria, can be found in Diagne et al. (2020a).

These data were further complemented with 5,212 cost entries extracted from literature in 15 languages other than English (Angulo et al. 2020, 2021). These cost estimates were collated through a) a standardised literature search that used the InvaCost protocol described in Diagne et al. (2020a) and b) a more targeted opportunistic search through

national databases, web pages of national institutions, NGOs and other organisations, as well as through contacts with regional national experts (Angulo et al. 2021).

We filtered the cost entries compiled ( $n = 10,005$ ) to select only costs of IAS in the 26 countries having a coastline on the Mediterranean Sea (or countries within these countries, i.e. Andorra, San Marino, Vatican City), or costs in the Mediterranean Sea. Costs of IAS explicitly occurring in overseas territories of these countries (e.g. French Guiana) were excluded from our analyses.

Prior to analyses, all cost entries in our database were expanded so that each entry was annualised (i.e. corresponding to a single year), given that original cost estimates may have corresponded to either a cost realised over a single year, a period of less than a year, or a cost reoccurring over a series of years. For the purpose of expanding these original cost entries, we used the *expandYearlyCosts* function of the ‘invacost’ R package (Leroy et al. 2020), based on the difference between the probable starting and ending years of each cost entry presented in the database. Note that this process removed any cost entries (including one for Israel, Morocco and Tunisia) that occurred over an unspecified time period following the procedure described in Diagne et al. (2020a). Our analysis is therefore based on the 4,786 “expanded” cost entries resulting from this process and occurring up until 2017 (the last complete year included in all systematic searches). These mostly originated from the following 15 Mediterranean countries: Albania, Bosnia and Herzegovina, Croatia, Cyprus, Egypt, France, Greece, Israel, Italy, Libya, Malta, Montenegro, Slovenia, Spain and Turkey.

All cost estimates were standardised to 2017 equivalent US dollars (US\$) using the market exchange rate (World Bank), and accounting for inflation (Consumer Price Index of the year the cost was estimated for in each study) (Diagne et al. 2020a, b). The dataset used for the analysis is provided as a Suppl. material (Suppl. material 1: Mediterranean database).

### Cost descriptors, temporal cost dynamics and correlation with socioeconomic variables

The extracted cost data were classified according to temporal, spatial, and taxonomic descriptors (see Diagne et al. 2020a for more details): (i) Publication year: referring to the year in which the study and/or costs were published; (ii) Method reliability: illustrating the perceived reliability of the type of publication and methodological approach used for cost estimation; estimates obtained from officially pre-assessed materials (peer-reviewed articles and official reports), or from grey material but with documented, repeatable and traceable methods, were designated as “High” reliability. All other estimates were designated as having a “Low” reliability; (iii) Implementation: referring to whether the cost estimate was actually realised or empirically incurred due to an invasive species within the invaded habitat (“Observed”), or whether it was not incurred but rather expected and/or predicted over time within or beyond its actual distribution area (“Potential”); (iv) Country: describing the origin country of the listed cost; (v) Taxonomy, referring to the taxonomic grouping of the cost; (vi) Habitat

of species: corresponding to where the species occurs (i.e. “Aquatic”, “Semi-aquatic”, “Terrestrial” or “Diverse/Unspecified”) (Suppl. material 2: Table S1a); (vii) Type of cost: grouping of costs according to the categories: (a) “Damage” referring to damages or losses incurred due to the invasion (i.e., costs for damage repair, resource losses, medical care), (b) “Management” comprising expenditure such as control, monitoring, prevention, eradication, (c) “Mixed” including a mix of categories (a) and (b) (cases where reported costs were undistinguishable damage and management costs); (viii) Impacted sector: the activity, societal or market sector that was impacted by the cost (Suppl. material 2: Table S1b); note that individual cost entries not allocated to a single sector were classified as “Mixed” in the “Impacted sector” column. Costs that were incurred from multiple or unspecified taxa, or countries, were categorised as “Diverse/Unspecified”.

To assess temporal trends of invasion costs in the Mediterranean over time, we considered 5-year means since 1990 (the first year with invasion costs in our database). We examined costs as a function of the “Impact year”, which reflects the time at which the invasion cost likely occurred based on probable starting and ending years (Leroy et al. 2020). This allowed for an estimation of annual average costs over the entire reported period.

In addition to the data included in our cost database, we collected complementary elements from the Centre for Agriculture and Bioscience International (CABI 2020) to obtain information on the geographic origin of each invasive species causing observed damage costs in the studied area, including their presence in each country, pathways of introduction, impacts and uses (if any). To improve our analysis and interpretation of invasion costs, we also extracted information on several country indicators from the World Bank (2020) (Suppl. material 2: Table S2) to further assess whether costs in each country could be correlated to key socioeconomic variables. To that aim, the `ggcorr` function of the ‘GGally’ package in R 4.0.0 was used. We found significant correlations between some of these indicators (Suppl. material 2: Fig. S1). However, since we aimed to study the relation of each indicator with the observed costs independently, we estimated Spearman rank correlations between each extracted indicator and country-level expenditures and damage costs using the ‘`ggpubr`’ package in R 4.0.0.

## Network analysis of costs

Spatial and taxonomic aspects of Mediterranean invasion costs were concurrently examined using a bipartite network of two types of nodes: (1) countries and (2) taxonomic groups (excluding studies reporting costs on diverse taxonomic groups, or in other words costs for species belonging to different taxonomic groups that were reported together). For taxa, broad groupings were created from combinations of habitat and animal taxonomic group (e.g. “terrestrial mammal”, “aquatic arthropod”) or plant guild e.g. (“terrestrial forb” or “aquatic floating”) to facilitate broad-scale taxonomic linking among countries. The taxonomic groupings used can be found

in Suppl. material 1: Mediterranean database. In brief, links were produced among nodes where a group had a cost in a given country, and the link thicknesses and node sizes were attributed to respective cost totals. As such, the size of the nodes, and thickness of the links, correspond to the magnitude of cumulative economic costs incurred for the 1990–2017 period. The network was illustrated in Gephi 0.9.2 using the Forceatlas2 algorithm (Bastian et al. 2009). We applied the Map Equation community-detection algorithm (version 0.19.12, [www.mapequation.org](http://www.mapequation.org); Rosvall and Bergstrom 2008, Rosvall et al. 2009) to examine clusters of countries which exhibited similar combinations of invasion costs. Clusters within this network reflect groups of nodes sharing costs (e.g., an invasive group that impacted multiple countries, or multiple groups that impacted altogether one to several countries). The network analysis was performed using the ‘biogeonetworks’ R package (Leroy et al. 2019; Leroy 2020), and based on the Map Equation algorithm optimised for a two-level partition of the network with 1,000 trials.

## Results

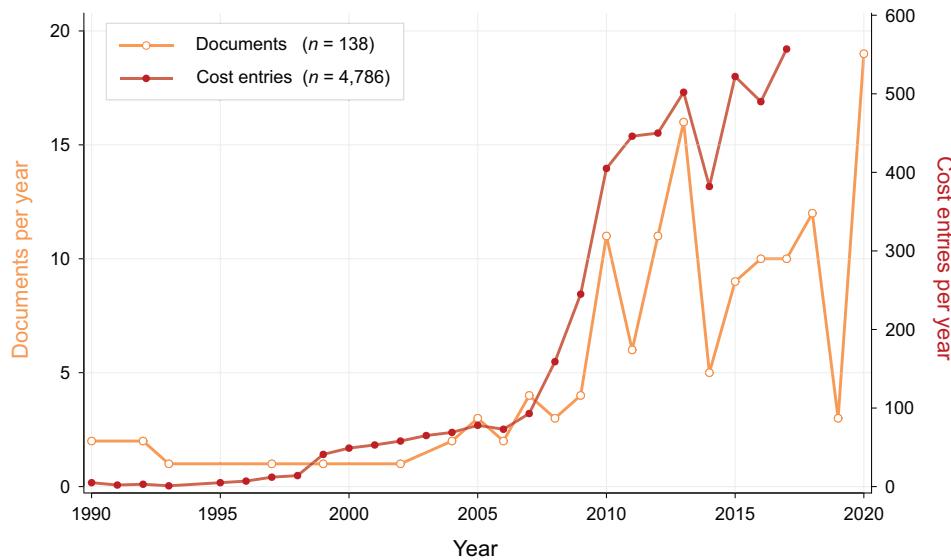
### Overview of invasion costs

Between 1990 and 2017, the total cost of IAS in the Mediterranean basin was estimated at \$27.31 billion (in 2017 US\$ values). The majority of the costs for the Mediterranean in our database were published after the mid-2000s (orange line, Fig. 2). The number of costs occurring per year exhibited a general increase over time, especially after 2006 (red line, Fig. 2).

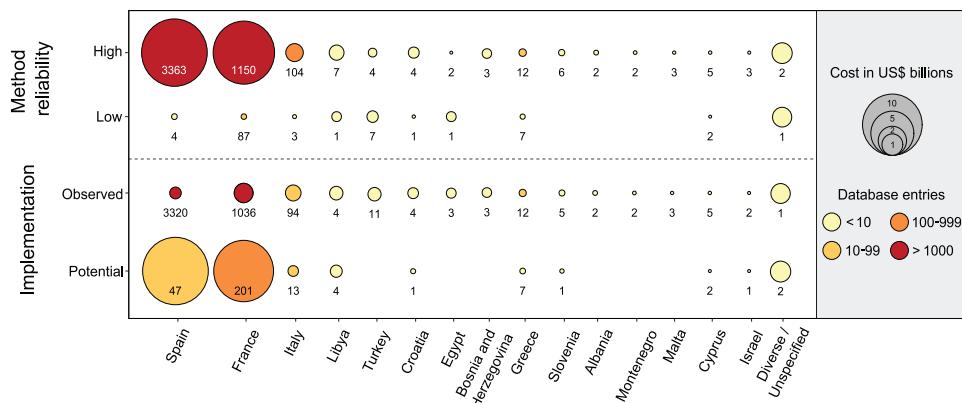
The vast majority (87%) of total costs for the region were derived from expectations or predictions (Potential, \$23.73 billion), rather than empirical observations (Observed, \$3.59 billion). However, these potential costs correspond to a relatively small number of database entries ( $n = 279$ ) with the majority of entries corresponding to empirical observations ( $n = 4,507$ , Fig. 3). Additionally, close to 98% of the cost entries for the Mediterranean basin ( $n = 4,672$ ), corresponding to \$25.89 billion, were deemed highly reliable based on the method of estimation (see also Suppl. material 2: Fig. S2, for method reliability in observed costs). Most of the costs (69%, \$18.81 billion) originated from English-language references.

### Spatial distribution of costs

Between 1990 and 2017, the majority of Mediterranean invasion costs were recorded in the western part of Europe: Spain (\$12.47 billion,  $n = 3,367$ ), France (\$10.85 billion,  $n = 1,237$ ) and Italy (\$680.76 million,  $n = 107$ ). Costs were also high in Libya (\$593.04 billion;  $n = 8$ ). The sum of costs in the remaining 11 countries for which data were available (i.e. Albania, Bosnia and Herzegovina, Croatia, Cyprus, Egypt, Greece, Israel, Malta, Montenegro, Slovenia and Turkey) were found to be relatively low, corroborating low numbers of cost entries (Fig. 4).

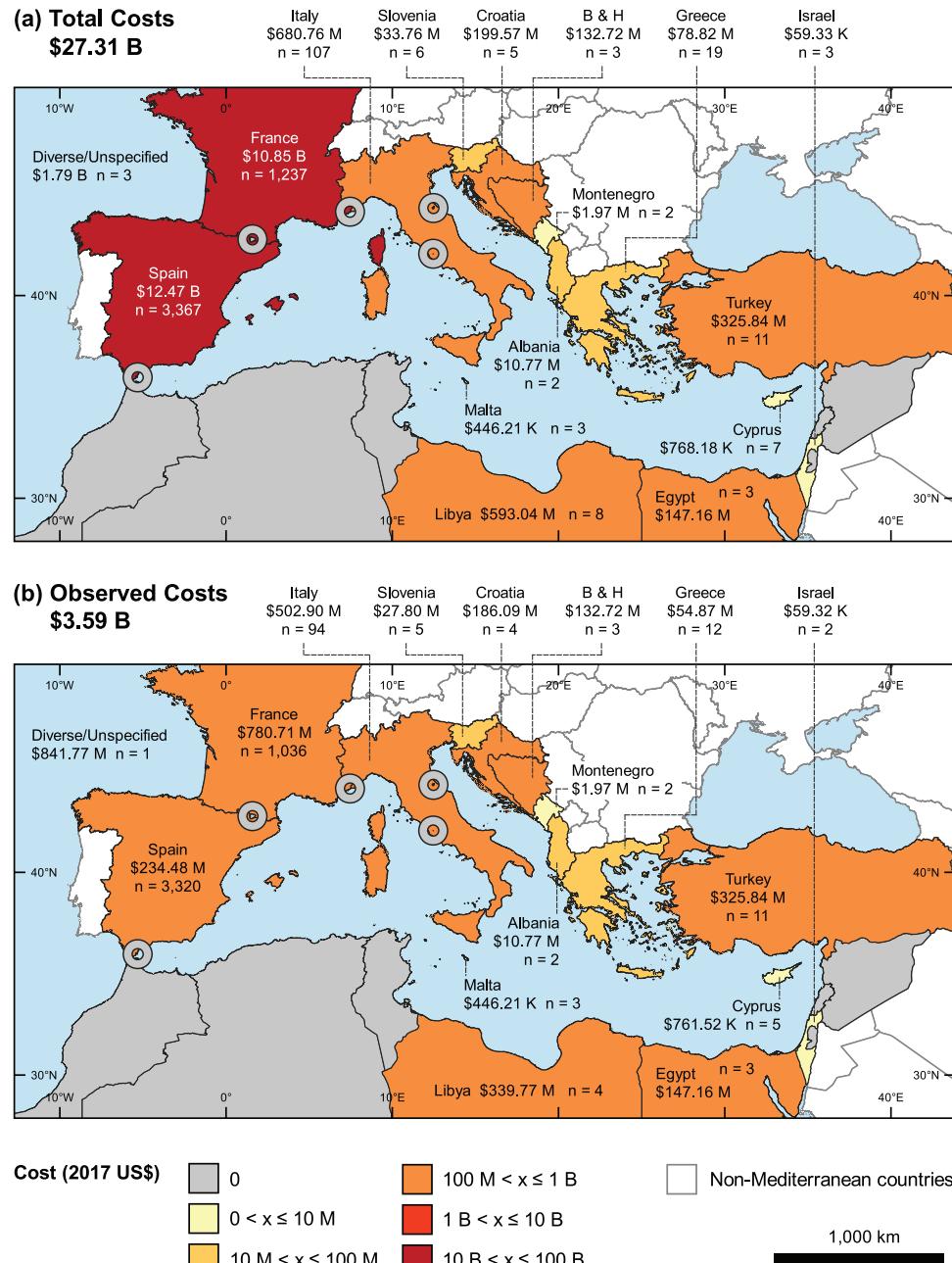


**Figure 2.** Temporal trends in numbers of documents reporting costs (left y-axis) and cost entries (right y-axis) concerning invasive alien species within the Mediterranean basin published during 1990–2020. Note the different scales for the two vertical axes. All data shown here reflect costs occurring in 2017 or earlier, as used in our analysis (note that some of these costs were published after 2017).



**Figure 3.** Balloon plot indicating invasion costs (total) and cost entry numbers for Mediterranean countries available, according to implementation type (Observed/Potential) and method reliability (High/Low). The numbers inside or adjacent to each balloon correspond to the sample size (also indicated by shading).

When “Observed” costs were considered, France (\$780.71 billion,  $n = 1,036$ ), Italy (\$502.9 million,  $n = 94$ ), and Libya (\$339.77 million,  $n = 4$ ) were the top three countries, with Turkey (\$325.84 million,  $n = 11$ ) ranking fourth and Spain (\$234.48 million,  $n = 3,320$ ) fifth. Our dataset contained no costs for the following 11 countries: Algeria, Andorra, Gibraltar, Lebanon, Monaco, Morocco, Palestine, San Marino, Syria, Tunisia and Vatican City.



**Figure 4.** Reported costs of IAS in countries of the Mediterranean basin over the period 1990–2017. Subplots display (a) total costs (observed and potential costs), and (b) observed costs only. n = number of cost entries in expanded InvaCost database, B: Billions, M: Millions, K: Thousands. Circles highlight small-sized countries (Andorra, Gibraltar, Monaco, San Marino, Vatican City, all with no recorded cost). National borders are based on data from <https://gadm.org/data.html> and are for illustration purposes only. Cyprus is represented as a single geographical unit; all costs were from the Greek part. Map Projection: World Mercator.

## Distribution of costs across taxonomic groups

Overall, close to two thirds of the costs (\$17.76 billion) were attributed to animals, and one third (\$9.54 billion) to plants, although the number of entries was much smaller for animals ( $n = 1,140$  entries) than for plants ( $n = 3,516$  entries). When considering “Observed” costs only, invasions from animals (\$1.81 billion,  $n = 998$  entries) were found to be slightly more costly than those from plants (\$1.76 billion,  $n = 3,399$  entries).

The vast majority of costs were caused by invertebrates, driven predominantly by the secernentean nematodes (\$14.08 billion, 52% of total costs,  $n = 110$  entries) and insects (\$3.55 billion, 13% of total costs,  $n = 143$  entries). Vertebrates accounted for <1% of total costs (\$74.01 million,  $n = 563$  entries), with mammals accounting for 88% of vertebrate costs (\$65.07 million,  $n = 272$  entries). Plant costs were driven primarily by the flowering plants Magnoliopsida (\$9.35 billion, 34% of total costs). When observed costs were considered solely, Magnoliopsida was the costliest class of species, with total reported costs of \$1.59 billion ( $n = 2,049$  entries), followed by insects, with \$1.74 billion ( $n = 128$  entries) (see also Suppl. material 2: Table S3).

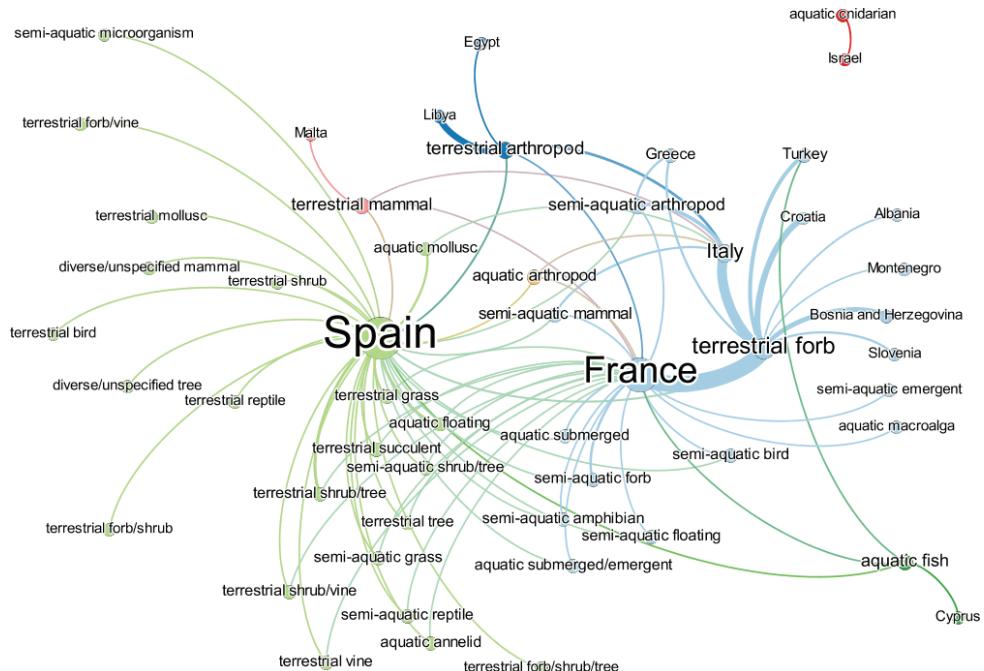
The database for the Mediterranean contains costs for 218 species and 187 genera (considering only costs attributable to individual species or genera). The pine wood nematode *Bursaphelenchus xylophilus*, the only species within the class of Secernentea, was by far the costliest invasive species across the Mediterranean basin, with total costs peaking at \$14.08 billion (Suppl. material 2: Table S3). The New World screwworm *Cochliomyia hominivorax* and the common ragweed *Ambrosia artemisiifolia* followed in the list of the top three most costly species, with total costs of \$1.54 and \$1.39 billion, respectively (Suppl. material 2: Table S4).

When accounting for “Observed” costs only, the common ragweed *Ambrosia artemisiifolia* was the costliest IAS (\$1.39 billion), followed by the olive fruit fly *Bactrocera oleae* with \$0.84 billion, the New World screwworm *Cochliomyia hominivorax* with close to \$0.34 billion and the tomato leafminer *Tuta absoluta* with \$0.22 billion.

## Spatial and taxonomic connectivity of costs

In examining spatial and taxonomic group connectivity across the Mediterranean basin, six clusters identified marked patterns of invasion costs (Fig. 5).

Two major clusters emerged in the Mediterranean basin. First, France, Italy, Greece, as well as Turkey and several Balkan countries constituted the largest cluster. All countries in this cluster were affected by terrestrial forbs; this cluster was also characterized by multiple groups of invaders affecting one to a few countries (notably, semi-aquatic arthropods). The second major cluster was composed of Spain and the highly diverse array of invasive groups impacting this country. The remaining clusters were composed of one to two countries economically impacted by a specific group of organisms: Libya and Egypt by terrestrial arthropods, Malta by terrestrial mammals, Cyprus by fishes and Israel by cnidarians. Nonetheless, despite these marked areas of interrelatedness, there were many inter-cluster linkages which indicate that most clusters are impacted

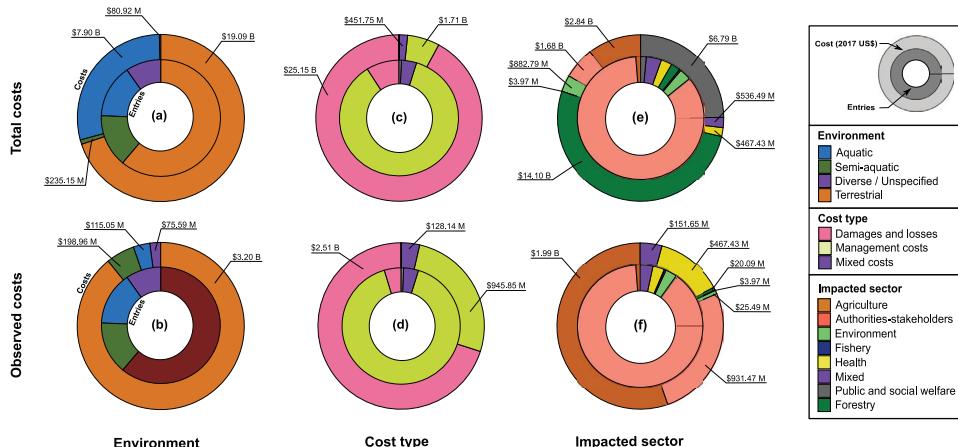


**Figure 5.** Network of observed invasive alien species costs per country in the Mediterranean. This bipartite network is composed of both species groups and country nodes. Links indicate the cumulative costs of species in countries over 1990–2017. Node size and link thickness corresponds to the cumulative costs. For species nodes, node size represents the total cost they had over all countries. For country nodes, the node size represents the total cost of all species in that country, so large country nodes imply that those countries had large invasion costs.

economically by several taxonomic groups. Note, for example, the numerous groups reported to impact both France and Spain. Overall, a relative lack of reported invasion costs for other Mediterranean countries negated their prominence in the network, indicating a disparity in cost reporting in the region.

### Distribution of costs across habitats, cost types and sectors impacted

Considering both “Total” and “Observed” costs, terrestrial species accounted for the vast majority of both total (\$19.09 billion, 70%) and observed costs (\$3.2 billion, 89%) (Fig. 6a, b). Costs characterised as purely “Aquatic” were estimated at \$7.9 billion (29% of all costs) and considering only observed costs at \$0.12 billion (3.2% of all costs) (Fig. 6a, b). In both cases, “Semi-aquatic” species contributions were relatively minor (Total costs: \$0.24 billion; Observed costs: \$0.20 billion). “Diverse/unspecified” costs were \$80.92 million and \$75.79 million, respectively. Costs from marine taxa comprised only a minor part (\$4.24 million,  $n = 18$ ) of the total aquatic cost (\$7.9 billion).



**Figure 6.** Invasion costs (outer circle) and cost entries (inner circle) in the Mediterranean basin by Environment (left), Type of cost (middle) and Impacted sector (right), considering all costs (upper) and observed costs alone (bottom).

The vast majority of costs associated with biological invasions in the Mediterranean basin were due to damages or losses (92.1% of total costs, \$25.15 billion), followed by much lower management costs (6.3% of total costs, \$1.71 billion) (Fig. 6c). The majority of damage costs were reported in Spain and France, and were largely due to the pine wood nematode invasion. When only observed costs were considered, damage costs again dominated (60% of observed costs, \$2.51 billion), but to a lesser extent compared to total costs (Fig. 6d). France incurred the highest damage costs (\$621.18 million observed) and Italy the second highest (\$400.26 million observed). Notably, more than half of the observed damage costs were attributed to the common ragweed (55%, \$1.39 billion).

The forestry industry was the most severely affected overall, with approximately \$14.1 billion ( $n = 114$  entries) in total costs (Fig. 6c). The high costs attributed to forestry in the Mediterranean basin are primarily due to the pine wood nematode invasion in Spain and France, and the predictions described earlier. Costs to “Public and social welfare” (\$6.79 billion,  $n = 68$  entries) followed by “Agriculture” (\$2.84 billion,  $n = 60$  entries) and “Authorities-Stakeholders” (\$1.68 billion,  $n = 4,059$  entries) were found to be the next highest among all other sectors. Costs that could not be assigned to a single sector (i.e., “Mixed”) were lower than costs incurred under the category “Environment” (\$536.49 million,  $n = 186$  and \$882.79 million,  $n = 145$  entries for “Mixed” and “Environment” respectively). The least impacted sectors according to data records were “Health” (\$467.43 million,  $n = 134$  entries) and “Fishery” (\$3.97 million,  $n = 20$ ) owing to the very low number of cost entries (20 in total) (Fig. 6e).

When “Observed” costs only were considered, “Agriculture” (\$1.99 billion,  $n = 51$  entries) came out as the most impacted sector, followed by “Authorities-Stakeholders” (\$931.47 million,  $n = 4,018$  entries), “Health” costs (\$467.43 million,  $n = 134$  en-

tries), and costs to “Mixed” sectors (\$151.65 million,  $n = 148$  entries) then “Environment” (\$25.49 million,  $n = 132$  entries) and “Forestry” (\$20.09 million,  $n = 4$ ) (Fig. 6c). Costs to the “Fishery” sector were found, again, to have the lowest cost value (\$3.97 million,  $n = 20$  entries), while there were no observed costs for “Public and social welfare”, despite high total costs for that sector. This is because all relevant costs were estimates based on models and/or theoretical assumptions such as for example scenarios under which the IAS under consideration were to spread beyond their current range.

A more detailed breakdown of costs per sector in each country is available in Suppl. material 2: Fig. S3.

### Correlations between costs and key socioeconomic variables

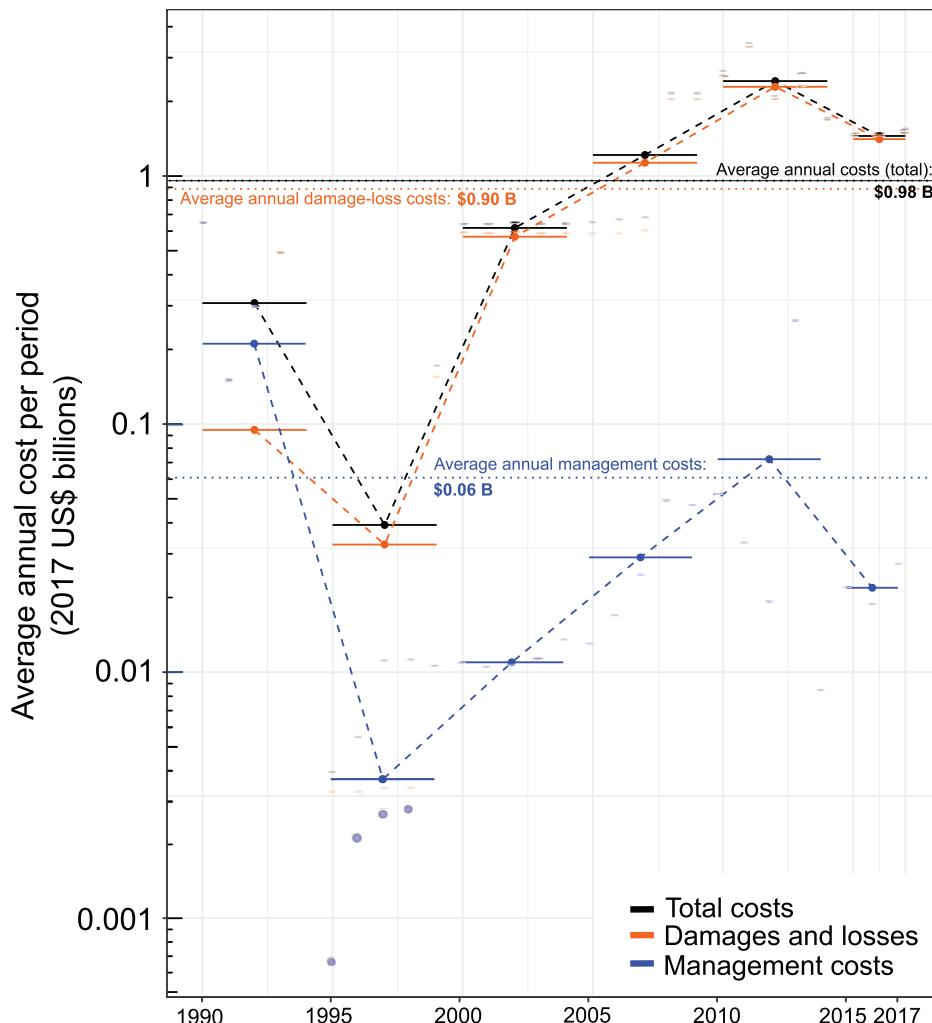
For observed cost entries, significant positive correlations were identified between both damages and management costs and research effort (reflected through expenditure in R&D). There were also positive strong correlations between a) observed damage-loss costs and the size of forest areas, GDP, international trade (reflected through container port traffic), and research effort (reflected also through number of journal publications, beyond just expenditure in R&D) and b) observed management costs and international trade (reflected through imports of goods and services) (Table 1).

### Temporal trends of costs

The average annual cost throughout the entire period of 1990–2017 was estimated at \$975.5 million, exhibiting an initial decrease throughout the 1990s, followed by a sharp increase in the early 2000s, and a further substantial increase afterwards (Fig. 7). Damages and losses comprised most of the average annual costs throughout this period, with management costs comprising less than 6% of all the costs. The average

**Table 1.** Relationships of observed “Damage” and “Management” costs of IAS in Mediterranean countries with country-specific indicators derived from the World Bank (2020). Details on these country-specific indicators are presented in Suppl. material 2: Table S2. Statistics shown are Spearman correlation coefficients and associated  $p$ -values (in brackets). Cells in bold indicate significance at the 0.05 level.

	Damage costs	Management costs
Total area (km <sup>2</sup> )	0.10 (0.670)	0.08 (0.740)
Agricultural area (km <sup>2</sup> )	0.11 (0.650)	0.03 (0.900)
Forest area (km <sup>2</sup> )	<b>0.63 (0.003)</b>	0.24 (0.310)
Urban area (km <sup>2</sup> )	0.34 (0.160)	0.31 (0.200)
Human population (thousands of people)	0.22 (0.360)	0.04 (0.880)
GDP (US\$)	<b>0.46 (0.039)</b>	0.39 (0.086)
Container port traffic (TEU: 20-foot equivalent units)	<b>0.47 (0.050)</b>	0.33 (0.180)
Research and development expenditure (US\$)	<b>0.49 (0.041)</b>	<b>0.61 (0.007)</b>
Scientific and technical journal articles	<b>0.47 (0.035)</b>	0.28 (0.230)
Number of researchers	0.41 (0.088)	0.45 (0.060)
Imports of goods and services (US\$)	0.44 (0.054)	<b>0.49 (0.027)</b>



**Figure 7.** Total (observed and potential) annual costs resulting from invasions in the Mediterranean region from 1990–2017 at five-year increments (except for the last three years of the dataset which cover the period 2015–2017). Data are presented for all costs combined, plus "Damage" and "Management" costs separately. Solid points and horizontal lines represent annual means over their respective 5-year intervals. Note that the y-axis is shown on a  $\log_{10}$  scale. The slight decrease observed for the last three years is likely indicative of the incomplete sampling of cost for these last years, because of the delay between cost occurrence and reporting/publication.

annual costs of damages and losses, estimated at \$898.3 million, have been steadily increasing through time, reaching their peak between 2010 and 2015 and declining over the last three years. Average annual management costs were estimated at \$61 million and had their peak in the early 1990s, reaching a low in the late 1990s and generally

did not exhibit a consistent pattern through time. Reductions in costs in recent years likely emanate from time lags (i.e. between timing of cost incurrence and publication) and thus reflect incompleteness, as there is no evidence that biological invasions are slowing down (Seebens et al. 2017).

## Discussion

Between 1990 and 2017, the total recorded economic costs of biological invasions in Mediterranean countries amounted to \$27.31 billion. However, most costs are the result of predictions or expectations (87% of total costs, \$23.73 billion) rather than realised costs, meaning that costs were projected in time and/or space by the original authors, so these costs have not necessarily been borne in practice. It is important to acknowledge this as a limitation in our understanding of actual economic impacts of invasions in the region. Observed costs of biological invasions were still substantial, at \$3.59 billion over the same time period. Note again though that our database includes reported costs only, implying that costs are likely a substantial underestimate. Additionally, and as suggested by our results, costs may reflect reporting effort as much as real costs. Biases and gaps in our database likely reflect an absence of published material or a failure of the InvaCost literature searches to find this or unpublished material, rather than a genuine absence of costs. Nevertheless, our analysis of temporal trends identified marked increases in invasion costs over time (during the last three decades), particularly for resource damages, in line with evidence of increasing rates of invasion worldwide (Seebens et al. 2017) and increasing publication rates.

Our understanding of the economic impacts of biological invasions in the Mediterranean basin is largely limited to studies from a subset of countries: cost data were found for only 15 out of 26 countries, with the Western European countries (France, Spain and Italy) dominating reported costs. While most of the invasive species causing the highest monetary losses in the Mediterranean are present in many countries, their observed costs are only reported by a few. For example, our database only contains observed costs for cnidarians in Israel, despite the presence of a number of invasive species of jellyfish all over the Mediterranean (Brotz and Pauly 2012). Furthermore, previous findings (Capinha et al. 2014; Essl et al. 2015; Schertler et al. 2020; Zhang et al. 2020) have shown that large areas of the Mediterranean basin are predicted to be currently climatically suitable for some of the IAS presenting observed damage costs in other regions. Assuming the presence of suitable dispersal vectors, costs are likely already occurring in these regions (but have not been reported or captured in our database) or likely to occur in additional countries as IAS distributions expand.

Not surprisingly and in line with earlier literature establishing correlations between economic development and invasions (Nuñez and Pauchard 2010), we identified research effort (reflected through expenditure in R&D) to be positively and significantly correlated with both damage and management costs of IAS. This significant correlation indicates that greater research investments enhance capacities to report economic

impacts, and may also bolster incentives for management actions. As expected, with greater economic activity in a country (e.g. higher GDP, greater value of imports etc), there is a larger scope for a) economic losses, which manifest especially through directly quantifiable damages to human infrastructure, health or different sectors of the economy, and b) increased expenditure on management driven by increased awareness of ecological damages and sufficient resources to invest in alleviating them (Dickie et al. 2014). However, there may also be reporting biases at play here, whereby more developed countries with more resources and higher expenditure on research (World Bank 2020) document invasion costs more thoroughly. Accordingly, France, Spain and Italy, the three countries found to dominate total reported costs in our data, are the highest-scoring Mediterranean countries in several of these indicators (World Bank 2020). Interestingly, we found no significant correlation between the observed costs and agricultural area, despite the fact that the sector bears a large proportion (55%) of the observed costs. However, these results should be carefully interpreted, given the aforementioned correlations between costs and research effort.

Impacts generally spanned various sectors affecting a diverse set of stakeholders; however, the vast majority of reported costs were attributed to damages or losses (92.1% of total costs, \$25.15 billion), possibly indicating relatively limited investments in management or, at best, limited reporting of management expenditure. Our results also provide evidence for strong taxonomic gaps and biases, with most costs derived from few invasive species or taxonomic groups. The top 10 costliest species (Suppl. material 2: Table S4) account for 70% of total costs and 91% of observed costs. A key cluster of reported costs was identified for terrestrial forbs in Western Europe and the Balkans. Costs from two publications and three species dominate the database, driving patterns in total costs. First, Issanchou (2012) estimated, by extrapolation, the economic losses to tourism and recreation caused by floating primrose willow *Ludwigia peploides* and water primrose *Ludwigia grandiflora*. Although this study focuses on a single French marsh, the annual cost is substantial and is described as extending over 13 years, resulting in a large total cost (\$7.74 billion), that comprises a large part of costs to "Public and social welfare" and contributes to the high ranking of France in the list of countries most affected by IAS. Second, Soliman et al. (2012) projected \$14.08 billion in damage costs of pine wood nematode *Bursaphelenchus xylophilus* in forests in Spain, France and Italy. Note that this is an approximate estimate given that our analysis of costs spans until 2017 (whereas the original paper projects costs to 2030) and assumes a linear accumulation of costs over time. This single reference greatly contributes to the dominance of: a) costs in terrestrial over other ecosystems, b) damages over other types of expenditure (e.g. management), c) effects on the forestry sector over other sectors/groups bearing costs, and d) Spain and France over all other countries. However, in reality, pine wood nematode has not spread extensively in the Mediterranean beyond Portugal, where it was introduced in 1999 (de la Fuente et al. 2018), implying that widespread damage has not yet occurred and therefore these damage costs have not yet been realised. This emphasises the importance of distinguishing between observed costs and total costs (which includes potential or expected costs; see Results

subsection “Overview of invasion costs”). At the same time, however, investments in understanding potential costs, along with efforts for control, early detection and rapid response measures for this species may reduce the likelihood of spread and therefore the likelihood of costs being realised (see for example 2012/535/EU in EU (2012)). The high reported costs for a single species may also highlight the role of research agendas along with researchers’ and research funders’ incentives, in determining those IAS of utmost importance and driving research investments in understanding their costs. These agendas and incentives, which differ across countries depending on e.g. national priorities on certain sectors of the economy, largely shape our understanding of costs at a regional scale, likely creating bias over ecosystems, sectors and countries affected (Kourantidou and Kaiser 2019).

Our database contains no information on the economic cost of several IAS known to have large costs in invaded habitats elsewhere in the world, or at the global scale. Such species present as aliens in the Mediterranean, include for example the diamond-back moth *Plutella xylostella*, the carpet sea squirt *Didemnum vexillum* and kikuyu grass *Cenchrus clandestinus* or *Pennisetum clandestinum* (Musil et al. 2005; Mendieta and Cardenas 2010; Ordóñez et al. 2015; Bradshaw et al. 2016). Similarly, the database is missing information on costs of several IAS or alien species known or expected to have large social and/or ecological impacts in the Mediterranean – which may be linked to high economic costs – such as the common myna *Acridotheres tristis*, the seaweed *Codium parvulum* and the Pacific oyster *Crassostrea gigas* (Katsanevakis et al. 2016; Peyton et al. 2019). An absence of such species from our database should not necessarily be interpreted as an absence of realised economic costs. In addition, several highly costly species in some countries are also invasive in others, but with no recorded costs. As an example, a study of the costs of invasions in France calculated the potential costs of all IAS known to be present but with no cost record, from the cost records in other countries (Renault et al. 2021). This estimation increased the economic costs of IAS in France by \$968 million over the period 1993–2018 (i.e. more than 8%). These examples highlight the need to expand research efforts quantifying the economic impacts of existing, ongoing and expected invasions.

These gaps in species reported are also reflected in the ecological literature for the region that describes the presence of many IAS (Zenetas et al. 2005; Di Castri et al. 2012; ISSG 2015), as well as in national and European legislation and regulatory instruments such as the EU (2014) Regulation 1143/2014. These knowledge gaps, which may also come along with a paucity of quantitative information on ecological impacts of invasions on goods and services, limit our ability to assess with accuracy the true costs of invasive species in the region and indicate that costs presented here are substantial underestimates.

Reported costs of aquatic species (\$7.9 billion, only \$0.12 billion of which were observed) were less than half of the reported costs for terrestrial species. These covered only 37 aquatic and 28 semi-aquatic species with species-specific costs. This is despite many reports of high-impact and newer high-risk invasions in Mediterranean aquatic environments, especially the Mediterranean Sea which is among the world’s most in-

vaded (Zenetas et al. 2005; Edelist et al. 2013; Kalogirou 2013; Giakoumi 2014; Katsanevakis et al. 2014; Clavero et al. 2015; Kletou et al. 2016; Zenetas and Galanidi 2020). Limited capacity for reporting costs of aquatic invasions may be related to the difficulty of understanding their social and economic dimensions, which may in turn lead to limited investments in research and management in these ecosystems. This becomes particularly important given that by the time aquatic invasions are observed and attract researchers' and/or resource managers' attention, they are typically at a quite advanced stage of the invasion (Beric and MacIsaac 2015), which increases the likelihood of more pronounced impacts. The absence of such reported expenditure in the Mediterranean is likely a combination of limited management at an early stage of the introduction and a lack of knowledge, strategies and/or frameworks for these types of investments. Despite the economic importance of coastal tourism and the socioeconomic value of fisheries in the Mediterranean, we do not exclude the possibility that economic impacts of IAS may be genuinely lower in aquatic than terrestrial systems, given that most human activities and infrastructure that could be affected by invasions are on dry land (e.g. 64% of costs in the U.S. linked to arable and livestock farming; Pimentel et al. 2005).

Notably, the costs from invasions identified in marine ecosystems (less than 0.01% of aquatic species costs) and were limited to a three species only, when there are multiple well-known invasive fish, marine mollusks and invertebrates, crustaceans, foraminifera, polychaetes and algae in the Mediterranean Sea (Rilov and Galil 2009; Edelist et al. 2013). Considering invasive fish, the Mediterranean has the most invasions worldwide, with at least 84 known Indo-Pacific fish that have invaded the eastern part since the opening of the Suez Canal, close to two thirds of which have established permanent populations in the Mediterranean (Edelist et al. 2013). Costs for marine invasions are generally underrepresented at a global scale, with about 2% of all aquatic invasion costs globally attributed to marine species (Angulo et al. 2020; Ballesteros-Mejia et al. 2020; Diagne et al. 2020b).

Costs to the fishery sector were only \$3.97 million (all observed), originating from two species: the tube worm *Ficopomatus enigmaticus*, and the red swamp crayfish *Procambarus clarkii*. Costs to the sector of several well-known marine invaders that have been affecting fishers directly (e.g. through damages to gear, injuries, bycatch costs etc) and/or indirectly (e.g. through ecosystem degradation, competition for food etc), such as the pufferfish *Lagocephalus sceleratus*, the round herring *Etrumeus golanii*, the lion-fish *Pterois miles* or the rabbitfishes *Siganus rivulatus* and *S. luridus* have not yet been quantified (e.g. see Kalogirou 2013; Giakoumi 2014).

Efforts to understand the spatial and taxonomic connectivity additionally highlighted the limits of the available data and the research effort conducted in the region to understand the different facets of invasion costs in the Mediterranean basin. Few broad taxonomic groups, such as terrestrial forbs and arthropods, as well as fish, had relatively far-reaching invasion costs, evidenced by network clustering. Conversely, other taxa were structurally disparate in the network, being linked to just single, or few, countries (e.g., cnidarians in Israel; aquatic plants in France and Spain), despite

the wider known extent and damages of such taxa across the Mediterranean region (e.g., Brundu 2015). Our network analysis revealed that the taxonomic composition of costs differed across countries, indicating that the reported assemblages of IAS impacts that drive economic impacts are strongly dictated by low publication effort (with the knowledge gaps and biases it entails), or that invaders have truly unique compositions with unevenly distributed impacts across nations.

## Conclusions

Having shed light on many of the limitations of the current understanding of economic impacts from invasions in the Mediterranean, we suggest that these shortcomings should be addressed in future research and also considered in resource managers' and policy makers' agendas. However, we also caution that management decisions should not be based on reported monetary costs alone, as difficult-to-quantify ecological invasion ramifications should also warrant interventions. As opposed to what one may have expected for an interconnected region such as the Mediterranean basin, no clear pattern can be identified regarding the origin of the invasive species causing costs in the area (Suppl. material 2: Table S5). This may be attributed to limited reporting of costs from several countries. Most of the terrestrial species occupy disturbed areas, cultivated lands or forests. No clear pattern has been identified for aquatic invasions which may reflect, among other factors, underreporting of invasions in aquatic systems. With 42% of countries in the Mediterranean basin completely absent from our database, very few recorded costs from the vast majority of the rest and collective action on combating invasions largely missing in the Mediterranean basin, it becomes clear that there is an urgent need for comprehensive, resolute and standardised reporting of how invasions impact human and social wellbeing and economies. This is especially the case in aquatic environments and the Mediterranean Sea in particular, which is known to be among the world's most invaded.

Such efforts will allow for specifying high-risk and/or high-impact invasive taxa and identifying with more accuracy the spatial and temporal scale of realized and expected impacts. Investments in standardising both costs of damages and management (Iacona et al. 2018; Diagne et al. 2021) can be of great value for an improved collective understanding of invasion impacts regionally as well as for designing cross-border collaborative policies that can help mitigate impacts in the Mediterranean, one of the world's richest biodiversity hotspots.

## Acknowledgements

The authors acknowledge the French National Research Agency (ANR-14-CE02-0021) and the BNP-Paribas Foundation Climate Initiative for funding the InvaCost project that allowed the construction of the InvaCost database. The present work was conducted following a workshop funded by the AXA Research Fund Chair of Inva-

sion Biology and is part of the AlienScenarios project funded by BiodivERsA and Belmont-Forum call 2018 on biodiversity scenarios. Funds for EA and LBM contracts come from the AXA Research Fund Chair of Invasion Biology. CD was funded by the BiodivERsA-Belmont Forum Project “Alien Scenarios” (BMBF/PT DLR 01LC1807C). RNC is funded through a Humboldt Research Fellowship from the Alexander von Humboldt Foundation. CC was supported by Portuguese National Funds through Fundação para a Ciência e a Tecnologia (CEECIND/02037/2017; UIDB/00295/2020 and IDP/00295/2020). DR thanks InEE-CNRS who supports the network GdR 3647 ‘Invasions Biologiques’, and BiodivERsA who supported the project ‘ASICS’ via the cofund call 2019–2020 ‘Biodiversity and Climate Change’. AN acknowledges funding from EXPRO grant no. 19-28807X (Czech Science Foundation) and long-term research development project RVO 67985939 (Czech Academy of Sciences). The authors also wish to acknowledge for the translation of the abstract in French, Gauthier Dobigny, in Italian, Paride Balzani, in Arabic, Ahmed Taheri, and in Croatian, Sandra Hodic.

Underlying data are publicly available in Ballesteros-Mejia et al. (2020), Diagne et al. (2020b), Angulo et al. (2020) and in the electronic Suppl. material (Suppl. material 1).

## References

- Angulo E, Diagne C, Ballesteros-Mejia L, Ahmed DA, Banerjee AK, Capinha C, Courchamp F, Renault D, Roiz D, Dobigny G, Haubrock PJ, Heringer G, Verbrugge LNH, Golivets M, Nuñez MA, Kirichenko N, Dia CAKM, Xiong W, Adamjy T, Akulov E, Duboscq-Carra VG, Kourantidou M, Liu C, Taheri A, Watari Y (2020) Non-English database version of InvaCost. Figshare. Dataset. <https://doi.org/10.6084/m9.figshare.12928136.v2>
- Angulo E, Diagne C, Ballesteros-Mejia L, Adamjy T, Ahmed DA, Akulov E, Banerjee AK, Capinha C, Dia CAKM, Dobigny G, Duboscq-Carra VG, Golivets M, Haubrock PJ, Heringer G, Kirichenko N, Kourantidou M, Liu C, Nuñez MA, Renault D, Roiz D, Taheri A, Verbrugge L, Watariaa Y, Xiong W, Courchamp F (2021) Non-English languages enrich scientific knowledge: the example of economic costs of biological invasions. *Science of the Total Environment* 775: 144441. <https://doi.org/10.1016/j.scitotenv.2020.144441>
- Arianoutsou M, Delipetrou P, Vilà M, Dimitrakopoulos PG, Celesti-Grapow L, Wardell-Johnson G, Henderson L, Fuentes N, Ugarte-Mendes E, Rundel PW (2013) Comparative patterns of plant invasions in the Mediterranean Biome. *PLoS ONE* 8: e79174. <https://doi.org/10.1371/journal.pone.0079174>
- Ballesteros-Mejia L, Angulo E, Diagne C, Courchamp F, InvaCost Consortia (2020) Complementary search database for Invacost. Figshare. Dataset. <https://doi.org/10.6084/m9.figshare.12928145.v2>
- Bastian M, Heymann S, Jacomy M (2009) Gephi: an open source software for exploring and manipulating networks. Third international AAAI conference on weblogs and social media.
- Beric B, MacIsaac HJ (2015) Determinants of rapid response success for alien invasive species in aquatic ecosystems. *Biological Invasions* 17: 3327–3335. <https://doi.org/10.1007/s10530-015-0959-3>

- Bradshaw CJA, Leroy B, Bellard C, Roiz D, Albert C, Fournier A, Barbet-Massin M, Salles J-M, Simard F, Courchamp F (2016) Massive yet grossly underestimated global costs of invasive insects. *Nature Communications* 7: 1–8. <https://doi.org/10.1038/ncomms12986>
- Brotz L, Pauly D (2012) Jellyfish populations in the Mediterranean Sea. *Acta Adriatica* 53: 213–232.
- Brundu G (2015) Plant invaders in European and Mediterranean inland waters: profiles, distribution, and threats. *Hydrobiologia* 746: 61–79. <https://doi.org/10.1007/s10750-014-1910-9>
- CABI (2020) Invasive Species Compendium. CAB International, Wallingford. [www.cabi.org/isc](http://www.cabi.org/isc)
- Capinha C, Rocha J, Sousa CA (2014) Macroclimate determines the global range limit of *Aedes aegypti*. *EcoHealth* 11: 420–428. <https://doi.org/10.1007/s10393-014-0918-y>
- Di Castri F, Hansen AJ, Debussche M (2012) Biological invasions in Europe and the Mediterranean Basin. Kluwer Academic Publishers, Dordrecht.
- CEPF (2020) Explore the Biodiversity Hotspots. Critical Ecosystem Partnership Fund. <https://www.cepf.net/our-work/biodiversity-hotspots>
- Clavero M, Hermoso V, Levin N, Kark S (2010) Biodiversity research: geographical linkages between threats and imperilment in freshwater fish in the Mediterranean Basin. *Diversity and Distributions* 16: 744–754. <https://doi.org/10.1111/j.1472-4642.2010.00680.x>
- Clavero M, Esquivias J, Qninba A, Riesco M, Calzada J, Ribeiro F, Fernández N, Delibes M (2015) Fish invading deserts: non-native species in arid Moroccan rivers. *Aquatic Conservation: Marine and Freshwater Ecosystems* 25: 49–60. <https://doi.org/10.1002/aqc.2487>
- Courchamp F, Fournier A, Bellard C, Bertelsmeier C, Bonnaud E, Jeschke JM, Russell JC (2017) Invasion biology: specific problems and possible solutions. *Trends in Ecology & Evolution* 32: 13–22. <https://doi.org/10.1016/j.tree.2016.11.001>
- Crystal-Ornelas R, Lockwood JL (2020) The “known unknowns” of invasive species impact measurement. *Biological Invasions* 22: 1513–1525. <https://doi.org/10.1007/s10530-020-02200-0>
- Cuthbert RN, Bacher S, Blackburn TM, Briski E, Diagne C, Dick JTA, Essl F, Genovesi P, Haubrock PJ, Latombe G (2020) Invasion costs, impacts, and human agency: response to Sagoff 2020. *Conservation Biology* 34: 1579–1582. <https://doi.org/10.1111/cobi.13592>
- Diagne C, Leroy B, Gozlan RE, Vaissière A-C, Assailly C, Nuninger L, Roiz D, Jourdain F, Jarić I, Courchamp F (2020a) InvaCost, a public database of the economic costs of biological invasions worldwide. *Scientific Data* 7: 1–12. <https://doi.org/10.1038/s41597-020-00586-z>
- Diagne C, Leroy B, Gozlan RE, Vaissière A-C, Assailly C, Nuninger L, Roiz D, Jourdain F, Jarić I, Courchamp F (2020b) InvaCost: references and description of economic cost estimates associated with biological invasions worldwide. Figshare. Dataset. <https://doi.org/10.6084/m9.figshare.12668570.v1>
- Diagne C, Catford JA, Essl F, Nuñez MA, Courchamp F (2020c) What are the economic costs of biological invasions? A complex topic requiring international and interdisciplinary expertise. *NeoBiota* 63: 25–37. <https://doi.org/10.3897/neobiota.63.55260>
- Diagne C, Leroy B, Vaissière A-C, Gozlan RE, Roiz D, Jarić I, Salles J-M, Bradshaw CJA, Courchamp F (2021) Increasing global economic costs of biological invasions. *Nature* 592: 571–576. <https://doi.org/10.1038/s41586-021-03405-6>
- Dick JTA, Laverty C, Lennon JJ, Barrios-O'Neill D, Mensink PJ, Britton JR, Médoc V, Boets P, Alexander ME, Taylor NG, Dunn AM, Hatcher MJ, Rosewarne PJ, Crookes S, MacIsaac HJ, Xu M, Ricciardi A, Wasserman RJ, Ellender BR, Weyl OLF, Lucy FE, Banks PB, Dodd

- JA, MacNeil C, Penk MR, Aldridge DC, Caffrey JM (2017) Invader Relative Impact Potential: a new metric to understand and predict the ecological impacts of existing, emerging and future invasive alien species. *Journal of Applied Ecology* 54: 1259–1267. <https://doi.org/10.1111/1365-2664.12849>
- Dickie IA, Bennett BM, Burrows LE, Nuñez MA, Peltzer DA, Porté A, Richardson DM, Rejmánek M, Rundel PW, Van Wilgen BW (2014) Conflicting values: ecosystem services and invasive tree management. *Biological Invasions* 16: 705–719. <https://doi.org/10.1007/s10530-013-0609-6>
- Dinerstein E, Olson D, Joshi A, Vynne C, Burgess ND, Wikramanayake E, Hahn N, Palominteri S, Hedao P, Noss R (2017) An ecoregion-based approach to protecting half the terrestrial realm. *BioScience* 67: 534–545. <https://doi.org/10.1093/biosci/bix014>
- Edelist D, Sonin O, Golani D, Rilov G, Spanier E (2011) Spatiotemporal patterns of catch and discards of the Israeli Mediterranean trawl fishery in the early 1990s: ecological and conservation perspectives. *Scientia Marina* 75: 641–652. <https://doi.org/10.3989/scimar.2011.75n4641>
- 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>
- Essl F, Biró K, Brandes D, Broennimann O, Bullock JM, Chapman DS, Chauvel B, Dullinger S, Fumanal B, Guisan A (2015) Biological flora of the British Isles: *Ambrosia artemisiifolia*. *Journal of Ecology* 103: 1069–1098. <https://doi.org/10.1111/1365-2745.12424>
- EU (2012) 2012/535/EU: Commission Implementing Decision of 26 September 2012 on emergency measures to prevent the spread within the Union of *Bursaphelenchus xylophilus* (Steiner et Buhrer) Nickle et al. (the pine wood nematode) (notified under document C(2012) 6543). <https://op.europa.eu/en/publication-detail/-/publication/2199d69e-6a9f-4cab-b70c-efebc662daf5>
- Faulkner KT, Robertson MP, Wilson JRU (2020) Stronger regional biosecurity is essential to prevent hundreds of harmful biological invasions. *Global Change Biology* 26: 2449–2462. <https://doi.org/10.1111/gcb.15006>
- de la Fuente B, Saura S, Beck PSA (2018) Predicting the spread of an invasive tree pest: the pine wood nematode in Southern Europe. *Journal of Applied Ecology* 55: 2374–2385. <https://doi.org/10.1111/1365-2664.13177>
- Galil BS, Marchini A, Occhipinti-Ambrogi A, Minchin D, Narščius A, Ojaveer H, Olenin S (2014) International arrivals: widespread bioinvasions in European Seas. *Ethology Ecology & Evolution* 26: 152–171. <https://doi.org/10.1080/03949370.2014.897651>
- Gasperi G, Bellini R, Malacrida AR, Crisanti A, Dottori M, Aksoy S (2012) A new threat looming over the Mediterranean basin: emergence of viral diseases transmitted by *Aedes albopictus* mosquitoes. *PLoS Neglected Tropical Diseases* 6: e1836. <https://doi.org/10.1371/journal.pntd.0001836>
- Gherardi F, Acquistapace P (2007) Invasive crayfish in Europe: the impact of *Procambarus clarkii* on the littoral community of a Mediterranean lake. *Freshwater Biology* 52: 1249–1259. <https://doi.org/10.1111/j.1365-2427.2007.01760.x>
- 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, North-eastern Mediterranean. *Marine Ecology* 35: 96–105. <https://doi.org/10.1111/maec.12059>

- Groves RH, di Castri F (1991) Biogeography of Mediterranean invasions. Cambridge University Press, New York. <https://doi.org/10.1017/CBO9780511525544>
- Hoffmann BD, Broadhurst LM (2016) The economic cost of managing invasive species in Australia. *NeoBiota* 31: 1–1. <https://doi.org/10.3897/neobiota.31.6960>
- Iacona GD, Sutherland WJ, Mappin B, Adams VM, Armsworth PR, Coleshaw T, Cook C, Craigie I, Dicks L V, Fitzsimons JA (2018) Standardized reporting of the costs of management interventions for biodiversity conservation. *Conservation Biology* 32: 979–988. <https://doi.org/10.1111/cobi.13195>
- Issanchou A (2012) Analyse économique d'une invasion biologique aquatique, le cas de la jussie (*Ludwigia* sp.). M.Sc. Dissertation. Institut National de la Recherche Agronomique – UMR LERNA.
- ISSG (2015) The Global Invasive Species Database. Version 2015.1. <http://www.iucngisd.org/gisd/> [September 17, 2020]
- Kalogirou S (2013) Ecological characteristics of the invasive pufferfish *Lagocephalus sceleratus* (Gmelin, 1789) in the eastern Mediterranean Sea-a case study from Rhodes. *Mediterranean Marine Science* 14: 251–260. <https://doi.org/10.12681/mms.364>
- 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, Zenetos A, Belchior C, Cardoso AC (2013) Invading European Seas: assessing pathways of introduction of marine aliens. *Ocean & Coastal Management* 76: 64–74. <https://doi.org/10.1016/j.ocecoaman.2013.02.024>
- Katsanevakis S, Coll M, Piroddi C, Steenbeek J, Ben Rais Lasram F, Zenetos A, Cardoso AC (2014) Invading the Mediterranean Sea: biodiversity patterns shaped by human activities. *Frontiers in Marine Science* 1: 1–32. <https://doi.org/10.3389/fmars.2014.00032>
- Kletou D, Hall-Spencer JM, Kleitou P (2016) A lionfish (*Pterois miles*) invasion has begun in the Mediterranean Sea. *Marine Biodiversity Records* 9: 1–7. <https://doi.org/10.1186/s41200-016-0065-y>
- Kourantidou M, Kaiser BA (2019) Research agendas for profitable invasive species. *Journal of Environmental Economics and Policy* 8: 209–230. <https://doi.org/10.1080/21606544.2018.1548980>
- Lasram FBR, Tomasini JA, Guilhaumon F, Romdhane MS, Do Chi T, Mouillot D (2008) Ecological correlates of dispersal success of Lessepsian fishes. *Marine Ecology Progress Series* 363: 273–286. <https://doi.org/10.3354/meps07474>
- Lasram FBR, Guilhaumon F, Albouy C, Somot S, Thuiller W, Mouillot D (2010) The Mediterranean Sea as a ‘cul-de-sac’ for endemic fishes facing climate change. *Global Change Biology* 16: 3233–3245. <https://doi.org/10.1111/j.1365-2486.2010.02224.x>
- Leroy B (2020) biogeonetworks: Biogeographical Network Manipulation And Analysis, R package version 0.1.2. <https://github.com/Farewe/biogeonetworks>
- Leroy B, Kramer A, Vaissière A-C, Courchamp F, Diagne C (2020) Analysing global economic costs of invasive alien species with the invacost R package. bioRxiv. <https://doi.org/10.1101/2020.12.10.419432>
- Leroy B, Dias MS, Giraud E, Hugueny B, Jézéquel C, Leprieur F, Oberdorff T, Tedesco PA (2019) Global biogeographical regions of freshwater fish species. *Journal of Biogeography* 46: 2407–2419. <https://doi.org/10.1111/jbi.13674>

- Leung B, Lodge DM, Finnoff D, Shogren JF, Lewis MA, Lamberti G (2002) An ounce of prevention or a pound of cure: bioeconomic risk analysis of invasive species. Proceedings of the Royal Society of London B: Biological Sciences 269: 2407–2413. <https://doi.org/10.1098/rspb.2002.2179>
- Mendieta JC, Cardenas TJ (2010) Lineamientos para la evaluacion del impacto economico de las plantas invasoras en Colombia. Informe 4: recopilación de todos los resultados.
- Muñoz-Adalia EJ, Colinas C (2020) The invasive moth *Paysandisia archon* in Europe: biology and control options. Journal of Applied Entomology 144: 341–350. <https://doi.org/10.1111/jen.12746>
- Musil CF, Davis GW, Milton SJ (2005) The threat of alien invasive grasses to lowland Cape floral diversity: an empirical appraisal of the effectiveness of practical control strategies: research in action. South African Journal of Science 101: 337–344.
- Novoa A, Richardson DM, Pyšek P, Meyerson LA, Bacher S, Canavan S, Catford JA, Čuda J, Essl F, Foxcroft LC (2020) Invasion syndromes: a systematic approach for predicting biological invasions and facilitating effective management. Biological Invasions: 1–20. <https://doi.org/10.1007/s10530-020-02220-w>
- Nuñez MA, Pauchard A (2010) Biological invasions in developing and developed countries: does one model fit all? Biological Invasions 12: 707–714. <https://doi.org/10.1007/s10530-009-9517-1>
- Ordóñez V, Pascual M, Fernández-Tejedor M, Pineda MC, Tagliapietra D, Turon X (2015) Ongoing expansion of the worldwide invader *Didemnum vexillum* (Ascidiacea) in the Mediterranean Sea: high plasticity of its biological cycle promotes establishment in warm waters. Biological Invasions 17: 2075–2085. <https://doi.org/10.1007/s10530-015-0861-z>
- Paini DR, Sheppard AW, Cook DC, De Barro PJ, Worner SP, Thomas MB (2016) Global threat to agriculture from invasive species. Proceedings of the National Academy of Sciences 113: 7575–7579. <https://doi.org/10.1073/pnas.1602205113>
- Peyton J, Martinou AF, Pescott OL, Demetriou M, Adriaens T, Arianoutsou M, Bazos I, Bean CW, Booy O, Botham M (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>
- Pimentel D, Zuniga R, Morrison D (2005) Update on the environmental and economic costs associated with alien-invasive species in the United States. Ecological Economics 52: 273–288. <https://doi.org/10.1016/j.ecolecon.2004.10.002>
- Pimentel D, Lach L, Zuniga R, Morrison D (2000) Environmental and economic costs of nonindigenous species in the United States. Bioscience 50: 53–65. [https://doi.org/10.1641/0006-3568\(2000\)050\[0053:EAECON\]2.3.CO;2](https://doi.org/10.1641/0006-3568(2000)050[0053:EAECON]2.3.CO;2)
- Pyšek P, Hulme PE, Simberloff D, Bacher S, Blackburn TM, Carlton JT, Dawson W, Essl F, Foxcroft LC, Genovesi P (2020) Scientists' warning on invasive alien species. Biological Reviews 95: 1511–1534. <https://doi.org/10.1111/brv.12627>
- Pyšek P, Richardson DM (2010) Invasive species, environmental change and management, and health. Annual Review of Environment and Resources 35: 25–55. <https://doi.org/10.1146/annurev-environ-033009-095548>
- Raitos DE, Beaugrand G, Georgopoulos D, Zenetos A, Pancucci-Papadopoulou AM, Theocaris A, Papathanassiou E (2010) Global climate change amplifies the entry of tropical

- species into the Eastern Mediterranean Sea. *Limnology and Oceanography* 55: 1478–1484. <https://doi.org/10.4319/lo.2010.55.4.1478>
- Renault D, Manfrini E, Leroy B, Diagne C, Ballesteros-Mejia L, Angulo E, Courchamp F (2021) Biological invasions in France: Alarming costs and even more alarming knowledge gaps. In: Zenni RD, McDermott S, García-Berthou E, Essl F (Eds) The economic costs of biological invasions around the world. *NeoBiota* 67: 191–224. <https://doi.org/10.3897/neobiota.67.59134>
- Rilov G, Galil B (2009) Marine bioinvasions in the Mediterranean Sea—history, distribution and ecology. In: Rilov G, Crooks JA (Eds) *Biological invasions in marine ecosystems: ecological, management and geographic perspectives*. Springer-Verlag, Berlin, 549–575. [https://doi.org/10.1007/978-3-540-79236-9\\_31](https://doi.org/10.1007/978-3-540-79236-9_31)
- Rosvall M, Bergstrom CT (2008) Maps of random walks on complex networks reveal community structure. *Proceedings of the National Academy of Sciences* 105: 1118–1123. <https://doi.org/10.1073/pnas.0706851105>
- Rosvall M, Axelsson D, Bergstrom CT (2009) The map equation. *The European Physical Journal Special Topics* 178: 13–23. <https://doi.org/10.1140/epjst/e2010-01179-1>
- Schertler A, Rabitsch W, Moser D, Wessely J, Essl F (2020) The potential current distribution of the coypu (*Myocastor coypus*) in Europe and climate change induced shifts in the near future. *NeoBiota* 58: 129–160. <https://doi.org/10.3897/neobiota.58.33118>
- Secretariat of the Convention on Biological Diversity (2020) *Global Biodiversity Outlook 5 – Summary for Policy Makers*. Montréal.
- Seebens H, Blackburn TM, Dyer EE, Genovesi P, Hulme PE, Jeschke JM, Pagad S, Pyšek P, van Kleunen M, Winter M (2018) Global rise in emerging alien species results from increased accessibility of new source pools. *Proceedings of the National Academy of Sciences* 115: E2264–E2273. <https://doi.org/10.1073/pnas.1719429115>
- 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: 1–9. <https://doi.org/10.1038/ncomms14435>
- Soliman T, Mourits MCM, Van Der Werf W, Hengeveld GM, Robinet C, Lansink AGJMO (2012) Framework for modelling economic impacts of invasive species, applied to pine wood nematode in Europe. *PLoS ONE* 7: e45505. <https://doi.org/10.1371/journal.pone.0045505>
- Tempesti J, Manganò MC, Langeneck J, Lardicci C, Maltagliati F, Castelli A (2020) Non-indigenous species in Mediterranean ports: a knowledge baseline. *Marine Environmental Research* 161: E105056. <https://doi.org/10.1016/j.marenvres.2020.105056>
- Traveset A, Brundu G, Carta L, Mprezetou I, Lambdon P, Manca M, Médail F, Moragues E, Rodríguez-Pérez J, Siamantziouras A-SD (2008) Consistent performance of invasive plant

- species within and among islands of the Mediterranean basin. *Biological Invasions* 10: 847–858. <https://doi.org/10.1007/s10530-008-9245-y>
- 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, Pujadas J (2001) Land-use and socio-economic correlates of plant invasions in European and North African countries. *Biological Conservation* 100: 397–401. [https://doi.org/10.1016/S0006-3207\(01\)00047-7](https://doi.org/10.1016/S0006-3207(01)00047-7)
- World Bank (2020) World Development Indicators. [www.data.worldbank.org](http://www.data.worldbank.org) [July 7, 2020.]
- Zenetas A, Galanidi M (2020) Mediterranean non indigenous species at the start of the 2020s: recent changes. *Marine Biodiversity Records* 13: 1–17. <https://doi.org/10.1186/s41200-020-00191-4>
- Zenetas A, Çinar ME, Pancucci-Papadopoulou MA, Harmelin JG, Furnari G, Andaloro F, Bellou N, Streftaris N, Zibrowius H (2005) Annotated list of marine alien species in the Mediterranean with records of the worst invasive species. *Mediterranean Marine Science* 6: 63–118. <https://doi.org/10.12681/mms.186>
- Zhang Z, Capinha C, Usio N, Weterings R, Liu X, Li Y, Landeria JM, Zhou Q, Yokota M (2020) Impacts of climate change on the global potential distribution of two notorious invasive crayfishes. *Freshwater Biology* 65: 353–365. <https://doi.org/10.1111/fwb.13429>

## Supplementary material I

### Mediterranean database

Authors: Melina Kourantidou, Ross N. Cuthbert, Phillip J. Haubrock, Ana Novoa, Nigel G. Taylor, Boris Leroy, César Capinha, David Renault, Elena Angulo, Christophe Diagne, Franck Courchamp

Data type: xlsx file database with cost entries for the Mediterranean basin

Explanation note: The dataset used for the analysis of costs of invasive species for the Mediterranean basin.

Copyright notice: This dataset is made available under the Open Database License (<http://opendatacommons.org/licenses/odbl/1.0/>). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

Link: <https://doi.org/10.3897/neobiota.67.58926.suppl1>

## Supplementary material 2

### Appendix

Authors: Melina Kourantidou, Ross N. Cuthbert, Phillip J. Haubrock, Ana Novoa, Nigel G. Taylor, Boris Leroy, César Capinha, David Renault, Elena Angulo, Christophe Diagne, Franck Courchamp

Data type: tables and figures

Explanation note: The Appendix contains additional tables and figures referred to in the text in the form of Fig. S4; Figs S1, S2; Table S2; Appendix, as required by the journal.

Copyright notice: This dataset is made available under the Open Database License (<http://opendatacommons.org/licenses/odbl/1.0/>). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

Link: <https://doi.org/10.3897/neobiota.67.58926.suppl2>