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Biological invasions in France: Alarming costs and even more alarming knowledge gaps

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Abstract

The ever-increasing number of introduced species profoundly threatens global biodiversity. While the ecological and evolutionary consequences of invasive alien species are receiving increasing attention, their economic impacts have largely remained understudied, especially in France. Here, we aimed at providing a general overview of the monetary losses (damages caused by) and expenditures (management of) associated with invasive alien species in France. This country has a long history of alien species presence, partly due to its long-standing global trade activities, highly developed tourism, and presence of overseas territories in different regions of the globe, resulting in a conservative minimum of 2,750 introduced and invasive alien species. By synthesizing for the first time the monetary losses and expenditures incurred by invasive alien species in Metropolitan France and French overseas territories, we obtained 1,583 cost records for 98 invasive alien species. We found that they caused a conservative total amount ranging between US\$ 1,280 million and 11,535 million in costs over the period 1993–2018. We extrapolated costs for species invading France, for which costs were reported in other countries but not in France, which yielded an additional cost ranging from US\$ 151 to 3,030 millions. Damage costs were nearly eight times higher than management expenditure. Insects, and in particular the Asian tiger mosquito *Aedes albopictus* and the yellow fever mosquito *Ae. aegypti*, totalled very high economic costs, followed by non-graminoid terrestrial flowering and aquatic plants (*Ambrosia artemisiifolia*, *Ludwigia* sp. and *Lagarosiphon major*).

Over 90% of alien species currently recorded in France had no costs reported in the literature, resulting in high biases in taxonomic, regional and activity sector coverages. To conclude, we report alarming costs and even more alarming knowledge gaps. Our results should raise awareness of the importance of biosecurity and biosurveillance in France, and beyond, as well as the crucial need for better reporting and documentation of cost data.

Abstract in Chinese

法国的生物入侵：造成令人震惊的经济损失和更令人震惊的知识差距

David Renault, Eléna Manfrini, Boris Leroy, Christophe Diagne, Liliana Ballesteros-Mejia, Elena Angulo, Franck Courchamp

快速增加的外来物种已经对全球生物多样性造成了严重威胁。虽然对于外来入侵物种的生态和进化影响受到关注持续增加，但对于外来物种经济影响却很少研究关注，特别是在法国。本项研究评估了法国外来入侵物种造成的直接经济损失和相关管理控制的经济花费。由于长期积极参与全球贸易活动、高度发达的旅游业以及在全球不同地区拥有多个海外领地，所以法国有着悠久的外来物种的引入历史，保守估计至少有2750种外来物种被引入了法国。本研究首次整理法国大都市和法国海外领地的外来入侵物种造成直接经济损失和相关管理支出的资料，我们查询到有关98种外来入侵物种1583条造成经济损失的相关研究。保守估算法国的外来物种在1993–2018年期间造成115.35亿美元的经济损失。对于那些已经入侵到法国但尚未有经济损失数据报道的物种，我们根据它们在其他国家已造成的经济损失估算它们造成的额外经济损失为1.51至30.3亿美元。在法国外来入侵物种造成的直接经济损失大约是对外来入侵物种管理控制费用的8倍。在所有外来入侵物种类群中，昆虫造成的非常高的经济损失，尤其是白纹伊蚊（*Aedes albopictus*）和埃及伊蚊（*A. aegypti*）。其次是非禾本科的陆生花卉和水生植物，如豚草（*Ambrosia artemisiifolia*）、蓼科植物（*Ludwigia spp*）和软管草（*Lagarosiphon major*）。目前超过90%的法国外来入侵物种缺乏研究其造成的经济损失，由于外来入侵物种分类类群，分布地区和使用部门不同，所以对其造成经济损失的研究存在很大的不平衡性。因此，我们这项研究报告外来入侵物种在法国造成巨大的经济损失，并存在更加巨大的知识差距。我们研究结果表明应提高对法国及其海外领地生物安全和生物监测重要性，急需更好的研究报告和记录外来入侵物种造成经济损失。

Abstract in French

Invasions biologiques en France : des coûts alarmants et des lacunes de connaissances encore plus alarmantes

David Renault, Eléna Manfrini, Boris Leroy, Christophe Diagne, Liliana Ballesteros-Mejia, Elena Angulo, Franck Courchamp

La croissance ininterrompue de transport et d'introduction d'espèces menace dangereusement la biodiversité mondiale. Bien que les conséquences éco-évolutives liées à la présence d'espèces exotiques envahissantes fassent l'objet d'un nombre d'études de plus en plus conséquent, les impacts économiques générés par les invasions biologiques restent insuffisamment étudiés, notamment en France. Dans cette étude, nous présentons une vue générale des pertes monétaires (dommages, dégâts) et des dépenses (gestion) induites par les espèces exotiques envahissantes en France. Ce pays dispose d'une longue histoire de présence d'espèces exotiques en raison d'importantes activités de commerce international de longue date, d'un tourisme fortement développé, et de nombreux territoires d'outre-mer dans différentes régions du monde; ceci contribue à expliquer l'estimation conservatrice de la présence de 2750 espèces exotiques (introduites ou envahissantes) en France. En synthétisant pour la première fois les pertes monétaires et les dépenses induites par la présence des espèces exotiques envahissantes en France métropolitaine et dans ses territoires d'outre-mer, nous avons pu identifier 1583 données de coûts concernant 98 espèces exotiques envahissantes. Nous avons estimé que les espèces exotiques envahissantes ont généré un montant conservateur de 1280 à 11535 millions \$US sur la période 1993–2018. Nous avons extrapolé les coûts pour les espèces envahissant la France, pour lesquelles

des données de coûts existent dans le monde mais pas en France, ce qui a abouti à un coût additionnel compris entre 151 et 3 030 millions \$US. Les coûts des dégâts étaient 8 fois plus élevés que les coûts liés aux dépenses de gestion. Les insectes, en particulier le moustique tigre, *Aedes albopictus*, et le moustique de la fièvre jaune, *Ae. Aegypti*, génèrent les coûts économiques les plus importants, suivis par les plantes à fleurs terrestres et les plantes aquatiques (*Ambrosia artemisiifolia*, *Ludwigia* sp. et *Lagarosiphon major*). Plus de 90% des espèces exotiques actuellement enregistrées en France ne font l'objet d'aucune mention de coût dans la littérature, ce qui traduit un fort biais taxonomique, et un fort biais de couvertures régionale et sectorielle des impacts de ces espèces. En conclusion, notre étude pointe des coûts alarmants et des lacunes de connaissances entre plus grandes au regard des impacts financiers liés aux espèces exotiques envahissantes. Nos résultats doivent alerter sur l'importance de la biosécurité et de la biosurveillance en France et, au-delà, sur le besoin crucial d'une meilleure documentation et d'une meilleure compilation des données de coût.

Abstract in Spanish

Invasiones biológicas en Francia: Alarmantes costos y lagunas de conocimiento aún más alarmantes.

David Renault, Eléna Manfrini, Boris Leroy, Christophe Diagne, Liliana Ballesteros-Mejia, Elena Angulo, Franck Courchamp

El número cada vez mayor de especies introducidas amenaza profundamente la biodiversidad mundial. Si bien las consecuencias ecológicas y evolutivas de las especies exóticas invasoras (EEI) están recibiendo cada vez más atención, sus impactos económicos han permanecido poco estudiados, especialmente en Francia. Nuestro objetivo en este artículo, fue proporcionar una descripción general de las pérdidas monetarias (daños causados por) y los gastos (gestión de) asociados con las especies exóticas invasoras en Francia. Este país tiene una larga historia de presencia de especies exóticas, debido a su tradición de actividades comerciales en todo el mundo, su turismo altamente desarrollado y presencia de territorios de ultramar en diferentes regiones del mundo, lo que nos lleva a tener un mínimo conservador de 2.750 especies exóticas introducidas e invasoras.

Esta primera síntesis de las pérdidas monetarias y los gastos incurridos por las EEI en la Francia metropolitana y sus territorios de ultramar, arrojó un total de 1.583 registros de costos para 98 especies exóticas invasoras. También descubrimos que durante el período de 1993 a 2018, las EEI causaron un monto total conservador de entre US \$ 1.280 millones y 11.535 millones en costos. Extrapolamos los costos de las especies que invaden Francia, cuyos costos se reportaron en otros países pero no en Francia, lo que generó un costo adicional que oscila entre los 151 y los 3.030 millones de dólares. Los costos de daños fueron alrededor de 8 veces más altos que los gastos de gestión. Los insectos, y en particular el mosquito tigre asiático *Aedes albopictus* y el mosquito de la fiebre amarilla *Ae. aegypti*, sumaron costos económicos muy altos, seguidos de plantas acuáticas y de flores terrestres no gramíneas (p. ej. *Ambrosia artemisiifolia*, *Ludwigia* sp. y *Lagarosiphon major*). Más del 90% de las especies exóticas registradas actualmente en Francia no tienen costos reportados en la literatura, lo que resulta en un alto sesgo en cuanto a la cobertura taxonómica, regional y en sectores socioeconómicos. En conclusión, reportamos costos alarmantes y lagunas de conocimiento aún más alarmantes. Nuestros resultados deberían crear conciencia sobre la importancia de la bioseguridad y el biocontrol en Francia y más allá, así como sobre la necesidad crucial de mejorar la calidad de la información y la documentación de los datos de costos sobre especies invasoras.

Abstract in Russian

Биологические инвазии во Франции: тревожные убытки и еще более тревожные пробелы в знаниях

David Renault, Eléna Manfrini, Boris Leroy, Christophe Diagne, Liliana Ballesteros-Mejia, Elena Angulo, Franck Courchamp

Постоянный рост числа интродуцированных видов серьезно угрожает глобальному биоразнообразию. Хотя экологическим и эволюционным последствиям инвазий чужеродных

винов уделяется огромное внимание, экономические потери от их деятельности в значительной степени остаются недостаточно изученными, особенно во Франции. Мы представляем обзор экономических потерь (в результате причиненных повреждений) и расходов на контроль инвазивных чужеродных видов во Франции. Эта страна имеет долгую историю присутствия на ее территории чужеродных видов, отчасти из-за давней глобальной торговой деятельности, высоко развитого туризма и наличия заморских французских территорий в разных регионах земного шара. Сегодня во Франции насчитывается 2750 интродуцированных и инвазивных чужеродных видов. Мы впервые обобщили данные по экономическим потерям в результате инвазий чужеродных видов во Франции и на ее заморских территориях, проанализировав 1583 позиции убытков в результате инвазий 98 чужеродного вида. В 1993–2018 гг. эти виды причинили ущерб на общую сумму 11,535 млн долларов США. Мы экстраполировали затраты на виды, вторгшиеся во Францию (расходы по которым были известны по другим странам, но не для Франции), что увеличило денежные потери в диапазоне от 151 до 3030 миллионов долларов США. Экономические потери в результате причиненных повреждений (прямые убытки) были в 8 раз выше, чем затраты на контроль инвазивных. Насекомые, в частности, азиатский тигровый комар *Aedes albopictus* и желтолихорадочный комар *Aedes aegypti*, являлись причиной самых высоких экономических потерь; за ними следовали травянистые (кроме злаков, бобовых и осоковых) и водные растения (*Ambrosia artemisiifolia*, *Ludwigia* sp. и *Lagarosiphon major*). Для более чем 90 % зарегистрированных во Франции чужеродных видов в литературе отсутствуют сведения об экономических потерях, что не может не сказываться на точности оценок экономических ущербов при анализе таксономических групп, регионов и секторов экономики. Таким образом, мы сообщаем о тревожных убытках и еще более тревожных пробелах в знаниях. Наши результаты должны повысить осведомленность о важности биологической безопасности и надзора за инвазивными во Франции и за ее пределами, а также о необходимости улучшения отчетности и документирования экономических потерь.

Abstract in Arabic

ملخص

الغزو البيولوجي في فرنسا: تكاليف مقلقة وفجوات معرفية مفرقة.

يشكل النمو المستمر في النقل وإدخال الأنواع تهديدًا خطيرًا للتنوع البيولوجي العالمي. وعلى الرغم من أن نتائج التطور الإيكولوجي لوجود "الأنواع الغازية" هي موضوع عدد متزايد من الدراسات، فإن الآثار الاقتصادية الناجمة عن الغزو البيولوجي لا تزال غير مدروسة بما فيه الكفاية، لا سيما في فرنسا. نقدم في هذه الدراسة لمحة عامة عن التكلفة المالية للأضرار والخسائر ونفقات التسيير التي تسببها الأنواع الغازية في فرنسا. لهذه الدولة تاريخ طويل فيما يخص تواجد الأنواع "الدخيلة" بسبب الأنشطة التجارية الدولية المهمة والطويلة الأمد، والسياحة المتطورة وامتدادها في العديد من الأقاليم "ما وراء البحار" المتواجدة في مناطق مختلفة من العالم؛ يساعد كل هذا في تفسير "التقديرات المتحفظة" لوجود 2750 نوعًا غازيًا في فرنسا. من خلال تجميعنا لأول مرة لمختلف الخسائر المالية والنفقات الناتجة عن وجود الأنواع الغازية في فرنسا وأقاليمها "ما وراء البحار"، استطعنا تحديد 1583 بيان تكلفة يتعلق بـ 98 صنفًا مختلفًا. ولقد قدرنا التكلفة الإجمالية للأنواع الغازية في 11535 مليون دولار أمريكي خلال الفترة 1993-2018. ومن خلال استقراءنا لتكاليف الأنواع التي تغزو فرنسا، والتي توجد بيانات عنها في العالم ولكن ليس في فرنسا، فإن هناك تكلفة إضافية تتراوح بين 151 و 3030 مليون دولار أمريكي. إضافة إلى ذلك، فإن التكاليف الناتجة عن الأضرار كانت أعلى 8 مرات من تكاليف مصاريف التسيير. وقد جاءت الحشرات، وخاصة بعوضة النمر وبعوضة الحمى الصفراء في الرتبة الأولى من حيث التكلفة الاقتصادية، تليها النباتات الزهرية الأرضية والنباتات المائية. وكان من اللافت أن أكثر من 90% من الأنواع الدخيلة المسجلة حاليًا في فرنسا لم تتم الإشارة إلى تكلفتها الاقتصادية في المراجع المعتمدة، مما يعكس وجود تحيز قوي لا من الناحية التصنيفية ولا من ناحية التغطية الإقليمية والقطاعية لتأثيرات هذه الأنواع. في الختام، نبلغ في هذه الدراسة عن تكاليف مقلقة وفجوات معرفية مهولة فيما يهم الآثار المالية المرتبطة بالأنواع الغازية. كما نأمل أن تزيد هذه النتائج في نسبة الوعي بأهمية الأمن البيولوجي والرصد البيولوجي في فرنسا وخارجها، وتساهم في تحسين عملية توثيق وتجميع مختلف بيانات التكاليف.

Keywords

damage costs, economic threat, exotic, InvaCost, invasive alien species, management costs, non-indigenous, non-native

Introduction

Biological invasions, alongside climate change, pollution, habitats destruction and over-exploitation, are direct drivers of change and loss in biodiversity (Bellard et al. 2012; Elbakidze et al. 2018; Hughes et al. 2020; Liu et al. 2020; Verma et al. 2020). With the continuous escalation in the number of transported species (Seebens et al. 2017), the threat to biodiversity incurred by invasive alien species, i.e. those populations introduced by humans and expanding in regions outside their past or current distribution areas, has become particularly concerning. Worse, recent predictions suggest that increasing shipping traffic may further enhance invasion phenomena, much more than climate change alone; for instance, models estimate a 3- to 20-fold increase of the marine invasion risks on the globe towards the 2050 horizon (Sardain et al. 2020). The resulting biogeographic changes in biodiversity distribution have several far-reaching ecological and evolutionary consequences (Alp et al. 2016; Carbonell et al. 2017; Colautti et al. 2017). In particular, the impacts of invasive alien species on biodiversity may profoundly alter the functioning of communities and ecosystems (Braun et al. 2019; Papier et al. 2019), in turn altering the delivery of ecosystem services (Castro-Diez et al. 2016), biodiversity and human health (Elbakidze et al. 2018; Shackleton et al. 2019; Kumar Rai and Singh 2020; Pyšek et al. 2020). When expanding their range, several invasive alien species can also act as ecosystem engineers, gradually transforming invaded communities and existing ecological structures (Guy-Haim et al. 2017; Lebouvier et al. 2020).

The accumulating evidence of the environmental impacts generated by biological invasions worldwide has considerably increased the attention of researchers towards invasive alien species over the years. In particular, databases documenting invasive alien species distributions are flourishing (e.g., Seebens et al. 2020; CABI; Global Register of Introduced and Invasive Species (GRIIS); The Invasive Species Specialist Group), in addition to investigations assessing existing vectors/pathways (Hulme 2009; Saul et al. 2017; Turbelin et al. 2017; Mohanty and Measey 2019) and the future distribution of invasive species (e.g., Bellard et al. 2013; Bertelsmeier et al. 2015; Fournier et al. 2019; Bazzichetto et al. 2020; Louppe et al. 2020). Continuous research effort improves our comprehension of the large array of effects incurred by invasive alien species, and contributes to identifying those species having the greatest impacts on ecosystems, habitats or biodiversity. These investigations subsequently allow for the establishment of action prioritisations for the management of invasive alien species. Yet, and surprisingly, while our understanding of the effects of biological invasions on biodiversity and the environment is growing (Simberloff et al. 2013; Castro-Diez et al. 2016; Braun et al. 2019; Verma et al. 2020), their impacts on economic activities, and the overall costs they are generating, have in parallel remained understudied (IUCN 2018). Information on the socio-economic impacts of invasive species is essential to identify effective management approaches and optimise transboundary legislation (Dana et al. 2013; Caffrey et al. 2014; Chaffin et al. 2016; Diagne et al. 2020a). Filling this gap in the invasion literature could also be beneficial to attract the attention of the non-academic actors (stakehold-

ers, industry, and the general public), as recommended in the assessments of the Intergovernmental Platform for Biodiversity & Ecosystem Services (IPBES, Elbakidze et al. 2018). Since the first estimations of economic costs of invasive alien species at large spatial scales by Pimentel et al. (2005), other studies have attempted to increase this knowledge (e.g., Scalera et al. 2010; Paini et al. 2017). However, available data remain scattered, and approaches remain methodologically questionable (Cuthbert et al. 2020).

To date, previous studies have suggested very high economic costs, i.e. damage and losses (e.g., damage repair, medical care, value of crop losses) incurred by an invasion, or means dedicated to understand or predict (research), prevent (education, biosecurity), early detect (monitoring, surveillance) and/or manage (control, eradication) invasive alien species. For instance, the global cost averages at about US\$ 76 billion per year globally for invasive insects (Bradshaw et al. 2016). In Europe, economic costs caused by invasive alien species were extrapolated at about 2017 US\$ 14 billion per year (Kettunen et al. 2009). In aquatic ecosystems, cumulated costs had reached at least US\$ 23 billion in the year 2020 (Cuthbert et al. 2021). Yet, detailed and thorough assessments of such costs at the national level are still lacking for most countries, while the country scale is often the first level of action regarding the management of biological invasions. In particular, France is highly impacted by the presence of invasive alien species, with a long history of global trade and tourism that has greatly favoured the introduction of non-native species. Currently, a conservative minimum of 2,750 introduced and invasive alien species with accepted names (as recorded on September 24th, 2020 in GRIIS; Pagad et al. 2018; Thevenot et al. 2020) have been recorded from metropolitan France. This large list of non-native records likely results from several concomitant factors. First, the central geographic position of France is unique, comparatively with the other countries of the European Union: France has frontiers with five other countries, coastlines on three different seas or oceans, and overseas territories distributed all over the world. This situation enhances the possibility for substantial national and transnational traffic from regions and countries hosting different native species. Second, France has the 7th highest gross domestic product worldwide (The World Bank, <https://www.worldbank.org/>), is the 7th largest importer of goods (World Trade Organization, <https://www.wto.org/>), is ranked 10th for transportation of persons and even ranked 1st in 2018 in terms of international tourist arrival (World Tourism Organization, UNWTO, <https://www.unwto.org/>). France welcomes over 80 million tourists annually (more than its own population) from all continents. Both trade of goods and transportation of people are known to increase biological invasions and their costs (Hulme 2009; Gippet et al. 2019; Essl et al. 2020; Haubrock et al. 2021a). Third, as is the case in general in Europe, the legislation concerning biological invasions in France is inadequate to slow down the flux of introductions of species (Caffrey et al. 2014). For example, there is no restriction of living species transportations from/to the many overseas territories.

In this context, a general overview of the monetary losses and expenditures associated with invasive species is urgently needed for France. This national cost assessment would be particularly important to fully capture the complex and diverse nature of costs incurred by biological invaders. To that aim, we synthesised for the first time the economic costs of invasive alien species in France (Metropolitan France and French

overseas) over a large time range. Then, we calculated the total economic costs caused by invasive alien species in France, and, using annualised cost values, examined how these costs have evolved over time. To obtain a comprehensive insight on the nature of the monetary impacts, we then examined the repartition of costs among different economic sectors and across French regions. Finally, we identified the distribution of economic costs across taxonomic groups of invasive alien species, and established a list of the costliest invasive alien species in France.

Material and methods

Data collection, compilation and filtering

To estimate the costs of biological invasions in France, we benefited from the Inva-Cost initiative (Diagne et al. 2020a, b) that compiles the most comprehensive and up-to-date information on the economic costs of invasive alien species worldwide. Data collection was mainly based on systematic literature searches, complemented by both opportunistic and targeted data collection through contacting experts and stakeholders. One of these searches targeted cost data in non-English languages, such as French (Angulo et al. 2021a), and is detailed below. All cost information retrieved were assembled in a common database structured following the descriptive columns of the InvaCost database (see ‘Descriptors’ file available at <https://doi.org/10.6084/m9.figshare.12668570> for a complete description of the descriptive fields considered). Thus, each cost entry refers to a unique cost value with specific descriptors (columns) about the document reporting the cost, the spatial and temporal information of the cost, the taxonomy of the species causing the cost and the typology of the cost (see Suppl. material 1 for details on the descriptors used in this manuscript). As cost entries were obtained from different years and currencies, all costs were standardised to a unique and common currency, i.e. 2017 equivalent US dollars (US\$) using official market exchange rates and taking into account the inflation since the year of cost estimation (see Diagne et al. 2020b for complete details about formulas and calculations associated with the cost standardisation, as well as Diagne et al. 2020a for a detailed description of the different steps of the construction of the InvaCost database). The latest version of this updatable database (9,823 cost entries), along with all related details and associated information, is fully accessible and openly available online (version 3.0; <https://doi.org/10.6084/m9.figshare.12668570>).

The InvaCost version 3.0 incorporates the cost data we collected when specifically searching for costs of invasive alien species in France. Indeed, we performed a double-stage strategy for collating more cost information for our study. First, monetized impacts of invasions were collected by screening the available literature containing invasion costs in the research engines Web of science and Google scholar. The topic search was restricted to the literature published in either English or French, with no timespan restriction. Second, we gathered additional – often unpublished – cost estimates from active communication efforts with conservation managers and practitioners to col-

lect information that we may have missed with more traditional searches. Specifically, we (i) directly contacted the French coordinator of IUCN (International Union for Conservation of Nature), the French Invasive Alien Species Resource Center (“*Centre des Ressources Espèces Exotiques Envahissantes*”), the National Botanical Conservatory (“*Conservatoire Botanique National*”), the Conservatories of Natural Spaces (“*Conservatoires d’Espaces Naturels*”) and their federation; and (ii) circulated a request among managers from French reserves and protected territories in order to collate specific cost data from these areas.

For the analyses, we filtered the InvaCost version 3.0 by the “Official country” descriptor to get the entries corresponding to France (Suppl. material 1). We carefully checked the data, identifying potential mistakes or double counting. Finally, we refined the data by excluding all cost entries deemed as less reliable from the database (i.e. assigned ‘low’ in the “Method reliability” column; Suppl. material 1), as well as those cost entries with partial temporal information. We restricted the temporal interval to the end of 2018, as it was the last year for which we had economic costs. After these filtering steps, our final dataset for France contained 1,118 entries for the 1993–2018 time period.

Total and annualised economic costs

Cost information could be reported for a single year in some documents, while it was occurring over several successive years in other studies. Therefore, we expanded the assembled French dataset to standardise all cost entries to yearly estimates using the *expandYearlyCosts* function of the *invacost* R package (Leroy et al. 2020). This function uses the original information about the time range, i.e. columns reporting the probable starting and ending years of each cost entry included in the database, to derive annual costs. This resulted in a total number of 1,583 annualised cost entries. We thus estimated both total and average annual costs by, respectively, totalling the annual costs of a given period of time (i.e. total costs), and then divided them by the number of years of this period of time (i.e. annual costs). We calculated the temporal trends of the invasion costs in France by using the function *summarizeCosts* in the *Invacost* package version 1.0 (Leroy et al. 2020) in R version 4.0.2 (R Core Team 2020), which allowed the calculation of mean annual cost between 1993 and 2018, providing averages in 4-year periods throughout the study period.

Description of impacted sectors and costliest species

To describe the patterns of invasive alien species costs in France, and their impacts on different sectors, we used different descriptors of the cost entries. First, we focused on the type of costs (column “Type of cost merged”) which categorises the cost reported as: ‘Damage’ referring to damages or losses incurred by the invasion (e.g., costs for damage repair, resource losses, medical care), or ‘Management’ comprising expenditure such as control, monitoring, prevention, or eradication of invasive alien species. For the analyses pertaining to these cost categories, we classified

as ‘mixed’ the cases where the specific nature of the reported costs was unclear, i.e. when it was not possible to separately attribute monetary values to either damages or management of invasive alien species. Second, we explored socio-economic sectors (column “Impacted sector”), which were classified into seven major categories reflecting the main activity, societal or market sectors impacted by costs (see Suppl. material 2 for a full description of the impacted sectors that are considered in the InvaCost database).

For the distribution of costs among taxa, we used the taxonomic information as reported in the InvaCost database. However, to understand how the different socio-economic sectors were impacted by invasive alien species, we also applied taxonomic groupings in combination with environment of the invasive species causing the cost (e.g., “terrestrial mammal”, “aquatic arthropod”, “semi-aquatic bird”). The list of environment-taxonomic groupings is available in Suppl. material 3.

To provide an InvaCost-based list of the costliest invasive species currently documented in France (i.e. those that had economic impacts exceeding US\$ 1 million in the period 1993–2018), the “Species” column was reclassified (i) to merge costs assigned to multiple species within the category diverse/unspecified, and (ii) to aggregate by genus all species with cost estimates provided at both the species and the genus level (i.e., *Impatiens glandulifera* and *Impatiens* spp.; *Ludwigia grandiflora*, *L. peploides*, *Ludwigia* spp., and *Ludwigia* sp., *Rattus norvegicus*, *Rattus* sp. and *Rattus* spp.; and *Reynoutria japonica* and *Reynoutria* sp.). Then, the geographic origin of the costliest invaders was collected from the Global Invasive Species Database (GISD 2020) and from the GRIIS (Pagad et al. 2018). Data were filtered and only ‘observed’ (incurred) costs were used for all these analyses; ‘potential’ (expected) costs (column “Implementation”, Suppl. material 1) were thus excluded.

Regional mapping of economic costs

To present a regional mapping of economic costs incurred by invasive alien species in metropolitan France and French overseas territories, data were filtered per region (column “Location”, Suppl. material 1), and only observed costs were selected (column “Implementation”, Suppl. material 1). The cost entries corresponding to multiple regions or with unspecified invasive alien species were removed from this analysis. Then, for each French region and French overseas, we mapped the total costs and the associated number of invasive alien species causing these costs.

Estimation of the cost of invasive alien species with no recorded cost in France

We also provide a coarse approximation of the potential costs of invasive alien species known to occur in France, but without cost data for France in InvaCost version 3.0, with a two-step extrapolation procedure based on available data. First, to identify the species reported from France that have no cost data, we collected (i) 2,750 introduced and invasive species with accepted scientific names from the GRIIS (Suppl. material 4, which also presents the distribution of species per taxonomic groups; Pagad et al. 2018;

Thevenot et al. 2020), (ii) 254 invasive alien species listed in GISD, and (iii) 630 alien taxa documented from French overseas territories (Soubeyran et al. 2015), of which some are also non-native in metropolitan France. We merged this information, and after having removed duplicated species and subspecies, we obtained a total of 2,621 introduced and invasive species occurring in France. From this list, we identified the species for which we had economic costs in InvaCost version 3.0: 67 species with both observed and potential costs, and 63 species with only observed costs. We used these species with economic cost data for both France and the world, to establish a linear regression model of the cost in France as a function of cost worldwide (all costs were log-10 transformed). Finally, we used this relationship to provide a coarse extrapolation of costs to the species known to occur in France, with cost data worldwide in InvaCost 3.0, but for which we had no cost information in France.

Data analysis

All analyses were conducted in R 4.0.2 (R Development Core Team 2020). We used the *invaCost* R package (Leroy et al. 2020) for all cost estimations (see above).

Results

Cost data collected

In a first step, the InvaCost database reported initially only 28 cost entries from 16 English-written articles. Then, our complementary search made using French as a language (Angulo et al. 2020) in the Web of Science and Google Scholar returned 26 papers mentioning economic costs caused by invasive alien species in France. Yet, only four articles, representing 14 cost entries, reported monetary cost values. In a third step, our efforts to personally contact experts allowed us to collect a high quantity of new cost information (1,106 cost entries from 39 documents written in French as of September 1st, 2020). In total, we obtained 1,583 annualised cost estimates, corresponding to 98 invasive alien species.

Overall costs and temporal trend

Invasive alien species incurred a total amount of US\$ 11,535 million in France over the period 1993–2018, with an average of US\$ 444 million annually (Figure 1A). The highest costs were documented in the time range 2009–2012 (ca. US\$ 4,172 million, corresponding to US\$ 1,043 million annually). A large part of the reported costs of invasive alien species for France were not empirically observed, i.e. they were obtained from extrapolations of the potential cost should these invasive alien species further invade favourable habitats/regions. Hence, the costs actually observed amounted up to US\$ 1,280 million for the 1993–2018 time period (average annual: US\$ 49.2 million) (Figure 1A).

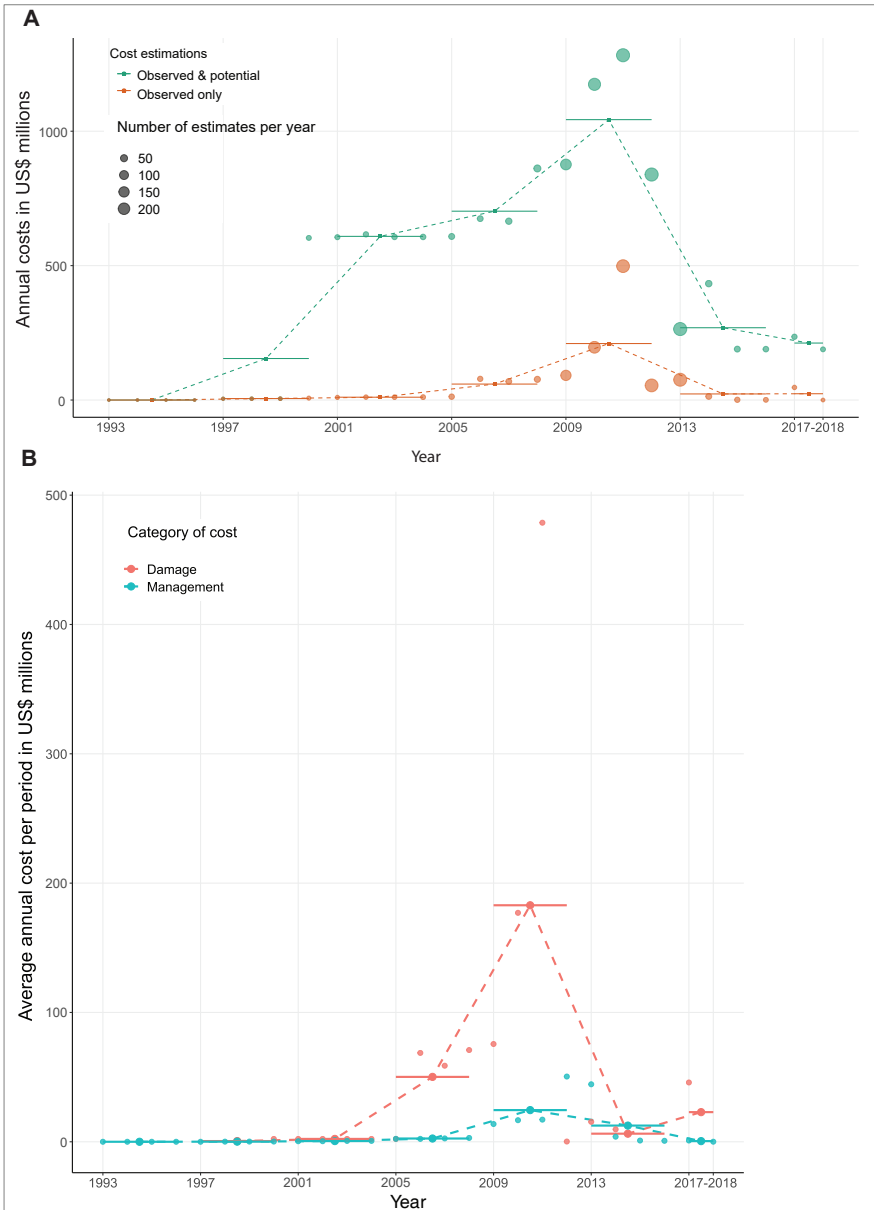


Figure 1. Presentation of the costs incurred by invasive alien species in France over the period 1993–2018 **A** total cost values (in 2017 US\$) per year of invasive alien species in metropolitan France and French overseas territories. The reported amounts are calculated from observed costs (orange), or from both observed (i.e. incurred) and potential (i.e. predicted to occur) costs (green). Each point represents the cumulative cost for a given year; the size of each point is proportional to the number of estimates for that year. Average annual costs for 4-year periods are represented by squares and horizontal solid lines; dashed lines connect the average annual costs across these 4-year periods **B** temporal changes in observed costs (2017 value) for ‘Damage-Loss’ (simplified as Damage in the figure legend) vs. ‘Management’ (control, monitoring, prevention, management, and eradication of alien invasive species) costs.

The number of cost entries per year was also the highest in this period (2009–2012), ranging from 168 to 283 entries per year. There were only 13 costs reported before 2000, and these documents only reported low cost values. The temporal trend in costs suggested that costs continuously increased from 1993 to 2012, and decreased afterwards. This decrease after 2012 is, however, concomitant with the decrease in the number of reported cost estimates and indicative of a time lag in cost reporting (see Suppl. material 5).

Nature of the costs and impacted sectors

As most of the costs started to be reported from the early 2000s in France, the paucity of information makes it impossible to obtain a comprehensive picture of how damage and management costs impacted the different sectors over time. Before 2000, it can only be mentioned that costs corresponded to damage and loss only, without any management expenditure. From 2000 to 2018, observed damage costs were almost always higher than observed management costs. For the most complete time period (2009–2012), observed damage costs were in general characterised by amounts 7–8 times higher than those observed costs documented for management, totalling to US\$ 732million for ‘Damage-Loss’ costs vs. US\$ 98 million for ‘Management’ costs (Figure 1B).

Four activity sectors were mainly impacted by invasive alien species in France over the time range (1993–2018) from which cost information was obtained: Health (US\$ 324 million; cumulative cost), Agriculture (US\$ 258 million) and Authorities and Stakeholders (US\$ 230 million) (Figure 2, Suppl. material 6). A fourth, mixed category (i.e., several sectors impacted together) was higher than the three above specific activity sectors (US\$ 425 million). We also found that each sector category could be affected by different groups of invaders (Figure 2). Semi-aquatic arthropods often had large impacts on a combination of sectors, as suggested by their large impact on the “Mixed” category (Figure 2). Costs to Agriculture and Health sectors were mostly caused by terrestrial forbs, whereas Authorities and Stakeholders were impacted by a diversity of invaders.

Regional mapping of economic costs

The reported economic costs and the number of associated species greatly varied among the different French regions, both metropolitan and overseas (Figure 3). Over the period 1993–2018, the regions with the lowest numbers of species and cumulative cost (< 10 species and < US\$5 million) were the northernmost regions (Grand Est, Ile de France, Hauts de France and Normandie). Auvergne-Rhône-Alpes and La Réunion were the regions with the highest cumulative costs (US\$238 million and US\$137 million, respectively) and had the highest number of invasive species with costs. Provence Alpes Côte d’Azur, Bretagne, Pays de la Loire, Nouvelle Aquitaine and New Caledonia had more than 15 invasive species with costs, and a cumulative cost ranging from US\$5 to US\$100 million. For each region, the listing of the genus / species for which we had cost information is available in Suppl. material 7.

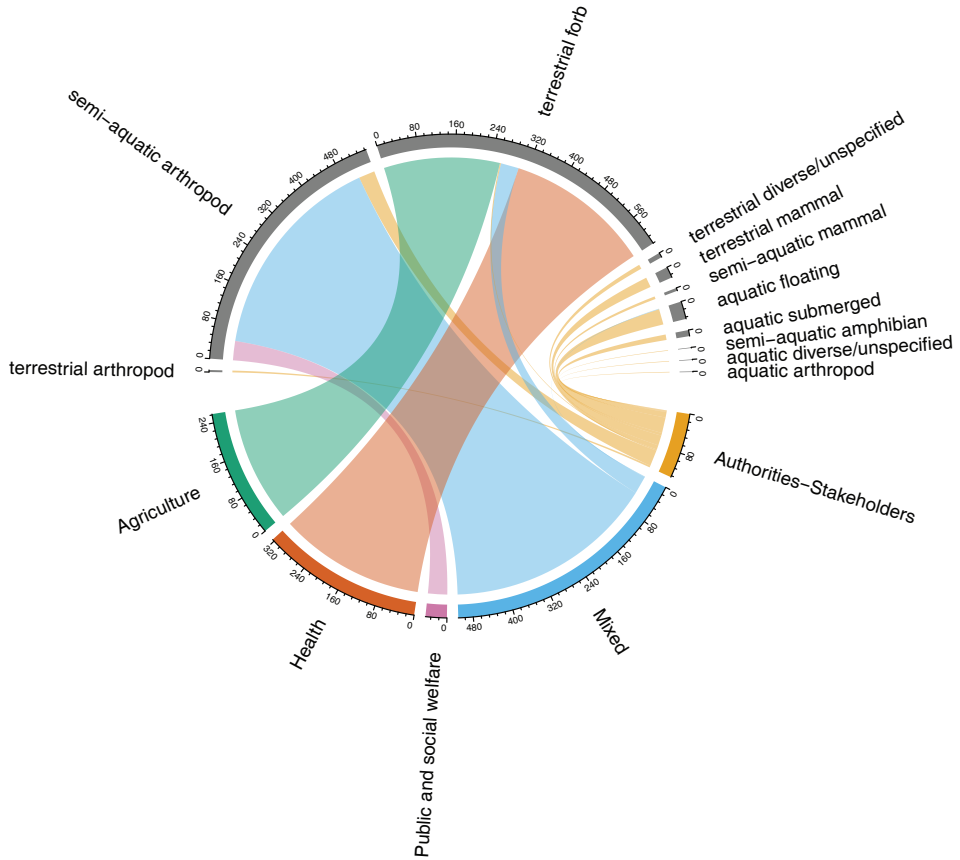


Figure 2. Cumulative costs (in 2017 US\$ million) incurred to each sector per major group of invaders in France in the period 1993–2018. The “Mixed” sector indicates that two or more sectors were economically impacted by invasive alien species. Note that diverse/unspecified groups of invaders were excluded, as well as groups of invaders whose cumulative impact was less than US\$ 1 million over the duration of the period (1993–2018).

Taxonomic group distribution and costliest species

The analysis of economic costs across taxonomic groups revealed that invasive alien plants and invertebrates accounted for most of the reported costs in France (Figure 4, Suppl. material 6). For plants, the great majority of the costs was attributed to the Magnoliopsida class, totalling US\$ 8,421 million in terms of potential costs, and US\$ 664 million for observed costs (Figure 4A, B); it included the 18 following plant taxa: *Acacia mangium*, *Acer negundo*, *Ambrosia artemisiifolia*, *A. polystachya*, *Baccharis halimifolia*, *Crassula helmsii*, *Elaeagnus angustifolia*, *Flemingia strobilifera*, *Ludwigia* spp., *Miconia calvenscens*, *Myriophyllum aquaticum*, *Opuntia rosea*, *Prunus serotina*, *Reynoutria* spp., *Robinia pseudoacacia*, *Rhododendron ponticum*, *Rubus alceifolius* and

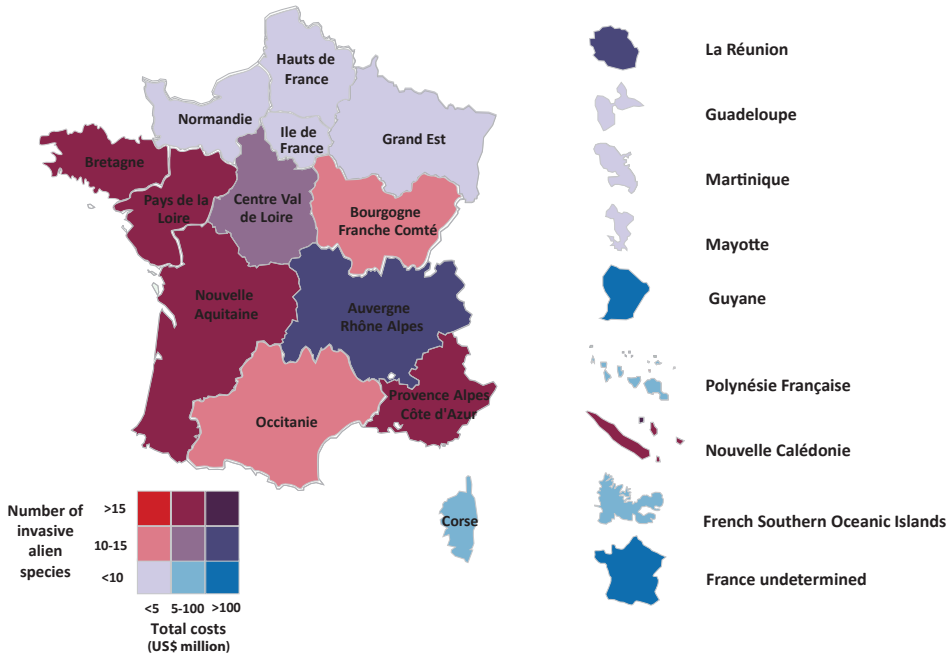


Figure 3. Gradient map of the cumulated numbers of invasive alien species and of total economic costs (US\$ million) recorded from each region of metropolitan France (and French overseas territories on the right) over the period 1993–2018. When the impacted region of the cost was not specified, it was mapped as ‘France undetermined’.

Table I. Listing of the costliest invasive alien species in France (> 1 million in observed cumulated costs).

Species/Genus	Common name	Sum of cost US\$2017	Geographic Origin
<i>Ambrosia artemisiifolia</i>	Common ragweed	551 261 394	North America
<i>Aedes aegypti</i>	Yellow fever mosquito	333 089 505	Africa
<i>Aedes albopictus</i>	Asian tiger mosquito	128 523 816	Asia
<i>Ambrosia polystachya</i>	Cuman ragweed	70 588 450	South America
<i>Ludwigia</i> spp.	Water primrose	35 226 942	America
<i>Rusa timorensis</i>	Javan rusa	8 300 398	Asia
<i>Rattus</i> spp.	Rats	2 811 942	Asia
<i>Vespa velutina</i>	Yellow legged-hornet	2 588 307	Asia
<i>Reynoutria</i> spp.	Knotweed	2 090 356	Asia
<i>Lagarosiphon major</i>	African elodea	1 605 914	Africa
<i>Lithobates catesbeianus</i>	American bullfrog	1 594 127	North America
<i>Procambarus clarkii</i>	Red swamp crayfish	1 394 047	North America
<i>Felis catus</i>	Feral cat	1 258 480	Africa
<i>Baccharis halimifolia</i>	Eastern baccharis	1 104 942	North America

Saururus cernuus. For invertebrates, most of the cost entries were attributed to insects, totalling US\$ 890 million for potential and observed costs, and US\$ 466 million for observed costs (Figure 4A, B); these costs were incurred from the nine following insect species: *Aedes aegypti*, *Ae. albopictus*, *Anoplolepis gracilipes*, *Anoplophora glabripennis*,

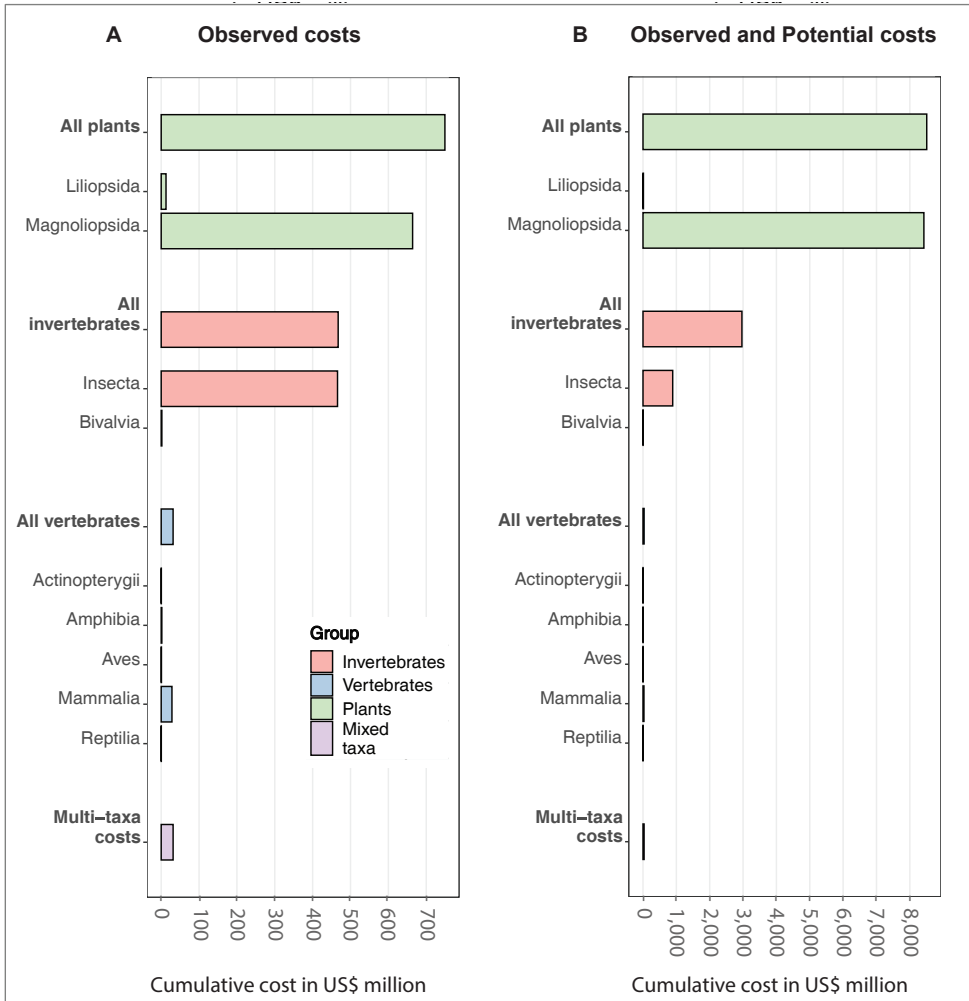


Figure 4. Cumulative costs (in 2017 US\$) by taxonomic groups of invasive alien species in France over the time range 1993–2018 for **A** observed cost amounts and **B** both observed and potential costs. The “Multi-taxa costs” group refers to entries that presented costs without separating the different taxa.

Apis mellifera, *Brontispa longissima*, *Bactrocera tryoni*, *Vespa velutina* and *Wasmannia auropunctata*. Little cost information was found for vertebrates in metropolitan France and French overseas territories.

The costliest invasive alien species in France are presented in Table 1. They include four invertebrates (*Ae. aegypti*, *Ae. albopictus*, *V. velutina*, *Procambarus clarkii*), four vertebrates (*Felis catus*, *Lithobates catesbeianus*, *Rattus* spp., *Rusa timorensis*,) and six plants (*A. artemisiifolia*, *A. polystachya*, *Baccharis halimifolia*, *Lagarosiphon major*, *Ludwigia* spp., *Reynoutria* spp.); these species originate from all continents except Europe and Oceania (Figure 5).



Figure 5. Representation of the geographic origin of the costliest invasive alien species in France over the period 1993–2018 (all those >1 million in cumulated cost). Some of the costliest invaders have multiple continental origins. The coloured bar on the right part of the figure shows the number of species for each continental area (North and South Americas, Arctic, Africa, Europe, Asia, Oceania). See Table 1 for the names of the costliest invasive taxa in metropolitan France and French overseas.

Estimation of the potential costs for species which cost information is missing in France

We found that costs in France represent a small proportion of worldwide species costs, weakly increasing with the global cost value (observed and potential costs):

$$\text{cost}_{\text{France}} = 0.172 \times \text{cost}_{(\text{Global-France})} + 3.500;$$

observed costs only:

$$\text{cost}_{\text{France}} = 0.163 \times \text{cost}_{(\text{Global-France})} + 3.462).$$

We used these relationships to make a first extrapolation of the costs of species known to occur in France, with cost data available worldwide, but no recorded costs in France, which resulted in an estimation of an additional US\$ 3,030 million for both observed and potential costs, and US\$ 151 millions when only considering observed costs.

Discussion

Based on 1,583 records for 98 invasive alien species, we found that biological invasions incurred a total cost ranging between US\$ 1,280 (only observed, incurred costs considered) and 11,535 (observed and potential costs) million in France over the period 1993–2018. These values are likely underestimated since we considered only highly

reliable costs and cost data were missing for the vast majority (97.6%) of invasive species in France. If we add to these numbers our coarse extrapolations of missing cost data, the total cost would range between US\$ 1,431 million (only observed costs) and 14,565 million (observed and potential costs). However, even these rough extrapolations still do not account for over 90% of the species invading France, for which there is no cost information whatsoever. The highest recorded costs correspond to the period 2009–2012, and overall most were damage and loss costs, with relatively few costs corresponding to management expenditures. Many regions had very little information on economic costs of biological invasions, whether in metropolitan France or in French overseas territories. The fractionary nature of the existing data pointed to aquatic insects (mosquitoes, in particular *Aedes* sp.) and terrestrial forbs (non-graminoid herbaceous flowering plants, in particular *Ambrosia* sp.) as belonging to the costliest invasive alien species in France, both severely impacting the human health sector. Yet, many more species had high costs in different sectors.

The economic costs incurred by invasive alien species in France greatly increased in the period 2009–2012. We suggest that the increasing consideration of biological invasions in France and elsewhere in the past years (decades), and the improved awareness of invasive species and biodiversity, may have contributed to explaining this pattern. In particular, the ‘Delivering alien invasive species in Europe’ initiative over the period 2002–2006 (DAISIE 2009), the development of GRIIS by the Species Survival Commission of the International Union for Conservation of Nature in 2006, the Aichi Biodiversity Target 9 for the period 2011–2020 (<https://www.cbd.int/sp/targets/rationale/target-9/>), and the European report published by Kettunen et al. (2009) may have significantly contributed to raising awareness of the ecological and economic burdens caused by invasive alien species. The emergence of these influential initiatives may have subsequently motivated the community to collect and publish information on invasive alien species costs. The decrease of recorded costs after 2012 is at least in part due to the time lag between occurrence of a cost, its record and its publication.

A large majority of the economic costs caused by invasive alien species in France are related to damages and losses. Regarding damages and losses, infrastructures and recreational activities were frequently reported as some of the sectors impacted by invasive alien species. As already reported in other countries, biological invasions can greatly interfere with recreational activities in France (Legrand 2002), especially in water bodies where, for instance, fishing or canoeing are practised; yet, these costs were not reported from several French regions where they are most probably occurring. Agriculture and Health were by far the most impacted sectors in France, followed by Authorities-Stakeholders (surveillance, prevention, control, and education), within which management costs were most often associated and of high reliability (Sarat et al. 2015a, Sarat et al. 2015b; Sarat et al. 2019). Agricultural, industrial or recreational losses, seem less straightforward to accurately estimate, most probably because of their intertwined relationships with several other confounding factors, but also because the invasive status species is not always specified in these sources (e.g. for “pests”), and may thus have been missed by our searches. For example, the lack of cost data of invasive insects on the agricultural sector is surprising given their known costs worldwide

(Bradshaw et al. 2016), and suggests a gap or bias in the reporting of their economic impacts in France. Recent research on invasive ants corroborates this hypothesis, suggesting a total cost over US\$ 45 million for France (Angulo et al. 2021b).

In this study, non-graminoid terrestrial flowering and aquatic plants totalled the highest economic costs followed by invertebrates, and more particularly insects. Five plants totalling a large proportion of the costs: *Ambrosia* spp., *Ludwigia* spp., *B. halimifolia*, *Reynoutria* spp., and *L. major*. *Ambrosia* and *Ludwigia* were also among the most costliest species in Europe (Haubrock et al. 2021a). Pollens produced by the different *Ambrosia* species, and more particularly by *A. artemisiifolia*, cause allergies to humans (Chen et al. 2018). In France, populations from the Auvergne-Rhône-Alpes region are particularly threatened by the pollens produced by *Ambrosia* spp., and pollen sensitivity of the inhabitants is increasing (from 5% in 1980 to about 13% in 2014; ORS Rhône-Alpes 2017). In Europe, the estimated health costs from treating pollen allergies have reached US\$ 8.3 billion annually (Schaffner et al. 2020). As predictive studies suggest that the numbers of inhabitants sensitive to *A. artemisiifolia* pollens should be at least doubled in France by 2041–2060 (Lake et al. 2017), it is likely that medical care costs will significantly rise in this country if mitigation measures aimed at limiting the proliferation of *A. artemisiifolia* are not further increased.

The curly waterweed *L. major* was introduced for aquariophilie and was first observed outdoors in France after the Second World War. By quickly forming very dense beds in ponds and lakes, this submergent plant has strong ecological (extirpation of native hydrophytes, accelerated sedimentation, enhanced transparency of the water), recreational (boating activities, fishing) and industrial (hydroelectric plants) impacts. As part of the invasive alien species list of EU concern (Roy et al. 2014), preventive measures are established to avoid new introductions of *L. major* in the EU, including France, and management plans are implemented for preventing its proliferation. Consistently, our study revealed that in many instances, available costs were related to harvesting of *L. major*, be it mechanised or manual, to labour costs, and to the cost of storage and destruction of this plant, which has 495 occurrences in France (over 3,102 occurrences worldwide; GRIIS, Pagad et al. 2018). Because manual or mechanical harvesting can cause propagation of invasive macrophytes, increased investment in biosecurity is warranted to prevent secondary spread (e.g. Crane et al. 2019). A similar observation can be raised for *Ludwigia* spp., also listed as an invasive alien species of EU concern due to its high ecological and socio-economic impacts (Thouvenot et al. 2013). In our study, all of the costs of *Ludwigia* spp., but one, were related to Authorities-Stakeholders, with more than 90% of the costs being associated with the management of this species.

Following plants, invertebrates (and in particular Insects) constitute the second costliest invasive alien taxonomic group in France. Among them, members of the Culicidae family, including the Asian tiger mosquito *A. albopictus* and the yellow fever mosquito *A. aegypti*, represent growing threats to human populations, due to being harmful mosquitoes swarming in both urban and peri-urban landscapes (Darriet 2014). Females of *A. albopictus* play a significant role in the transmission of many pathogens, and this results in a strong threat to the public health system (Schaffner et al. 2013). Vega-Rua et al. (2013) showed that this species was particularly efficient in

transmitting chikungunya and dengue in the southeast of France, and can also harbour and transmit yellow fever virus (Amraoui et al. 2016). The *Aedes* genus has also been shown to cause the greatest costs of all aquatic and semi-aquatic taxa (Cuthbert et al. 2021). In this study, we found that monitoring, surveillance prevention, research and control costs reached ca. US\$ 62 million in France over the period 2009–2013 for *A. albopictus*, and US\$ 48 million for *A. aegypti* in the same time range. Wittmann and Flores-Ferrer (2015) previously reported that 55% of the costs related to invasive alien species in France in 2013 were related solely to *A. albopictus*, with the number of cost data growing over the period they studied (76 cost entries in 2009 for *A. albopictus*, 81 in 2010, 101 in 2011, 144 in 2012, and 133 in 2013). Yet, the direct medical costs resulting from the expanding populations of vector mosquitoes remain poorly documented. High costs for *Aedes* species were expected in the French territories located in the Americas (French Guiana, Martinique and Guadeloupe), as these species were also the costliest species in the Central and South America region and in specific countries therein such as Ecuador or Argentina (Ballesteros-Mejia et al. 2021; Duboscq-Carra et al. 2021; Heringer et al. 2021). For these French territories in the Americas, Uhart et al. (2016) documented 4,574 hospitalisations of approximately 4.3 days each for patients affected by dengue, with a mean cost per stay of US\$ 2,849. These monetary values are, however, region-dependent, and thus cannot be used for obtaining accurate estimates of the economic impacts of the species in other regions. As an illustration, the direct medical cost per person (hospitalisation, diagnosis, specialised services, drug usage and medical supplies) from dengue fever was about US\$ 48.10 per dengue episode in Vietnam (Vo et al. 2017), US\$ 307 in Central America and Mexico, and US\$ 3,154 in North America (Shepard et al. 2011). Also, we highlight that many costs incurred by invasive alien vectors have not been recorded or monetised (for instance, lost income of hospitalised patients). Finally, as global warming is rapidly boosting the fecundity, development, survival rate and the frequency of blood meals of hematophagous insects, and hence the intensity with which they transmit pathogens (Ryan et al. 2019; Iwamura et al. 2020), the geographic expansion of vector-borne disease insects in France should be considered urgently. In Corsica for instance, there remains a major reintroduction risk of *Plasmodium falciparum* with the presence of populations of *Anopheles labranchiae* on the island (this species is native to northern Africa and vector of the most serious form of malaria, Toty et al. 2010). Given this background, and despite the continuous expansion of *Aedes* sp. in France and Europe, and the massive medical costs they cause, it is surprising that these insects have remained absent from the European list of invasive alien species of concern to the EU (Roy et al. 2014; Consolidated version of the Union list 2019: https://ec.europa.eu/environment/nature/invasivealien/list/index_en.htm).

In the context of global warming, another alien insect species could further expand its range in France, and could potentially have huge monetary impacts: the pinewood nematode *Bursaphelenchus xylophilus*. As several entries corresponded to potential costs for this species in InvaCost, and because we worked with entries of high reliability only, relatively low costs are reported from the pinewood nematode in France in our work. Meanwhile, Soliman et al. (2012) suggested that the species could be distributed in the southern part

of France, as well as in Bourgogne, Poitou-Charentes, Aquitaine, Midi-Pyrénées, Limousin, Rhône-Alpes, Provence-Alpes Côte d'Azur and Auvergne, with potential huge direct impacts varying from US\$ 18 to 102 per km² of infested pinewood, depending on the considered region. Globally, these authors projected US\$ 14.08 billion in damage costs of pinewood nematode *B. xylophilus* in forests in Spain, France and Italy, should the species not be contained. These were not considered in our national estimate, but constituted 99% of the costs in Spain if potential costs were included (Angulo et al. 2021c); a similar amount of annual losses was estimated in Russia (Kirichenko et al. 2021).

The Asian hornet, accidentally introduced in southwestern France in 2004, is the second costliest insect genus (after *Aedes* sp.) in France. This species has colonised urban, agricultural and forest areas, and continues its expansion throughout Europe (Monceau et al. 2014). The Asian hornet has severe impacts on beekeeping and pollination services provided by domestic bees on which it predares (Rome et al. 2011). A study dedicated to the monetary cost of the control of *V. velutina* suggested a US\$ 26 million cost for the destruction of nests in France from 2006 to 2015, and mentioned that this cost could increase by US\$ 13.4 million per year due to the expansion of the species (Barbet-Massin et al. 2020). Yet, this study had no data to report on the probable high costs to beekeepers or to decreased pollination due to the hornet's predation on wild and domestic pollinators. Given that the apiculture revenue was € 135 million in France (corresponding to 2017 US\$ 152.5 million) (Barbet-Massin et al. 2020) and the yearly pollination services to agriculture were estimated at € 2 billion in France (2017 US\$ 2.26 billion) (Gallai et al. 2009), the actual economic impact of the Asian hornet is probably massive. The high costs found for France are very similar to the costs found in Spain for the same species (US\$ 5.33 billion; Angulo et al. 2021c).

Overall, our study revealed very high economic costs of biological invasions, and yet, they remain very conservative, for several reasons. First, we remained conservative here and used only highly reliable cost entries. Second, many existing costs are simply unknown, or unreported, because the scientific literature reporting the economic consequences of biological invasions is still in its infancy in France, as evidenced by the 3% of currently introduced or invasive species having cost entries in InvaCost in France (Diagne et al. 2020b, Angulo et al. 2020). Out of the 2,621 invasive species in total, the remaining 97% of species likely represent a very high additional cost, as shown by the high extrapolations derived for invasive alien species invading France but with known costs only outside France. During our literature search, we also observed that a large number of studies (22 out of 26) stated that invasive alien species have monetary impacts in France, without supplying cost information or referring to published material reporting these costs. Third, monetising the costs remains a difficult task, and we found that pricing the effects of invasive alien species was often achieved by different ways (e.g., costs based from direct observations, estimations, models, extrapolations,...) (Diagne et al. 2020a; Angulo et al. 2021a), with all of these procedures being challenging to synthesise. Fourth, access is probably one of the major hurdles, as cost information exists in relatively large amounts of (a) unpublished and not publicly available documents, (b) documents not published in English, and (c) documents aggregated by

non-academic entities. In France, it is especially difficult to obtain cost values because of the large diversity of entities running investigations on alien species and the diversity of protection designations for terrestrial and aquatic areas (Guignier and Prieur 2010).

As reported elsewhere (e.g., IUCN 2018), direct contacts with academic and non-academic actors had here too proven the most efficient means of retrieving cost information, and partially resolved the issue of the paucity of publicly available cost information. By using phone calls, e-mailing, and by circulating questionnaires, we have been able to collect the majority of cost information (1,106 cost entries collected from 39 documents, as compared with 26 cost entries with the classical InvaCost Database search), revealing that even if cost data were poorly documented in France and overseas territories, those data do exist as grey literature. High percentages of non-English costs were also reported in other countries, such as in Spain or Japan (98%, Angulo et al. 2021c; and 100%, Watari et al. 2021, respectively), and this percentage was lower but also important in countries such as Germany or Ecuador (69%, Haubrock et al. 2021b; 52%, Ballesteros-Mejias et al. 2021) or in general in the Central and South America continent and in Asia (Heringer et al. 2021; Liu et al. 2021). In line with the recent suggestion from Blackburn et al. (2020), this observation proves that academics must continue their engagements towards a more collaborative science for improving the sharing of knowledge and having adequate communication of invasion science findings to the public (Mattingly et al. 2020), and ultimately an ability to better tackle the issues caused by invasive alien species.

The paucity of literature reporting the monetary impacts of invasive alien species in France is problematic, as it results in decision-makers failing to be convinced at local and national levels of the need to make investments towards improving our understanding of ecological and economic impacts linked with invasion. The absence of more quantitative studies on costs is startling, as many introduced populations present very serious risks to public health in France, including the allergenic common ragweed and the irritant giant hogweed (*Heracleum mantegazzianum*), both of which mobilize significant economic resources for their control (Sarat et al. 2015a, b) and for medical care (Schaffner et al. 2020). Some years ago, the overview published by Mazza et al. (2014) summarised the different threats posed by invasive alien species to human health, reemphasising the crucial need for stringent policies to reduce invasion-driven health effects. Our study points out the crucial need for considering invasive alien species costs more generally, i.e. not only the species having health impacts or being listed as invasive alien species of union concern, to reveal and address the significant burden invasive alien species have on the economy in France and beyond.

Conclusion

Our knowledge of the ecological effects of invasive alien species is progressing constantly (Laverty et al. 2017; Cuthbert et al. 2019), and results in frequent warning of the deleterious effects they cause on biodiversity and human societies (e.g., Simberloff et al. 2013; Pyšek et al. 2020). Climate change is additionally enhancing the

geographic expansion of aliens (Bellard et al. 2013; March-Salas and Pertierra 2020), in turn increasing their role as drivers of biodiversity decline (Butchart et al. 2010; McGeoch et al. 2010; Lebouvier et al. 2020). The increased scientific awareness and communication of the negative effects of alien species on biodiversity and ecosystem services have fostered their consideration by a wide array of actors, and a complete and robust assessment of economic costs was hitherto missing. In this study, we provided the first synthesis on the economic costs incurred from invasive alien species to the French economy. We report alarming costs and even more alarming knowledge gaps. The growing number of invasive alien species in France, while budgets dedicated to their management remain very low, has pushed managers to optimize the use of limited funds. By collecting information on the costs incurred by invasive alien species, we hope to raise awareness on the need to monitor and prevent new invasions, but also to supply managers with additional information to better prioritise the species already invasive in France. The costs that we are reporting provide evidence of the significant damages invasive alien species can cause to economies, in addition to their threats to biodiversity. At present, a national coordination compiling the effects of all known invasive alien species in monetary terms is missing. This aspect should be urgently solved, as it would greatly enhance communications towards decision-makers and the public, facilitating our ability to raise awareness of the importance of biosecurity and biosurveillance in France and overseas. The InvaCost initiative partially addresses this need, and offers a platform for standardised cost reporting by environmental managers.

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Supplementary material I

Datasets of the economic costs of invasive alien species in France and descriptive variables (from Diagne et al. 2020b)

Authors: David Renault, Eléna Manfrini, Boris Leroy, Christophe Diagne, Liliana Ballesteros-Mejia, Elena Angulo, Franck Courchamp

Data type: Description of the structure of the database

Explanation note: Spreadsheet 'DB-Descriptor': summary of the content of the descriptive columns of the database used in this study (from Diagne et al. 2020b). The different columns (i.e. descriptive variables) are presented by alphabetical order and between inverted commas (""); note that the 'Taxonomy' information groups several columns. The categories used for each descriptive variable are italicized. Spreadsheet 'RawData': Raw data for France from InvaCost v3.0. Spreadsheet 'DB_Expanded_High': expanded data filtered with only high reliable cost entries. Spreadsheet 'DB_Expanded_High_Observed': expanded data filtered with only high reliable and observed costs.

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Link: <https://doi.org/10.3897/neobiota.67.59134.suppl1>

Supplementary material 2

Description of the different sectors of the InvaCost database

Authors: David Renault, Eléna Manfrini, Boris Leroy, Christophe Diagne, Liliana Ballesteros-Mejia, Elena Angulo, Franck Courchamp

Data type: Description of the structure of the database

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Supplementary material 3

Listing of the environment-taxonomic groupings

Authors: David Renault, Eléna Manfrini, Boris Leroy, Christophe Diagne, Liliana Ballesteros-Mejia, Elena Angulo, Franck Courchamp

Data type: Description of the structure of the database

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Link: <https://doi.org/10.3897/neobiota.67.59134.suppl3>

Supplementary material 4

Listing of the 2750 introduced or invasive alien species with accepted names in France

Authors: David Renault, Eléna Manfrini, Boris Leroy, Christophe Diagne, Liliana Ballesteros-Mejia, Elena Angulo, Franck Courchamp

Data type: listing of Invasive Alien Species

Explanation note: Data were extracted from the Global Register of Introduced and Invasive Species database.

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Link: <https://doi.org/10.3897/neobiota.67.59134.suppl4>

Supplementary material 5

Number of cost estimates per year for France

Authors: David Renault, Eléna Manfrini, Boris Leroy, Christophe Diagne, Liliana Ballesteros-Mejia, Elena Angulo, Franck Courchamp

Data type: cost data

Explanation note: The dashed line illustrates the sudden decrease in the number of cost estimates after 2013.

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Link: <https://doi.org/10.3897/neobiota.67.59134.suppl5>

Supplementary material 6

Categorical representation of the cumulated costs caused by invasive alien species in metropolitan France and French overseas over the period 1993–2018

Authors: David Renault, Eléna Manfrini, Boris Leroy, Christophe Diagne, Liliana Ballesteros-Mejia, Elena Angulo, Franck Courchamp

Data type: distribution of costs incurred by Invasive Alien Species

Explanation note: Categorical representation of the cumulated costs caused by invasive alien species in metropolitan France and French overseas over the period 1993–2018 per (a) activity sectors, (b) cost types, and (c) taxonomic groups. Pie charts show the cost contribution of alien invasive species to the different categories; inner circle shows information based on all costs (i.e. observed and potential costs), whereas the outer circle restricts the information to the costliest invaders ((i.e. observed costs > 1 US\$ million) from France (*Aedes* sp., *Ambrosia* sp., *Lagorasiphon* sp., *Lithobates catesbeianus*, *Ludwigia* sp., *Procambarus clarkii*, *Rattus* sp., *Reynoutria* sp., *Rusa timorensis russa*, *Vespa velutina*, *Felis catus*, *Baccharis halimifolia*).

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Link: <https://doi.org/10.3897/neobiota.67.59134.suppl6>

Supplementary material 7

For each French region, listing of the taxa for which we had cost information in the InvaCost database over the time range 1993–2018

Authors: David Renault, Eléna Manfrini, Boris Leroy, Christophe Diagne, Liliana Ballesteros-Mejia, Elena Angulo, Franck Courchamp

Data type: occurrences

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Link: <https://doi.org/10.3897/neobiota.67.59134.suppl7>

Supplementary material 8

List of the 68 invasive alien species in metropolitan France for which no economic cost was documented in our database

Authors: David Renault, Eléna Manfrini, Boris Leroy, Christophe Diagne, Liliana Ballesteros-Mejia, Elena Angulo, Franck Courchamp

Data type: Listing of Invasive Alien Species

Explanation note: The potential costs incurred by these 68 invasive alien species in France were estimated from cost data obtained from other countries (see Material and methods).

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Link: <https://doi.org/10.3897/neobiota.67.59134.suppl8>