

# Using species ranges and macroeconomic data to fill the gap in costs of biological invasions

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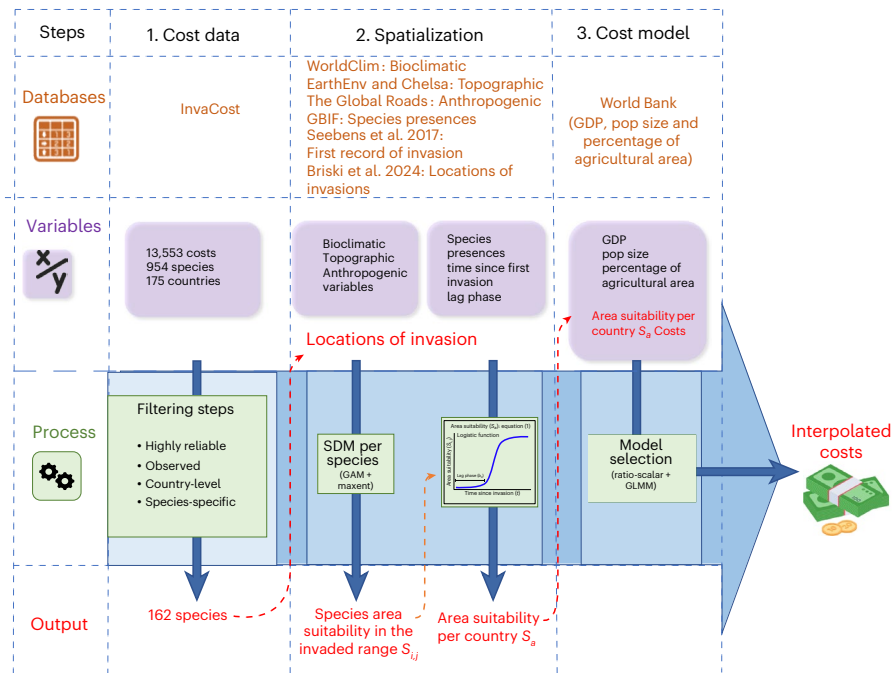
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Biological invasions threaten global biodiversity, human well-being and economies. Many regional and taxonomic syntheses of monetary costs have been produced recently but with important knowledge gaps owing to uneven geographic and taxonomic research intensity. Here we combine species distribution models, macroeconomic data and the InvaCost database to produce the highest resolution spatio-temporal cost estimates currently available to bridge these gaps. From a subset of 162 invasive species with ‘highly reliable’ documented costs at the national level, our interpolation focuses on countries that have not reported any costs despite the known presence of invasive species. This analysis demonstrates a substantial underestimation, with global costs potentially estimated to be 518% higher for these species than previously recorded. This discrepancy was uneven geographically and taxonomically, respectively peaking in Asia and for plants. Our results showed that damage costs were primarily driven by gross domestic product, human population size, agricultural area and environmental suitability, whereas management expenditure correlated with gross domestic product and agriculture areas. We also found a lag time for damage costs of 46 years, but management spending was not delayed. The methodological predictive approach of this study provides a more complete view of the economic dimensions of biological invasions and narrows the global disparity in invasion cost reporting.

Biological invasions pose a global threat to biodiversity, ecosystem services and economies<sup>1</sup>. They are recognized as one of the five main biodiversity threats, contributing to 60% of recorded global extinctions<sup>2,3</sup>. Alongside the massive environmental and health impacts, the estimated monetary cost of biological invasions exceeds those for most natural hazards<sup>4</sup>, totaling a multi-trillion-dollar cost globally<sup>5,6</sup>. These monetary impacts are escalating worldwide, in line with the rising rates of introduction<sup>7,8</sup>.

The InvaCost database has begun to address the global knowledge gap in costs of biological invasions by compiling and synthesizing data on their monetary burden<sup>9</sup>. However, current estimates are mostly based on published studies and thus represent only a subset of monetary costs, often reflecting geographic and taxonomic biases in underlying research<sup>6,10,11</sup>. Most of the documented costs are concentrated in Europe and North America<sup>9</sup>, thereby misrepresenting the economic burden of invasive species present in other regions, including most

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**Fig. 1 | Schematic representation of the methodology used to interpolate monetary costs.** The scheme is split into the following: extraction of monetary cost data (step 1), SDMs (step 2) and cost model selection (step 3). Each step is

not solely dependent on the listed databases; some variables are derived from previous steps. Each colour corresponds to the factor input in each step. GLMM, general linear mixed model.

of the global south<sup>12,13</sup>. This skew leads to an underestimation of costs in less-studied regions that has remained unresolved.

Considering the extensive data deficiencies, the growing economic implications of biological invasions and the limited budgets allocated to conservation, new approaches are urgently needed to assess their monetary burden more accurately. Species distribution models (SDMs) are used to predict the potential range of species by quantifying their environmental suitability<sup>14</sup>. These models work by correlating the known locations of species with environmental factors in these locations. By combining the species occurrences predicted by SDMs with the economic costs associated with these species, it is possible to perform spatial interpolations that include regions where economic costs have not yet been reported<sup>14,15</sup>. Despite strong links between species range size and economic impacts of invasions<sup>16</sup>, the range estimates from SDMs and the invasion cost data reported by InvaCost have yet to be fully synthesized. Considering the dynamic nature of invasive species costs over space and time, SDMs could thus be used to improve global monetary estimates.

We integrate SDMs into invasion cost estimates by linking the predicted suitable habitat area for invasive species in each country to potential economic impacts, while integrating further invasional and macro-economic characteristics (Fig. 1). Specifically, cost predictions could be made in combination with data on the time since invasion which in turn informs how economic costs might evolve temporally, including potential time lags between the invasion and the appearance of measurable impacts<sup>17</sup>. Macro-economic indicators, such as gross domestic product (GDP), human population or agriculture area size could also be relevant predictors of the monetary impact of invasive species because they are directly tied to macro-economic factors (for example, labour, capital)<sup>18</sup>. Moreover, different types of cost, such as damage costs and management expenditure, might exhibit divergent spatio-temporal patterns. These costs are compounded by increased economic activities and the potential for more extensive damage to goods, production and infrastructure in densely populated or agriculturally intensive areas. Damage costs might rise rapidly with longer invasion duration and expanding suitability area, whereas management

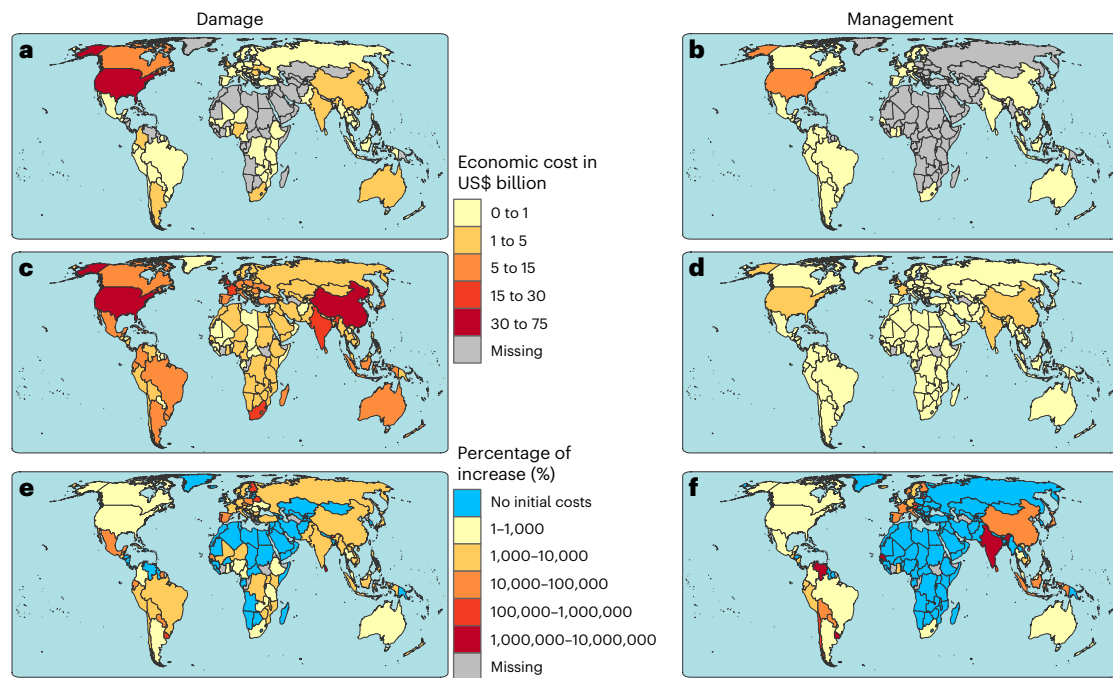
expenditure might start off lower and increase more gradually over time or decrease as it becomes more efficient<sup>5</sup>.

Our study aims to estimate the monetary cost of invasive species based on a method combining SDMs with macro-economic indicators and spatio-temporal predictors. To achieve this, we (1) analyse the differential patterns of damage and management expenditure; (2) assess the interpolated monetary costs and their potential to provide a more accurate representation of costs in under-documented regions, thereby shedding light on geographic biases; and (3) provide a fine-scale map of global monetary costs. By relating range size to costs within a country, we obtain unprecedented granularity in cost estimation per unit area. This is critical because per unit costs underpin the efficient allocation of resources, making it possible to assess returns on investment and prioritize mitigation strategies<sup>19</sup>.

## Results

Based on 162 invasive species in 172 countries, the assessment of the missing costs showed a 17-fold discrepancy, that is, the difference between costs reported in InvaCost and the total estimated costs. It represents a discrepancy of global cost of these species from US\$126.81 billion (reported in InvaCost) to US\$784.24 billion (approximately +518%; range, US\$228–5,025 billion) over the period 1960–2022, resulting in an annual average of US\$12.45 billion (Supplementary Table 1). The ensemble economic model for damage costs (Supplementary Tables 2 and 3) predicted a discrepancy in damage cost of 529%, corresponding to an increase from US\$117.73 to US\$740.91 billion (range, US\$213–4,539 billion). For management expenditure, the ensemble economic model (Supplementary Tables 2 and 3) predicted a discrepancy of +378%, equal to an increase from US\$9.07 to US\$43.38 billion (range, US\$14–486 billion) (Supplementary Table 1).

For damage costs, the mixed model provided the best model (fitted  $R^2 = 0.52$ ), with GDP, agricultural area and environmental suitability showing significant positive relationships (see Supplementary Table 2 for details, including both fitted and validation dataset results). The best ratio-scalar model additionally found population size, time since invasion and lag phases as significant predictors (fitted  $R^2 = 0.34$ ;



**Fig. 2 | Global economic cost associated with invasive species at the country level. a,b,** Costs are split into data from the InvaCost database for damage costs (a) and management expenditure (b). **c,d,** Total economic costs (that is, data from the InvaCost plus estimated costs) for damage costs (c) and management

expenditure (d). **e,f,** Percentage increase (that is, discrepancy) of the economic cost from InvaCost to the total economic costs for damage costs (e) and management expenditure (f).

Supplementary Table 2). By contrast, for management expenditures, the ratio-scalar model was the strongest approach (fitted  $R^2 = 0.26$ ), with GDP and agricultural areas providing the main predictors (Supplementary Table 2). For the mixed model, only GDP was significant for management expenditures (fitted  $R^2 = 0.23$ ; Supplementary Table 2). Importantly, similar patterns were observed for both fitted and validation datasets, supporting the robustness of our models. Ensemble models of ratio-scalar and the mixed model were used for final cost projections.

### Geographic cost distributions

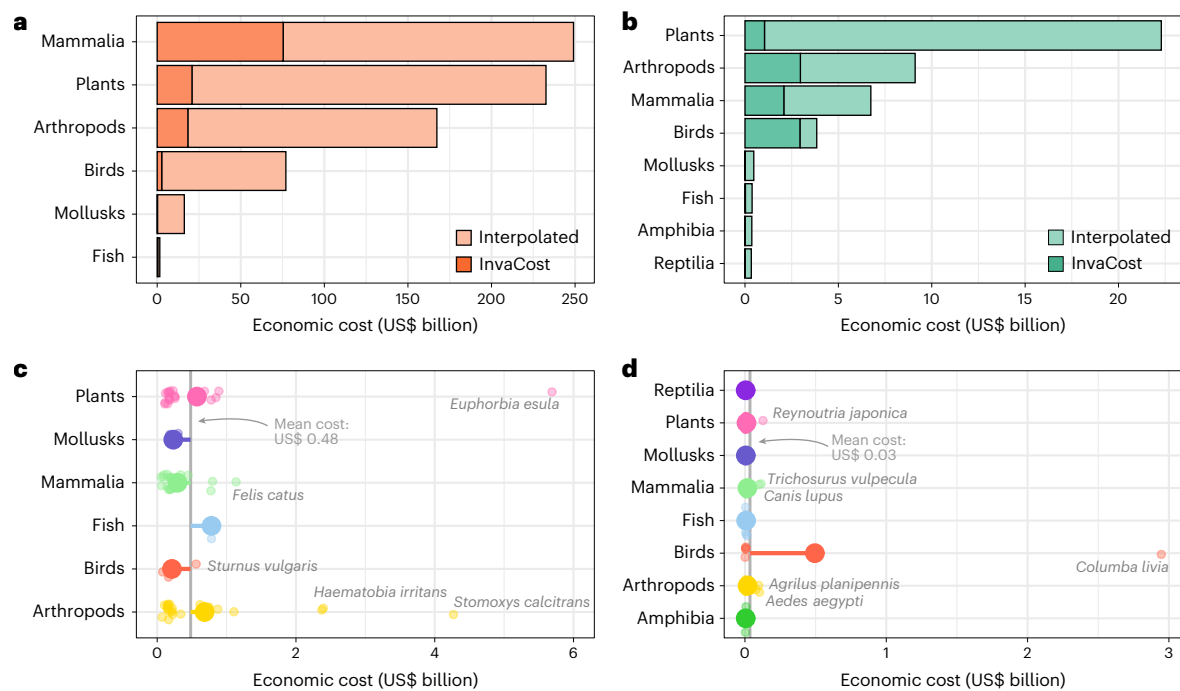
In addition to completing costs for undocumented species in some countries, our cost interpolations also revealed costs for 78 countries for which no data were previously available. Based on our interpolation, at the continental level, Europe had the highest potential impacts from biological invasions, reaching US\$213.45 billion (27.22% of global costs), followed by North America (US\$201.26 billion, 25.66%), Asia (US\$20.23 billion, 8.21%), Africa (US\$116.92 billion, 14.91%), South America (US\$67.52 billion, 8.61%) and Oceania (US\$28.11 billion, 3.58%). Asia reported a disproportionate discrepancy in costs corresponding to +2,679%, followed by Europe (+1,939%), Africa (+1,768%), South America (+809%), Oceania (+654%) and lastly, North America (+116%) (Supplementary Fig. 1 and Supplementary Table 4). When focusing on damage costs, Europe again had the highest estimated economic burden, at US\$199.18 billion, whereas the percentage discrepancy for Asia was again the most substantial at +2,790%, rising from US\$5.21 to \$150.78 billion (Supplementary Fig. 1 and Supplementary Table 4). For management expenditures, Europe had the highest estimates costs at US\$14.27 billion and Africa the steepest percentage rise, reaching +1,618%, from US\$0.29 billion to US\$4.99 billion (Supplementary Fig. 1 and Supplementary Table 4).

At the country level, the median cost discrepancy was +3,243% (3,100% and 4,098% for damage and management, respectively). However, there was a major discordance among countries, with some

showing remarkably higher increments were India (+973,077,392%), followed by Sri Lanka (+11,406,804%) and the Netherlands (+11,367,006%). The estimated costs were particularly acute for countries in Africa and Asia, where most had not previously recorded any economic costs (see Fig. 2). In terms of absolute estimated costs from biological invasions, China had the highest estimates costs, at US\$131 billion. When examining the discrepancy in damage costs, Sri Lanka reported the most significant rise at +11,406,904%, although the United States had the highest absolute damage costs, amounting to US\$46.44 billion. As for management expenditure related to these invasions, India had the highest percentage discrepancy at +973,077,492%. Yet, the United States again topped the list in terms of total expenditure with US\$10.47 billion (Supplementary Table 5).

### Taxonomic cost interpolations

The estimated monetary burden of biological invasions varied across taxonomic groups and types of cost. For damage costs, mammals were the group with the highest estimates cost (US\$247.75 billion; discrepancy of +229%), followed by plants (US\$231.62 billion; +1,013%), arthropods (US\$167.25 billion; +811%), birds (US\$76.47 billion; +2,715%), mollusks (US\$16.23 billion; +8,810%) and fish (US\$1.56 billion; +347%) (Fig. 3a). For management expenditures, plants were the costliest group with the highest estimates cost (US\$22.28 billion, +2,033%), followed by arthropods (US\$9.00 billion; +203%), mammals (US\$6.73 billion; +224%) and birds (US\$3.79 billion; +28%), while mollusks (+5,866%), fish (+1,658%), amphibians (+22,702%) and reptiles (+14,914%) had negligible costs totaling US\$1.41 billion (Fig. 3b). Fish had the greatest average estimated damage costs (US\$0.78 billion) and birds for management expenditures (US\$0.49 billion) (Fig. 3c,d). We also identified variations within each taxonomic group influenced by both the number of cost estimates available and the individual magnitudes of these estimates, with plants, fish and arthropods exhibiting above-average damage costs, whereas birds exceeded the global average in management expenditures (Fig. 3c,d).



**Fig. 3 | Monetary cost of invasive species by taxonomic order and type of cost.** **a,b**, Stacked bar plot based on the type of cost according to InvaCost for damage (**a**) and management (**b**). **c,d**, Average economic costs per species across taxonomic groups for damage (**c**) and management (**d**). Each dot represents the

average cost for a given species, whereas the larger dot refers to the taxonomic average. Two species (*Pontederia crassipes* and *T. absoluta*) were excluded to enhance visualization clarity.

### Monetary costs per unit area (km<sup>2</sup>)

Our high-resolution assessment of the monetary costs of biological invasions revealed a complex pattern of spatial heterogeneity in costs estimated across the globe. We found large disparities at sub-national level, with apparent ‘cost hot spots’ (that is, locations where the costs are highest). Notably, we identified that these cost hot spots are predominantly located in densely populated urban areas, particularly in coastal zones. Regionally, Europe, the east coast of China and the east and west coasts of the USA were highly affected.

Among the species causing damage costs, *Heracleum mantegazzianum* (giant hogweed) was estimated to be the most economically burdensome, with an average cost of US\$630,928 km<sup>2</sup> (Fig. 4). This was followed by *Carduus platytypus* (plumeless thistle; US\$532,510 km<sup>2</sup>), *Capra hircus* (domestic goat; US\$503,387 km<sup>2</sup>), *Sus scrofa* (wild boar; US\$456,536 km<sup>2</sup>) and *Coptotermes formosanus* (Formosan subterranean termite; US\$296,369 km<sup>2</sup>). For management expenditure, *Phelipanche aegyptiaca* (Egyptian broomrape) was the costliest species with an average cost US\$1,335,975 km<sup>2</sup>, followed by *Cryptotermes brevis* (West Indian drywood termite, US\$433,828 km<sup>2</sup>), *Reynoutria japonica* (Japanese knotweed, US\$72,403 km<sup>2</sup>), *Aedes aegypti* (yellow fever mosquito; US\$44,937 km<sup>2</sup>), and *Anolis carolinensis* (Green Anole, US\$31,410 km<sup>2</sup>).

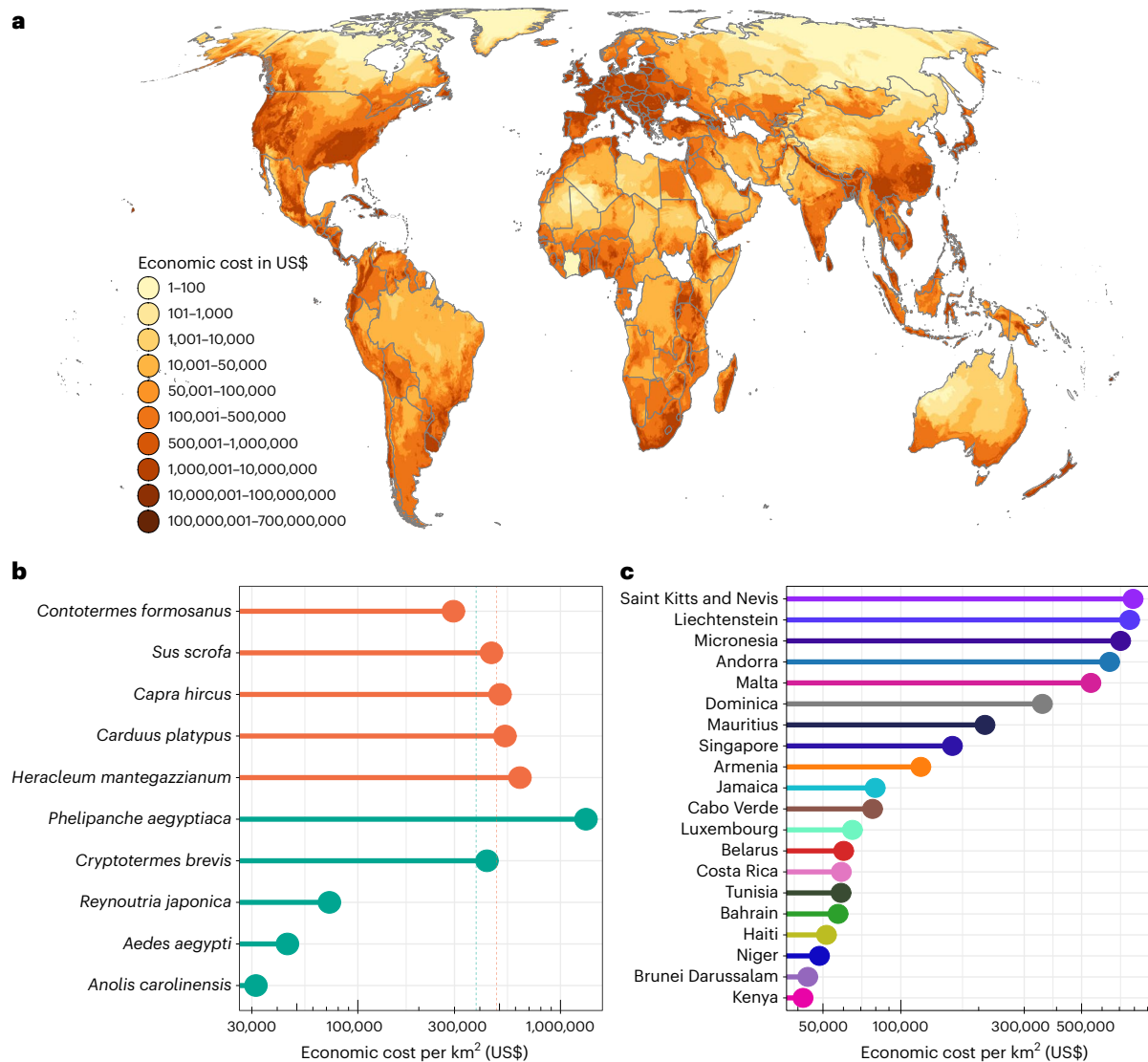
Area-based cost estimates revealed unprecedented marginal costs in Asian and North American countries, amounting to US\$25.71 billion km<sup>2</sup> and US\$10.48 billion km<sup>2</sup> respectively, followed by Oceania (US\$4.64 billion km<sup>2</sup>), Africa (US\$4.01 billion km<sup>2</sup>), Asia (US\$2.74 billion km<sup>2</sup>) and South America (US\$0.17 billion km<sup>2</sup>) (Supplementary Fig. 2). Saint Kitts Nevis had the highest estimates cost per unit area, amounting to approximately US\$790,712 km<sup>2</sup> followed by Liechtenstein and Micronesia, both exceeding costs of US\$700,000 km<sup>2</sup>. Lastly, Andorra with a cost of US\$641,838 km<sup>2</sup> and Malta (US\$543,072 km<sup>2</sup>) complete the top-five costliest countries per km<sup>2</sup> (Fig. 4).

### Discussion

Integrating SDMs with cost prediction models based on socio-economic factors enabled us to draw up a more complete picture of the monetary costs of invasive species, marking a notable advancement in quantifying their impacts. We revealed a considerable discrepancy of +518% from US\$126.81 billion to US\$784.24 billion in estimated costs at the global scale (focusing on the subset of 162 species). Our approach therefore offers insight into the magnitude of missing costs, particularly in less-documented regions, such as Africa and Asia, alongside a granular assessment of the monetary costs of invasive species by country and square kilometre. These results place the monetary cost of biological invasions on a similar scale to the global costs of extreme weather attributable to climate change<sup>20</sup> and surpass previous comparative estimates for natural hazards<sup>4</sup>.

We included moderating factors in our models to account for differences in socioeconomic contexts based on the data available. Damage costs were driven mainly by GDP, human population size, agriculture area and environmentally suitable area (adjusted by time since invasion) common in both models (that is, ratio-scalar and mixed models). Larger human populations result in higher damage costs through more economic activities and greater invasion risks<sup>21</sup>, impacting goods, production and infrastructure. Agriculture—the sector most vulnerable to invasions<sup>22</sup>—faces reduced yields and compromised livestock health, elevating economic burdens<sup>23,24</sup>. Nevertheless, invasive species impacts are not confined to agriculture sectors and extend to others, such as public health and forestry. For instance, cats *Felis catus* are one of the costliest invasive species, affecting many sectors, including the environment, authorities and stakeholders, and agriculture<sup>25</sup>. The extent of suitable area is an indicator of invasion susceptibility affecting both damage and management costs. Lastly, regions with high GDP indicate more resources and financial capacity to invest in invasive species management but may also face greater establishment rates and potential for spread, making management





**Fig. 4 | Monetary costs of invasive species per unit area. a**, Total costs (that is, reported and estimated) of invasive species per unit area (km<sup>2</sup>) at a resolution of 0.083. **b**, Monetary costs per km<sup>2</sup> on a log<sub>10</sub> scale of the top five invasive

species with highest impacts, categorized by the type of cost (orange refers to damage costs and green to management expenditure). **c**, Monetary cost per km<sup>2</sup> on a log<sub>10</sub> scale of the top 20 countries with highest cost.

more difficult and costly. Nevertheless, management and damage costs often occur simultaneously, as management efforts typically respond to or coincide with damages. While our model accounts for the variation in damage and management levels associated with socioeconomic contexts, the complex interactions between damage and management effectiveness remain unexplored and are challenging to test on a global scale.

We identified a time lag of ~46 years between species introduction and the peak of damage costs, suggesting that the monetary cost may not be immediate (that is, the cost debt)<sup>26</sup> but increase over time, as presumably the invasive species becomes more abundant or occupies more surface area. This indicates that pre-emptive measures to mitigate the costs of invasive species should be implemented as soon as possible to limit the economic burden of invasive species in the future. Management expenditure was, conversely, not characterized by a lag phase. This suggests that measures are often implemented soon after (for example, rapid response) or even before (for example, prevention) the impacts of invasive species. The potential early application of management actions is a positive sign and consistent with recent theoretical analyses showing the importance of swift action<sup>27</sup>.

Our research addressed the bias presented in InvaCost database towards high-income nations by estimating invasion costs in countries previously undocumented, which is a common bias across all fields of biodiversity science, as for example, global meta-analyses often overlook a substantial proportion of the globe<sup>5,11,28,29</sup>. Moreover, the observed distribution of species occurrences is also biased, with most data in the Global Biodiversity Information Facility (GBIF) occurring in North America and Europe and less than 7% of the surface sampled even at 5 km<sup>2</sup> (ref. 30). By projecting species occurrences more broadly, we include a greater geographic scope in our analysis and enhance the representativeness and applicability of our findings across diverse economic contexts. We showed that several countries—mainly those with lower GDPs or little research into the cost of invasive species—had in fact substantial monetary costs, in some cases exceeding their annual GDP (for example, Dominica). Collectively, the estimated economic costs of invasive species exceed 3% of the global GDP. The initial geographical bias was further exacerbated when the two categories of costs were distinguished, with a greater bias towards management expenditure suggesting lower investment in invasion mitigation in developing regions<sup>31</sup>. This disparity could stem from both limited resources and a recording

bias in the InvaCost database, which may overlook reports in languages predominant in Africa and Asia<sup>12</sup>. In addition, the geographic origin of costly invasions, primarily from Asia to Europe and the USA, contrasts with the minimal reported costs flowing to Africa and Asia, highlighting a need for broader, more inclusive data collection and analysis efforts<sup>32</sup>.

Monetary costs varied also in magnitude across taxonomic groups and within types of cost. Based on the reported costs in InvaCost, plants were respectively ranked second and fourth in damage and management spending. After accounting for interpolated costs, plants reported a substantial increase (1,062%), becoming the second most economically impactful group, confirming the underestimation bias that has been previously highlighted for this group<sup>5,33</sup>. Although they represented a sizable fraction in InvaCost, our results suggest that plant invasions were even more widespread in nature compared to other taxonomic groups, relative to their frequency in InvaCost<sup>34–36</sup>. Nonetheless, arthropods, mammals and birds also reported considerable total costs (Fig. 3), while other groups, such as molluscs, fish, reptiles and amphibians generally had relatively low economic costs (Fig. 3). However, this may be due to their lower observability in terms of damage costs (that is, particularly to human infrastructure)<sup>37</sup>, research biases towards high-profile and more charismatic species<sup>38</sup> or disparities resulting from the filtering process used in the study.

Quantifying the monetary cost of invasive species per spatial unit allows for a better impact assessment, aiding policymakers and conservationists in prioritizing management efforts. Our analysis revealed that a small fraction of locations (that is, hot spots)—often with high human density or key industries—are associated with most of the costs, as well as coastal regions—vulnerable due to trade and tourism<sup>37</sup>. The highest costs per km<sup>2</sup> were predominantly in small countries which might be explained by their relatively high population density and/or dependence on the agricultural sector.

Our results indicate that *H. mantegazzianum*, *C. platypus*, *C. hircus*, *S. scrofa*, *C. formosanus* were the costliest species in terms of damage costs, while *P. aegyptiaca*, *C. brevis*, *R. japonica*, *A. aegypti*, and *A. carolinensis* required the highest management expenditure per square kilometre. The reasons for their important impact vary among species, such as prominent traits (for example, rapid reproduction or high adaptability) that allow them to outcompete native species and disrupt ecosystems but also the economic sectors they affect, such as agriculture or public health that represent substantial portions of the global economy<sup>22</sup>. Management strategies for these species focus on control and eradication of populations, which can be costly due to the necessity for ongoing, intensive efforts<sup>39</sup>.

While our approach provides a more complete estimate of the monetary costs of invasive species and addresses many geographical gaps in existing literature, it is not without limitations. Our study included only species for which sufficient data were available for model calibration (distribution and economic cost data), limiting our sample to 162 species out of 954 (17%) in the InvaCost database, thus likely under-representing true costs. Economic estimates are subject to potential measurement errors, as cost data inherently vary in accuracy and completeness; however, by focusing on most reliable costs from InvaCost, we tried to minimize these uncertainties, although they may still influence the overall cost assessments presented. For instance, interpolated costs for certain countries appear disproportionately large, surpassing their entire GDP. These high estimates may arise from inherent limitations in the modelling process. Notably, such cases often involve small economies, such as Kiribati (GDP<sub>2020</sub> ≈ US\$0.22 billion), where low GDP values make such discrepancies more likely. As with any statistical model, both overestimations and underestimations are inevitable. While most values align well with predicted relationships, some deviations are expected, warranting caution when interpreting individual cases.

In addition, our approach spans several interconnected modelling steps, each of which necessarily comes with their own source of uncertainty and limitations (for example, transferability of SDMs<sup>40</sup>). While

we included a temporal dimension, the lack of complete data on species' first occurrences limited its effectiveness. While we acknowledge that species distribution predictions may vary due to the exclusion of ecological and socio-economic factors<sup>30</sup>, they provide the best projections available, and our model framework allows for the integration of additional data where possible. Although we tried to account for the socio-economic context of each estimated cost, we acknowledge that estimates from developed countries may not translate fully to less developed nations, where such data are often lacking. Finally, improved investment and management policies, such as transitioning to alternative crops that are less susceptible to damage, might affect economic cost estimates.

Therefore, the conclusions of this study must necessarily be based on currently available data (and its limitations), in particular, interpolation based on different socio-economic and agricultural contexts when considering the varying cost effectiveness of management strategies between developed and developing nations. Despite limitations in our assumptions, our analysis reveals that adjusted costs are likely around 518 times higher than those recorded in InvaCost. Our findings not only bolster the robustness of these results but also lay the foundation for future research by refining analyses with, for example, mapping crop-specific pest impacts, extending models to include sectors such as fisheries and forestry as predictors or other potential relevant predictors such as transportation volume or split management costs by private agents or public sector. These advances pave the way for better assessment of the costs of these species in space and time and provide information on their marginal costs, enabling cost-effective management to be put in place worldwide.

## Methods

### Approach

Using the InvaCost database, we filtered country-level costs for a set of 162 invasive species (out of 954 species in InvaCost) with highly reliable economic cost data at the national level, while separately considering damage and management costs (Supplementary Fig. 3). For each species, we used ensemble SDMs (generalized additive models (GAMs) and maximum entropies (maxents)) to determine the amount of suitable area in each invaded country and incorporated two temporal predictors by considering the time since invasion and lag phases in the detection of the impacts that can modulate economic costs. Finally, we modeled costs against a set of macro-economic factors (that is, GDP, population size and agriculture area<sup>18</sup>) and, using the best ensemble economic model (averaging ratio-scalar and mixed model), we interpolated the missing costs in the countries where these species have been reported but no monetary costs have been recorded (Supplementary Fig. 3). Translocation of species that are native to other areas within the same country (e.g., the signal crayfish *Pacifastacus leniusculus* in the United States), were not considered in this analyses. The following sections describe the main steps of this methodology in detail.

### Monetary costs

We first identified species whose costs were recorded in InvaCost, a 'living' database of the monetary cost of invasive species worldwide reported in over 22 languages, to interpolate the monetary cost of invasive species on a global scale<sup>9,12,41</sup>. Each cost entry is standardized in annual US\$ (2017 value) and has 65 descriptors, including the type of the invaded ecosystem and the taxonomy of the species. We excluded from the InvaCost database (1) less reliable and potential costs (the former referring to costs lacking documented, repeatable and traceable methods, typically from grey/non-peer-reviewed sources, the latter to costs expected and/or predicted over time within or beyond their actual distribution area), (2) costs at a lower scale than the country level and (3) costs for which data were insufficient or entries were unspecified (that is, with respect to spatial dimension, habitat type or nature of cost) (see Supplementary Information, Material 1 for more

details). This filtering process resulted in the retention of 162 species (70 plants, 37 arthropods, 29 mammals, 10 birds, 5 molluscs, 4 reptiles, 4 fish and 3 amphibians; Supplementary Table 6). The total cost for each estimate and species was divided by the corresponding duration of the cost entry, determined by the time elapsed between the 'Probable\_starting\_year\_adjusted' and the 'Probable\_ending\_year\_adjusted' columns using the `expandYearlyCosts` function, to standardize cost estimates as annual costs<sup>42</sup>.

## SDMs

We fitted SDMs using occurrences retrieved from the GBIF ([gbif.org](http://gbif.org))<sup>43</sup> database for each of the 162 species (Supplementary Table 6) alongside a combination of bioclimatic, anthropogenic and human-mediated spread variables (Supplementary Fig. 3 and Supplementary Table 7). These were compared against 10,000 background points, generated for each taxonomic group (plants, arthropods, reptiles, amphibians, mammals, birds, molluscs and fish). To minimize sampling bias in presence-only data, we used the 'target-group background' approach<sup>44</sup>, basing the pseudo-absences on randomly sampling GBIF records for each taxonomic group. This reduces observation and spatial biases because pseudo-absences would be chosen using the same observation processes<sup>44,45</sup>.

For environmental variables, we downloaded 19 bioclimatic variables at global scale and at  $5 \times 5$  arc min resolution ( $0.0833^\circ$ ) from WorldClim, which describe means, extremes and seasonality in temperature and precipitation from 1970–2000 (ref. 46) (Supplementary Table 7). We complemented these with anthropogenic and environmental variables demonstrated to provide high predictive power for determining the presence of invasive species. Environmental variables included elevation, slope, rugosity and potential evapotranspiration<sup>47,48</sup> (Supplementary Table 7), while also including density of roads extracted from the Global Roads Open Access Data Set, version 1<sup>49</sup>, which was used as a proxy for ease of human-mediated spread<sup>50</sup>. We standardized the predictors into grid cells to match the resolution of the WorldClim dataset (that is,  $5 \times 5$  arc min). We minimized the collinearity among predictors by calculating the variance inflation factor of all variables using the `vifstep` function of the `usdm` R package (version 2.1.7)<sup>51</sup> and removing variables using a threshold value of 10 (Supplementary Table 7).

We used two versatile algorithms that can handle non-linear relationships to predict the potential suitable distribution for each invasive species: GAMs using the `mgcv` R package (version 1.8)<sup>52</sup> and `maxnet` using the `maxnet` R package<sup>53</sup>. While our approach to SDMs focused on the fundamental principles of the methodology, we meticulously adhered to the established standards<sup>54</sup> (ODMAP (Overview, Data, Model, Assessment and Prediction) protocol; Supplementary Note 1), thereby ensuring the replicability of our analysis and the transparency, robustness and reliability of our results. For GAMs, we limited the number of knots (that is, smooth terms) to 5 and used the selection function and cross-validation option to prevent overfitting of the model to our data. Furthermore, we examined the concurvity (that is, the correlation of the smooth functions of the predictors) for each variable and removed variables with high concurvity ( $>0.8$ ) using the concurvity function from the `mgcv` R package to reduce multicollinearity<sup>52</sup>. For `maxnets`, we used 'transformed features'—modified versions of the original predictors, for example, linear, quadratic—to enhance the model's predictive capabilities. To mitigate the risk of possible overfitting, we limited the model complexity to linear, quadratic and product features<sup>55</sup> while using the default settings in the `maxnet` package<sup>53</sup> for all other parameters with the regularization applied<sup>40</sup>. Lastly, we created a weighted ensemble SDM that integrates both algorithms, weighting by the area under the curve of each modelling approach. Predictions from the ensemble models were then used to estimate the suitable area, which was calculated as the sum of the probabilities for a given species in a country.

To evaluate the performance of the models, we used a fivefold cross-validation and three metrics for evaluating predictive models: the area under the curve, the true skill statistic and the Boyce index (Supplementary Information, Materials 2 and 3).

## Suitable area per country

We would expect that countries are not uniformly environmentally suitable for each species. Furthermore, as invasions tend to spread, we would expect that costs might also not be constant over time. We tested these predictions by modelling a temporal suitability and cost impact model. This model accounts for variations in environmental suitability and the associated economic costs over time within each country. It uses a logistic growth function to encapsulate the changing suitability of an area for a species (denoted as  $S_a$ ), parameterized by both a constant ( $b_0$ ) and a time-varying coefficient ( $b_1$ ). This allows us to capture a possible initial phase of delay with costs initially minimal and gradually increasing as the species becomes established and spreads.

$$S_a = \frac{\sum_{i=1}^G S_{i,j}}{1 + e^{-(b_0 + b_1 t')}}; \quad t' = \{0 \text{ if } t \leq b_2; t - b_2 \text{ if } t \geq b_2\} \quad (1)$$

where  $S_{i,j}$  = summed suitability area of a country scores across  $G$  grid cells  $i,j$  and  $t$  = time (years) since invasion. In addition, we modeled a potential lag phase ( $b_2$ ). This was done by fitting an additional temporal threshold ( $t'$ ), where if  $t$  is lower than  $b_2$ ,  $t'$  was set to 0, such that cost would be at the minimal level (set by  $b_0$ ). Our model does not incorporate economic discounting of future costs. Instead, all costs are weighted equally over time, with temporal variations in cost strictly governed by the logistic function in equation (1). While SDMs come with several limitations, our use of SDMs for interpolation helps mitigate these challenges. We address observation biases in occurrence records through a target-background sampling approach. Although SDMs provide only relative probabilities of occurrence and may indicate habitat suitability, they do not imply that damages occur uniformly across the species' entire range. These gaps are addressed in our ratio-scalar approach ('Economic cost model' section), which integrates both observed and interpolated areas. In addition, invasions are dynamic over time, whereas SDMs are often treated as static. To account for this, we incorporated a temporal threshold ( $t'$ ), with the SDM acting as the asymptote in our model.

We used a comprehensive database detailing the locations of these invasions<sup>56</sup> to identify countries that have not reported any costs despite the known presence of invasive species. We retrieved the initial period of invasion in each country from the Global Alien Species First Record database version 1.1<sup>7</sup>. When there was no estimate of time since invasion, we used the earliest record of the species in the target country from GBIF<sup>40</sup>. If neither the Global Alien Species First Record nor GBIF had records of an invasion in a country for a species, we used the asymptotic cost based on the suitability alone (that is, we treated it as an old invasion).

## Economic cost model

We built an interpolation cost model that allowed species-specific costs estimates to be used, context-specific factors to be included and easy interpretation (that is, directional effect of context-specific factors). We used two approaches which conformed to these criteria—a general linear mixed model, using context-specific predictors as fixed factors, and species as a random factor, and a 'ratio-scalar' approach<sup>18</sup> described below (equation (2)). For context-specific predictors, in addition to the suitability area ( $S_a$ , from equation (1)), we used three anthropogenic predictors: GDP, human population size and agricultural area from the World Bank 2021 ([worldbank.org](http://worldbank.org))<sup>57</sup> to predict the monetary costs of invasive species ( $\hat{C}$ ) across their global invaded geographic range (Supplementary Fig. 3). GDP and human population size were chosen due to their well-documented relationships with economic impacts<sup>18</sup>. Similarly, agricultural area was selected as a key predictor because agriculture represents the highest overall and most prevalent sector



impacted across countries in the InvaCost database<sup>22</sup>. In notation, for the ratio-scalar model,

$$\hat{C}_{s,ci,j} = \frac{1}{n} \sum_{k=1}^n C_{s,c_k,j} \prod_{m=1}^M \left( \frac{V_{m,c_i}}{V_{m,c_k}} \right)^{y_m} \quad (2)$$

where  $C$  is the monetary cost documented in InvaCost per country;  $s$  denotes species;  $c$  denotes country;  $j$  denotes the type of cost (damage or management);  $V$  denotes each of the four predictors  $m$ ;  $c_i$  denotes country  $i$  where species  $s$  has been reported, and  $c_k$  denotes country  $k$  where species  $s$  has been reported and where a monetary cost has been recorded. We set boundaries on scalar ratios using the highest (or lowest) values in the fitted economic model, to not interpolate beyond the range of the fitted data. The model handles a null effect of the predictors and either positive or negative effects<sup>18</sup>. The model calibrates suitable areas estimates using real cost data, accounting for the proportion of areas impacted. This approach does not assume that the entire suitable areas are susceptible to monetary costs and allows deviations where spatial extent is not correlated with costs (the fitted coefficient would approach 0). In addition, our ratio-scalar model allows us to account for the socio-economic context of each country through macro-economic predictors, ensuring that our predictions remain flexible.

We fit each economic model separately for each cost type (that is, damage and management), acknowledging that different types of cost can exhibit different underlying processes or be driven by different factors. Before modelling, we excluded outlier costs as those costs exceeding US\$5 billion for damage ( $n = 3$ ) and US\$0.6 billion for management ( $n = 3$ ). We examined all possible combinations of the predictor variables (ranging from a single-variable model to all four predictor variables) and used maximum likelihood with a Gaussian error distribution in the ratio-scalar model to determine the optimal set of parameters for each model, using the optim function in R<sup>58</sup>. For mixed models, the initial model included all predictors as fixed effects, with species as a random intercept. Subsequently, the model was refitted based on a reduced set of predictors that had statistically significant effects (that is,  $P < 0.05$ ).

We calculated the Akaike's information criterion for each combination of variables to evaluate the relative economic model performance and selected the economic models (that is, mixed model and ratio-scalar) with the lowest Akaike's information criterion score. To validate the model's performance, we used leave-one-out cross-validation by excluding each row and refitting the model. Subsequently, we estimated the economic cost of invasive species that were recorded but whose costs have not been assessed by the mixed model with the predict function and using equation (2) for the ratio-scalar model. In addition, we conducted 1,000 bootstrap samples with replacement to estimate the uncertainty of each model parameter (reporting the standard deviation). This methodology offers a more robust estimation of cost by offering an average and a range of each estimated cost (Supplementary Table 1). Final model predictions were based on combined predictions from both models (that is, mixed and ratio-scalar models), weighted by the  $R$ -square of each model.

### Economic cost per unit area

To estimate the monetary cost of invasive species per spatial unit ( $\text{km}^2$ ) in a given country, we first estimated the total monetary cost of each species in each country as described in the section 'Economic cost model'. We calculated the size of each cell  $A$  ( $\text{km}^2$ ), as follows:

$$A \approx 8.3 \text{ km} \times 8.3 \text{ km} = 68.89 \text{ km}^2 \quad (3)$$

where 8.3 km is based on the raster resolution of 0.0833° in both latitude and longitude, giving an approximation of the actual area of the

cell. The cost per  $\text{km}^2$  per species and per country is the total cost of the species in the country divided by the suitable area  $S_a$ .

### Reporting summary

Further information on research design is available in the Nature Portfolio Reporting Summary linked to this article.

### Data availability

All data generated and analysed during this study are publicly available and can be accessed via GitHub at [https://github.com/IsmaSA/InvaCost\\_SDM](https://github.com/IsmaSA/InvaCost_SDM). Source data are provided with this paper.

### Code availability

All codes generated during this study are available and can be accessed via GitHub at [https://github.com/IsmaSA/InvaCost\\_SDM](https://github.com/IsmaSA/InvaCost_SDM).

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## Author contributions

I.S. and B. Leung conceived the study, led on coding the analyses and data interpretation, designed and assembled the figures, designed the methodology, wrote the original draft and revised subsequent drafts. The following authors participated in the data acquisition or provided and approved the final draft: P.C., A.P., E.T., E.M., E.A., C.B., E.B., M.B., R.N.C., A.K., M.K., R.L.M., B. Leroy, P.J.H. and F.C.

## Competing interests

The authors declare no competing interests.

## Additional information

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Software and code

Policy information about [availability of computer code](#)

|                 |                                                                                           |
|-----------------|-------------------------------------------------------------------------------------------|
| Data collection | Economic cost of invasive species from InvaCost database (DOI:10.1038/s41597-020-00586-z) |
| Data analysis   | All code and analyses have been conducted in R software v.4.3.1                           |

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Reporting on sex and gender

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## Life sciences study design

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Sample size

n/a

Data exclusions

n/a

Replication

n/a

Randomization

n/a

Blinding

n/a

## Behavioural & social sciences study design

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Study description

n/a

Research sample

n/a

Sampling strategy

n/a

Data collection

n/a

Timing

n/a

Data exclusions

n/a

Non-participation

n/a

Randomization

n/a

# Ecological, evolutionary & environmental sciences study design

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|                          |                                                                                  |
|--------------------------|----------------------------------------------------------------------------------|
| Study description        | Interpolation of monetary burden of invasive species                             |
| Research sample          | 162 species with high-realible economic cost data                                |
| Sampling strategy        | n/a                                                                              |
| Data collection          | Data is extracted from open databases (InvaCost, Global Alien First Records)     |
| Timing and spatial scale | Time period 1960-2022. Spatial scale: Global                                     |
| Data exclusions          | 3 outliers (n =2 Damage costs and n =1 Management) were excluded of the analysis |
| Reproducibility          | Dataset and R code can be found at GitHub                                        |
| Randomization            | n/a                                                                              |
| Blinding                 | n/a                                                                              |

Did the study involve field work? ☐ Yes ☒ No

## Field work, collection and transport

|                        |     |
|------------------------|-----|
| Field conditions       | n/a |
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| Access & import/export | n/a |
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| <input checked="" type="checkbox"/> | <input type="checkbox"/> Antibodies                    | <input checked="" type="checkbox"/> | <input type="checkbox"/> ChIP-seq               |
| <input checked="" type="checkbox"/> | <input type="checkbox"/> Eukaryotic cell lines         | <input checked="" type="checkbox"/> | <input type="checkbox"/> Flow cytometry         |
| <input checked="" type="checkbox"/> | <input type="checkbox"/> Palaeontology and archaeology | <input checked="" type="checkbox"/> | <input type="checkbox"/> MRI-based neuroimaging |
| <input checked="" type="checkbox"/> | <input type="checkbox"/> Animals and other organisms   |                                     |                                                 |
| <input checked="" type="checkbox"/> | <input type="checkbox"/> Clinical data                 |                                     |                                                 |
| <input checked="" type="checkbox"/> | <input type="checkbox"/> Dual use research of concern  |                                     |                                                 |
| <input checked="" type="checkbox"/> | <input type="checkbox"/> Plants                        |                                     |                                                 |

## Antibodies

|                 |     |
|-----------------|-----|
| Antibodies used | n/a |
| Validation      | n/a |

## Eukaryotic cell lines

Policy information about [cell lines and Sex and Gender in Research](#)

|                                                                      |     |
|----------------------------------------------------------------------|-----|
| Cell line source(s)                                                  | n/a |
| Authentication                                                       | n/a |
| Mycoplasma contamination                                             | n/a |
| Commonly misidentified lines<br>(See <a href="#">ICLAC</a> register) | n/a |

## Palaeontology and Archaeology

|                     |     |
|---------------------|-----|
| Specimen provenance | n/a |
| Specimen deposition | n/a |
| Dating methods      | n/a |

☐ Tick this box to confirm that the raw and calibrated dates are available in the paper or in Supplementary Information.

|                  |     |
|------------------|-----|
| Ethics oversight | n/a |
|------------------|-----|

Note that full information on the approval of the study protocol must also be provided in the manuscript.

## Animals and other research organisms

Policy information about [studies involving animals](#); [ARRIVE guidelines](#) recommended for reporting animal research, and [Sex and Gender in Research](#)

|                         |     |
|-------------------------|-----|
| Laboratory animals      | n/a |
| Wild animals            | n/a |
| Reporting on sex        | n/a |
| Field-collected samples | n/a |
| Ethics oversight        | n/a |

Note that full information on the approval of the study protocol must also be provided in the manuscript.

## Clinical data

Policy information about [clinical studies](#)

All manuscripts should comply with the ICMJE [guidelines for publication of clinical research](#) and a completed [CONSORT checklist](#) must be included with all submissions.

|                             |     |
|-----------------------------|-----|
| Clinical trial registration | n/a |
| Study protocol              | n/a |
| Data collection             | n/a |
| Outcomes                    | n/a |

## Dual use research of concern

Policy information about [dual use research of concern](#)

### Hazards

Could the accidental, deliberate or reckless misuse of agents or technologies generated in the work, or the application of information presented in the manuscript, pose a threat to:

| No                                  | Yes                                                 |
|-------------------------------------|-----------------------------------------------------|
| <input checked="" type="checkbox"/> | <input type="checkbox"/> Public health              |
| <input checked="" type="checkbox"/> | <input type="checkbox"/> National security          |
| <input checked="" type="checkbox"/> | <input type="checkbox"/> Crops and/or livestock     |
| <input checked="" type="checkbox"/> | <input type="checkbox"/> Ecosystems                 |
| <input checked="" type="checkbox"/> | <input type="checkbox"/> Any other significant area |

## Experiments of concern

Does the work involve any of these experiments of concern:

| No                                  | Yes                                                                                                  |
|-------------------------------------|------------------------------------------------------------------------------------------------------|
| <input checked="" type="checkbox"/> | <input type="checkbox"/> Demonstrate how to render a vaccine ineffective                             |
| <input checked="" type="checkbox"/> | <input type="checkbox"/> Confer resistance to therapeutically useful antibiotics or antiviral agents |
| <input checked="" type="checkbox"/> | <input type="checkbox"/> Enhance the virulence of a pathogen or render a nonpathogen virulent        |
| <input checked="" type="checkbox"/> | <input type="checkbox"/> Increase transmissibility of a pathogen                                     |
| <input checked="" type="checkbox"/> | <input type="checkbox"/> Alter the host range of a pathogen                                          |
| <input checked="" type="checkbox"/> | <input type="checkbox"/> Enable evasion of diagnostic/detection modalities                           |
| <input checked="" type="checkbox"/> | <input type="checkbox"/> Enable the weaponization of a biological agent or toxin                     |
| <input checked="" type="checkbox"/> | <input type="checkbox"/> Any other potentially harmful combination of experiments and agents         |

## Plants

|                       |     |
|-----------------------|-----|
| Seed stocks           | n/a |
| Novel plant genotypes | n/a |
| Authentication        | n/a |

## ChIP-seq

### Data deposition

- ☒ Confirm that both raw and final processed data have been deposited in a public database such as [GEO](#).
- ☒ Confirm that you have deposited or provided access to graph files (e.g. BED files) for the called peaks.

|                                                                    |     |
|--------------------------------------------------------------------|-----|
| Data access links<br><i>May remain private before publication.</i> | n/a |
| Files in database submission                                       | n/a |
| Genome browser session<br>(e.g. <a href="#">UCSC</a> )             | n/a |

### Methodology

|                         |     |
|-------------------------|-----|
| Replicates              | n/a |
| Sequencing depth        | n/a |
| Antibodies              | n/a |
| Peak calling parameters | n/a |
| Data quality            | n/a |



Flow Cytometry

Plots

Confirm that:

- ☐ The axis labels state the marker and fluorochrome used (e.g. CD4-FITC).
- ☐ The axis scales are clearly visible. Include numbers along axes only for bottom left plot of group (a 'group' is an analysis of identical markers).
- ☐ All plots are contour plots with outliers or pseudocolor plots.
- ☐ A numerical value for number of cells or percentage (with statistics) is provided.

Methodology

Sample preparationn/a

Instrumentn/a

Softwaren/a

Cell population abundancen/a

Gating strategyn/a

☐ Tick this box to confirm that a figure exemplifying the gating strategy is provided in the Supplementary Information.

Magnetic resonance imaging

Experimental design

Design typen/a

Design specificationsn/a

Behavioral performance measuresn/a

Imaging type(s)n/a

Field strengthn/a

Sequence & imaging parametersn/a

Area of acquisitionn/a

Diffusion MRI

☐ Used

☐ Not used

Preprocessing

Preprocessing softwaren/a

Normalizationn/a

Normalization templaten/a

Noise and artifact removaln/a

Volume censoringn/a

Statistical modeling & inference

Model type and settingsn/a

Effect(s) testedn/a

Specify type of analysis: ☐ Whole brain ☐ ROI-based ☐ Both

Statistic type for inference 

n/a

(See [Eklund et al. 2016](#))

Correction 

n/a

Models & analysis

- n/a
- Involvement in the study
- ☒ ☐ Functional and/or effective connectivity
- ☒ ☐ Graph analysis
- ☒ ☐ Multivariate modeling or predictive analysis

Functional and/or effective connectivity 

n/a

Graph analysis 

n/a

Multivariate modeling and predictive analysis 

n/a

