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Biological invasions on Indigenous peoples' lands

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Biological invasions are a growing challenge in a highly interconnected and globalized world, leading to the loss of native biodiversity. Indigenous peoples' lands (IPLs) play a vital role in biodiversity conservation through activities such as land stewardship and management practices. Similar to protected areas, they are also often remote, with fewer connections to international trade networks. The extent to which IPLs are threatened by the spread of invasive species is still unknown. Here we provide a global study detailing the distribution and drivers of alien species on IPL. On average, IPLs host 30% (in absolute numbers: 11 ± 3.5) fewer alien species relative to other lands, after controlling for sampling intensities. Alien species numbers remained consistently lower on IPLs even after accounting for potentially confounding factors such as differences in accessibility and ecological integrity. The difference may result from land management practices of Indigenous peoples. In the relatively small number of cases where IPLs host disproportionately higher numbers of alien species than other lands, the most likely reason is high alien species propagule pressure arising from proximity to large urban areas. Overall, our results highlight the importance of IPLs in protecting nature in the face of increasing biological invasions.

Indigenous peoples play vital roles in the protection and long-term persistence of biological diversity[1,2] through land stewardship, management practices and applications of knowledge that help conserve biodiversity worldwide[3]. For example, biodiversity loss is lower on Indigenous peoples' lands (IPLs) (defined as terrestrial lands managed or owned by Indigenous peoples) than on other lands[4]. In addition, the sustainable use of wild species is central to the identity and existence of many Indigenous peoples[5]. Both the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services[4,5] and the Kunming–Montreal Global Biodiversity Framework of the Convention on Biological Diversity emphasize the importance of Indigenous peoples and their knowledge and practices to enhance global biodiversity conservation and ecosystem management.

At present, IPLs cover at least 28% of Earth's terrestrial surface in at least 87 countries worldwide, of which a major proportion is still free from most transformative human impacts[6]. In addition, IPLs have more areas (67%) considered as natural (Human Footprint score <4)[7] compared with other lands (44%), and they comprise large portions (66%) of the most remote and least inhabited regions globally[6]. Recent studies revealed that at least 36% of intact forests are within IPLs (areas that are crucial carbon sinks)[8]. Further, the rate of loss of intact forests has been considerably lower on IPLs relative to other

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lands. Ref. 9 found that 2,695 species of mammals (60% of assessed mammals) had ≥10% of their ranges on IPLs, and 1,009 species (23%) had >50% of their ranges on these lands (47% and 26%, respectively, for threatened species).

Many IPLs are under pressure from anthropogenic threats[10] commonly generated beyond their borders, including biological invasions, a main driver of biodiversity loss[4,11]. Biological invasions are introductions by humans of non-native species outside their native ranges. While such introductions have occurred for thousands of years, their frequency has sharply increased in recent centuries[12]. Colonialism was the major driver of biological invasions before 1900, particularly by European empires[13]. In the process of colonization of Indigenous peoples and Indigenous places, colonizers both intentionally and inadvertently spread an uncountable number of species far beyond their natural ranges[14]. Acclimatization societies and botanical gardens were founded to support the cultivation and introduction of new species[15]. The activities of colonial empires strongly influenced the distribution of alien species, the imprint of which is still visible today in the current global distribution of alien plants[15]. In more recent decades, the ongoing globalization of trade and transport has drastically accelerated the spread of alien species to new environments[16]. Consequently, alien species are now found in all countries and nearly all ecosystems worldwide, including remote places lacking strong ties to global trade networks[17]. The spread of alien species by humans has considerably changed the distribution of biota worldwide[18], with some alien species negatively impacting human well-being on IPLs[11,19,20].

Like many protected areas, IPLs are often remote and have fewer connections to international trade networks, potentially slowing alien species introductions[21]. Protected areas have been shown to be less affected by biological invasions due to greater ecological intactness and fewer introduction events[22], which is also probably the case for IPLs. For example, remote IPLs in Australia often have fewer alien species than lands near developed areas[23]. However, remote areas can also be prone to biological invasions due to the vulnerability of their unique ecological communities[24]. Whether IPLs generally host lower numbers of alien species compared with other lands is unknown. If they do host lower numbers, it is uncertain whether this is because IPLs are more remote and ecologically intact, benefit from different land management practices or a combination of these factors.

In this study, we quantified the level of biological invasions (the number of alien species present) on IPLs and other lands at the global scale to test the hypothesis that IPLs harbour lower numbers of alien species than other lands. In addition, we investigated the factors that drive potential differences and asked the following research questions. (1) How are alien species distributed across IPLs globally? (2) Do IPLs have fewer alien species than other lands? (3) Can the number of alien species on IPLs be explained by accessibility and habitat characteristics alone, or does IPL consistently support fewer alien species even after accounting for these drivers? (4) Where are IPLs with disproportionally high and low alien species numbers?

To answer these questions, we distinguished between IPLs and 'other lands'. In doing so, we follow ref. 6, who distinguished IPLs, defined as "terrestrial lands managed or owned by Indigenous peoples", from lands not mapped as IPLs in publicly available documentation. We acknowledge that such a dichotomy between IPLs and other lands simplifies reality, both because Indigenous peoples were expelled from many lands classified here as other lands that they often aspire to reclaim, and because Indigenous peoples continue to face barriers influencing management of lands mapped as IPL. Unfortunately, we were able to consider in our analysis only lands that have been mapped as IPL because information on Indigenous peoples' engagement with lands outside these areas is not available at a large geographic scale. The definition of IPL excludes marine waters and lands managed or owned exclusively by local or traditional communities that do not meet the definition of Indigenous[6].

Table 1 | Mean values of characteristics of grid cells on IPL and other land

	IPL	Other land
Mean and standard deviation of alien species numbers (after controlling for sampling effort)	27±2.6	39±3.8
Mean species abundance index (MSA)	0.60	0.48
Number of GBIF records	2.367	13.494
Percentage agriculture (%)	14	28
Percentage forest (%)	37	35
Percentage settlements (%)	0.13	0.87
Night-time light index	0.55	2.65
Road density (km)	96	259
Travel time (min)	1.072	447

Mean values of the number of alien species were calculated on the basis of grid cells with similar sampling efforts on IPLs and other lands in a resampling design (see Methods for further details).

Results

Integrating the spatial layers of IPLs and alien species occurrences revealed 128,515 records of 6,192 alien species on IPLs worldwide (Supplementary Fig. 1). We found a high correlation between the total number of alien species in a country with the number of alien species on IPLs within the same country (t test: $t = 12.8$, d.f. = 77, $P < 0.001$). Thus, countries with the highest numbers of alien species, such as Australia (Supplementary Fig. 1), also tended to have high numbers of alien species on IPL. The comparison between IPLs and other lands based on equal-area grid cells revealed that, on average, IPLs had less than one-third (30%) of the number of alien species found on other lands after controlling for differences in sampling effort (Table 1). In absolute terms, this meant that 11 ± 3.5 fewer alien species were found on IPLs after accounting for sampling. Several metrics of human disturbance on IPLs clearly deviated from other lands: IPLs had higher forest cover, less cultivated land and fewer settlements (Table 1). The night-time light index, a proxy for human population density and wealth (see Methods), was 5 times lower on IPLs, road densities were 2.7 times lower and travel times to cities were 2.4 times longer, indicating that IPLs were less accessible. However, IPLs had also been under-sampled in terms of available Global Biodiversity Information Facility (GBIF) records, with five times fewer GBIF records than were available for other land areas.

To test our hypothesis that the number of alien species is lower on IPLs compared with other lands, we applied a generalized linear mixed model (GLMM), thereby taking covariates and potential confounding factors such as data availability into account. As predicted by the model and shown by original data, the number of alien species on IPLs was particularly high in Australia, northern Europe and North America (Fig. 1a and Supplementary Fig. 1); these regions also represented areas with consistently high numbers of alien species on other lands (Fig. 1b and Supplementary Fig. 1). The GLMM analysis revealed that all predictor variables significantly influenced the number of alien species (Fig. 2a). Sampling intensity, as estimated by the number of GBIF records per grid cell, had the largest effect size. Accessibility, expressed by travel time to the nearest cities, was the second most important predictor, followed by human population density and wealth. Thus, more-accessible sites with larger and wealthier human populations in the vicinity generally had higher numbers of recorded alien species than sites lower on each scale. Furthermore, the number of alien species was positively correlated with the proportion of land under cropping. Most important, even after accounting for the variation in sampling, human infrastructure, population size and land cover, the numbers of alien species remained significantly lower on IPLs than on other lands of a similar type (Fig. 2a). The GLMM had a high predictive

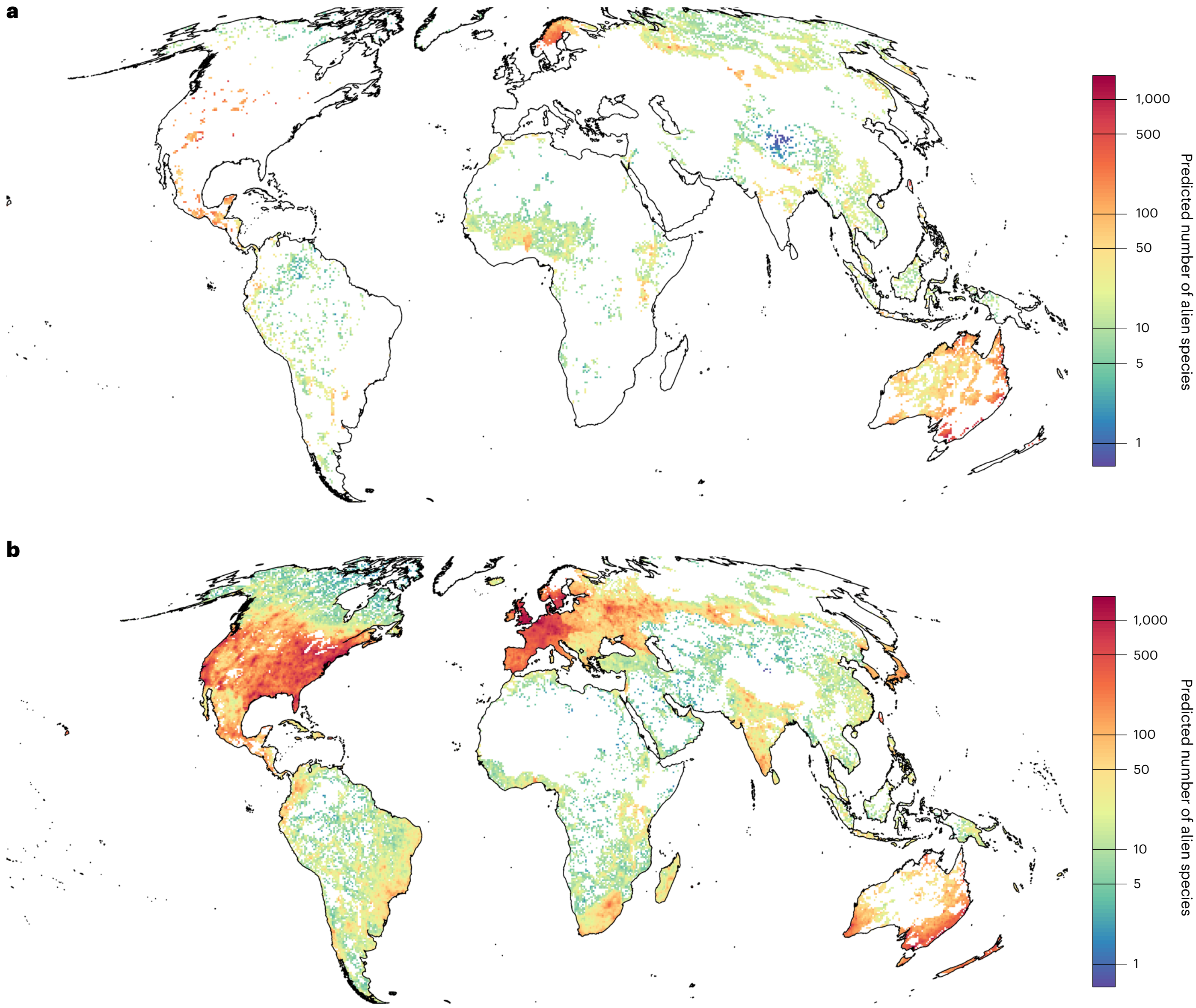


Fig. 1 | Predicted numbers of alien species per equal-area grid cell (50 km × 50 km) of IPLs and other lands. a, IPLs. **b**, Other lands. The numbers of alien species were predicted by a GLMM and shown separately for each land type. Individual cells of high alien species richness (red) can be found all over the world, particularly in Australia, northern Europe and North America. White areas denote regions without information of alien species numbers.

power, indicated by a conditional R^2 of 0.87. This was due partly to the effect of the region, which was considered as a random effect in the GLMM, thereby reflecting the variation in data availability and alien species distributions across regions. A sensitivity analysis testing for influences of nonlinearity, spatial autocorrelation or using an alternative regression approach revealed that the estimated coefficients of this analysis remain robust (Supplementary Figs. 2 and 3). A map of residuals of the GLMM (anomalies between observed and predicted values) illustrated areas overestimated by the model, particularly in the eastern United States and central Europe (Supplementary Fig. 4). Areas where the model underestimated alien species numbers were prevalent in central North America and eastern Europe. For most other regions, the modelled and reported numbers of alien species were similar.

Across major taxonomic groups, the GLMM provides similar results (Fig. 2b–f): in all cases, except fish, the number of available GBIF records (that is, sampling) had the largest effect on species numbers, followed by travel time (that is, accessibility). For fish, the most important predictor variable was the night-time light index, which may indicate that fish are often released for recreational fishing and as a food source near inhabited areas. In general, the influence of land cover on alien species numbers was low. Except for birds, the numbers of alien species were consistently lower on IPLs than on other lands across all taxonomic groups, with the strongest effects for arthropods, although the effect was not always significant. For mobile species, such as birds and mammals, the effect was less pronounced than for more-stationary species, such as plants and fish, the latter being restricted by the availability of connections between catchments. This pattern remained similar across continents: GBIF records, night-time light index and travel time remained important predictor variables, while the effect of IPL differed among continents (Supplementary Fig. 5). The effect of IPL was positive for Africa and North America and lower for all other continents.

For a more direct comparison of alien species numbers between land types, a resampling analysis was conducted, thereby comparing species numbers of grid cells of similar characteristics from IPLs and other lands. By randomly selecting grid cells, this analysis also

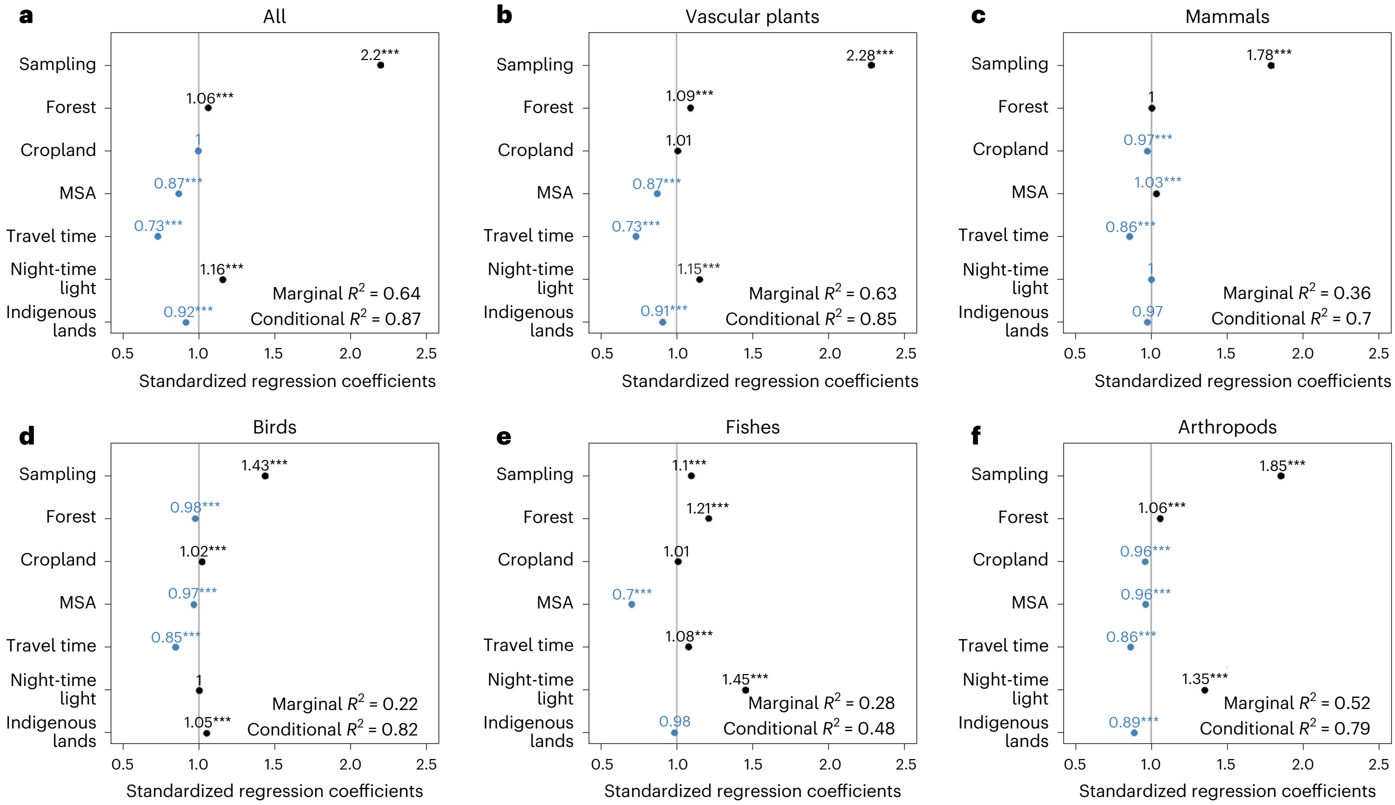


Fig. 2 | Influences of predictor variables on alien species numbers on ILPs by taxonomic group. a–f, Standardized regression coefficients for individual predictor variables obtained from GLMMs for all alien species combined (**a**), vascular plants (**b**), mammals (**c**), birds (**d**), fish (**e**) and arthropods (**f**). Predicted increases are shown in black and reductions in blue. Significance levels are indicated by asterisks (*$P < 0.05$; **$P < 0.01$; ***$P < 0.001$). Standard errors of the estimates were very small and not visible at this scale. Note that results for the interaction terms are not shown. MSA, mean species abundance.

accounted for uneven numbers of grid cells for different land types and spatial autocorrelation. This analysis revealed that alien species numbers differed by 70% when sampling randomly from both land types (Fig. 3). The difference decreased when, for example, comparing grid cells only from the same region (the average number of alien species on IPLs was 62% lower than on other lands in the same region). The number of alien species was 64% lower when comparing grid cells of similar land-cover distributions, 30% lower after taking sampling intensities into account and 13% lower when all of these criteria are considered together (Fig. 3). Similar results were obtained for other variables and combinations. For all cases shown in Fig. 3, the number of alien species was significantly lower (t test; $P < 0.001$) on IPLs than on other lands.

Alien species were unevenly distributed across IPLs both within and across countries with some IPLs appearing to have comparatively high alien species loads (Supplementary Fig. 6). Most of the IPL areas with disproportionally high numbers were located in Australia (37% of all grid cells with high alien species numbers; mostly eastern Australia), followed by Russia (23%), China (13%), the United States (9%) and Argentina (7%). These grid cells were characterized by considerably higher road densities, higher night-time light intensities, higher accessibility and more settlements (compare Table 1 and Supplementary Table 1). By contrast, disproportionately low alien species numbers were found mostly in grid cells located in Australia (61%, mostly western Australia), the United States (20%), India (12%), South Africa (4%) and Finland (1%). The characteristics of these areas were similar to those found for average IPL grid cells, except that they had a lower percentage of settlements and higher accessibility scores than did average IPL grid cells (compare Table 1 and Supplementary Table 1).

Case study Australia

Australia has been identified in our analysis as a country with both disproportionally high and disproportionately low alien species numbers on IPLs. This supports our finding that high numbers of alien species result from an interplay of regional factors rather than high numbers in a country per se. The IPLs close to large urban areas or with main roads nearby, such as those in the intensively developed areas of eastern Australia, are also likely to share high alien species numbers (Fig. 4). These lands are often developed for agriculture with a well-developed infrastructure that facilitates biological invasions. Such lands are also areas where opportunities for land management by Indigenous peoples have been most compromised and where they have the fewest opportunities to practice active land management[25]. By contrast, in remote IPLs such as those in central and northwestern Australia, alien species numbers are generally low, with the greatest diversity of alien species occurring mostly along roads (Fig. 4). However, remote areas in Australia are not free of alien species, and the lack of diversity does not mean that the species that can establish in often challenging Australian environments do not then thrive. Australia has the greatest diversity of naturalized alien megafaunas of any country[26], and the pastoral industry has promoted the spread of alien grasses and legumes of which a small number of species are coming to dominate large areas of remote tropical and arid Australia[27,28].

Indigenous peoples are at the forefront of alien species control in remote Australia, with the substantial resources invested into Indigenous ranger groups for feral animal eradication and exotic weed control[29] being seen as having major benefits for local economic development[30]. However, Indigenous perspectives on alien species are culturally complex, nuanced, diverse and dynamic. Some species brought in by Asian traders centuries before Europeans colonized Australia

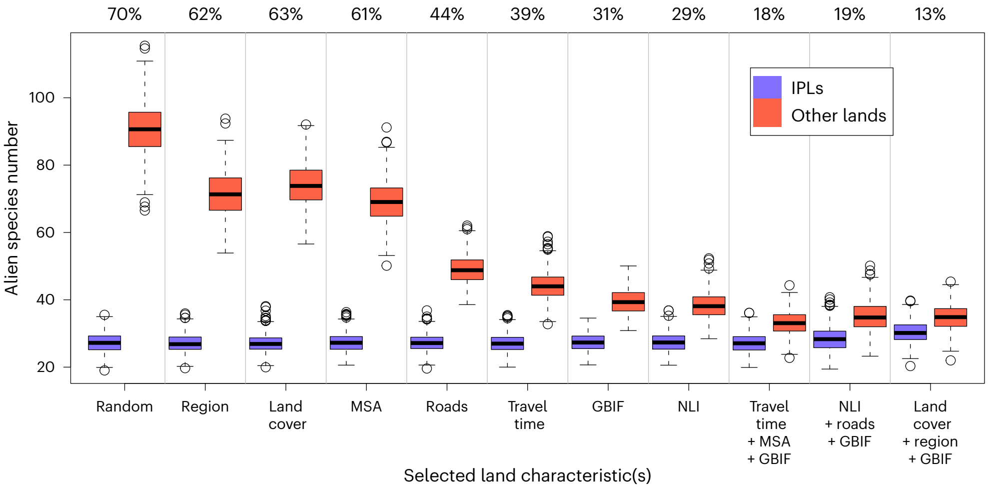
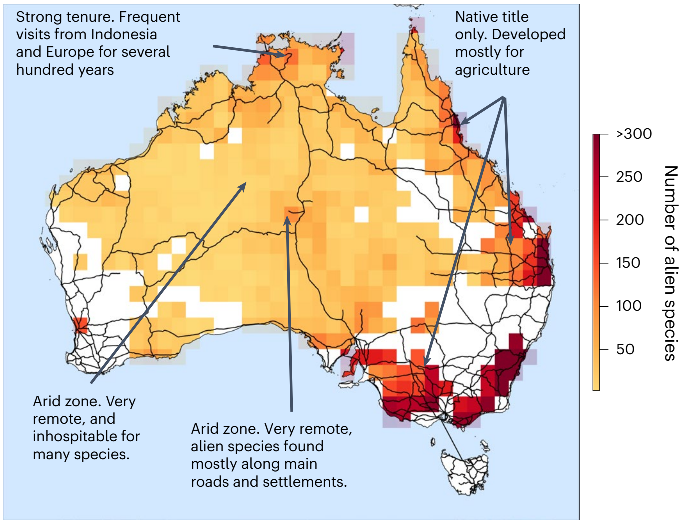


Fig. 3 | Comparison of mean alien species numbers on IPLs and other lands. The box plots were generated from 500 mean values, each calculated from 500 randomly selected grid cells per land type (IPLs or other lands). The numbers of alien species in both were selected either purely randomly (Random) or from those grid cells from the same region (Region), with similar land-cover distributions, mean species abundance (MSA), road densities, travel times to nearest cities, sampling intensities (GBIF) and night-time light index (NLI). See Methods for a description of the selection process. In all cases, alien species numbers were significantly lower on IPLs according to the results of *t* tests. The differences between mean alien species numbers on both land types are indicated by percentages at the top of the figure. In all cases, differences between land types were statistically significant (two-sided *t* test; $P < 0.001$). Box plots show the median (thick line), the first and third quartiles (lower and upper box edges) and 1.5 times the interquartile range as whiskers. Outliers are indicated by circles.


Strong tenure. Frequent visits from Indonesia and Europe for several hundred years

Native title only. Developed mostly for agriculture

Arid zone. Very remote, and inhospitable for many species.

Arid zone. Very remote, alien species found mostly along main roads and settlements.

Fig. 4 | Alien species numbers on IPLs in Australia. Numbers of alien species on IPLs per grid cell are shown in colour. Roads are indicated by black lines. White areas indicate grid cells without recognized IPL at the time of the study. 'Native title' refers to land ownership by Indigenous peoples.

have developed deep cultural roots[31]. More-recently introduced species have also been incorporated into Indigenous cosmologies and become important components of local livelihoods[32,33]. Collaborative research with Indigenous traditional owners emphasizes approaches to engagement with newly arrived species, even aggressive weeds, which are consistent with cultural responsibilities and traditional knowledge of environmental processes[34–37].

Discussion

Indigenous peoples and their lands are vital for nature conservation[3] because ecosystems on IPLs are, on average, more intact, with lower biodiversity loss[6,8]. Several studies reported occurrences and impacts of alien species on IPLs, but it was unclear to what degree IPLs are affected by biological invasions, a major driver of global biodiversity loss. Our study provides a global analysis about the distribution and drivers of alien species on IPLs. While data on alien species impacts on IPLs remain incomplete, we showed that there are considerably fewer (30%; Fig. 3 and Table 1) alien species on IPLs than on other lands after controlling for variation in data availability. The lower numbers of alien species on IPLs are due partly to lower levels of disturbance, which reduces vulnerability to biological invasions[38], and greater inaccessibility, which hinders the introduction and spread of new alien species[21] (Fig. 2). However, even after controlling for major drivers such as ecosystem disturbance, human population size, wealth and accessibility, IPLs still have significantly fewer alien species (Fig. 2a). These results are robust and independent of the analytical methodology applied (Supplementary Figs. 2 and 3). Our study indicates that IPLs are more resistant to biological invasions, which may result from different land management. Indigenous peoples often apply land management practices that are more sustainable than most modern methods[3], which in turn can affect the prevalence of biological invasions[39]. More-sustainable land management practices on IPLs may have resulted in fewer disturbances and reduced the likelihood of new alien species establishment. Furthermore, Indigenous peoples often consider the risks associated with biological invasions[40] and actively protect their lands from invasive alien species[33]. Thus, in addition to remoteness and intactness, land management practices and stewardship may explain the consistently lower number of alien species on IPLs.

The effect of IPLs on the number of alien species varied by taxonomic group and continent. The strongest effects were found for arthropods and vascular plants, which have often been introduced unintentionally, while the effects were weaker for vertebrates, which are more likely to have been introduced intentionally. The strong effect found in Europe might be a result of the location of IPLs in northern Europe, which is generally less affected by biological invasions than, for example, central Europe, which hosts exceptionally high numbers of alien species, but where no IPLs are recognized (Fig. 1). For Africa, numbers of alien species were significantly higher on IPLs. As all other factors remained fairly similar across continents, an explanation for differences among these regions may be that data availability is biased towards urban areas and well-sampled regions, such as protected areas.

Indeed, data are lacking for large areas of Africa, with most records unevenly distributed for a few countries and coastal areas[41].

Interestingly, IPLs with disproportionately high and low numbers of alien species sometimes occur within the same country. Hence, although high alien species numbers in a country correlate with high numbers on IPLs, the underlying reasons for having high or low alien species numbers are not necessarily country specific. As shown in the Australian case study, the number of alien species is highly influenced by proximity to urban areas and land-use history. Moreover, IPLs are not free of industry and transport hubs, which increase the probability of new alien species introductions. Consequently, some IPLs under particularly high anthropogenic pressure can host disproportionately higher numbers of alien species than regions with similar characteristics on other lands.

Conducting this analysis inevitably required assumptions that simplified reality. One assumption is the separation of lands into two classes, IPLs and other lands. The category other lands contains lands that are not mapped as being managed by Indigenous peoples. In many cases, Indigenous peoples have been expelled from their lands, and policies have been put in place that prevent them from exercising their own biocultural land management and conservation practices[42]. Thus, the category other lands also contains lands originally or still inhabited by Indigenous peoples that are often not fully under the control of Indigenous peoples and have often been managed in non-traditional ways. The reverse can also be true. While we assume that Indigenous peoples have an important influence on land management on most lands identified as IPL, there are many places where their influence is being challenged even when they have legal rights; for example, in Nicaragua, the agricultural frontier is being pushed into IPLs despite land title being granted to Indigenous peoples[43,44]. Using the number of alien species is also a relatively crude proxy for alien species' impact. However, to move from the simplistic assumptions we have made here to any more precise assessment of the influence of Indigenous peoples on alien species occurring on their lands would require a level of detail that is rarely available at a local scale and is not available globally.

We acknowledge the diverse views about biological invasions. While biological invasions are generally considered to be a threat to nature and human livelihoods[4], a dichotomy between native and alien species is not necessarily consistent with all Indigenous peoples' conceptions of nature[42]. There are several examples where alien species have improved local livelihoods and well-being[45–48], and a single species can have multiple and contrasting relationships with Indigenous peoples[49]. For example, feral animals such as water buffalo (*Bubalus bubalis*) in northern Australia have been adopted as a totem animal by some Indigenous people[50] and have long been a source of protein[51] and income[52] while, at the same time, being considered a major threat to the cultural and ecological integrity of Indigenous-owned land[53] where they are subject to major control programs[54]. As another example, feral pigs (*Sus scrofa*) negatively affect Hawaiian ecosystems but are important to Native Hawaiians both culturally and as a source of food[55,56]. Overall, however, alien species are considered to have more negative than positive impacts on natural environments[11], a risk acknowledged by Indigenous peoples[57,58].

In conclusion, our study contributes to the increasing body of literature highlighting the role of Indigenous peoples in protecting nature and providing refuge for native species that are under threat globally[1,2]. Our study provides a basis for exploring the drivers of biological invasions on IPLs at a large geographic scale. It identifies areas that are particularly affected and vulnerable to biological invasions and that require more efforts and support to halt the spread of alien species and to protect biodiversity. A better understanding of drivers and influences of land management practices on biological invasions would be obtained by comparing IPLs with different levels of invasions and different practices. This, however, requires more information about land management practices at the local scale, which is currently lacking. As emphasized throughout the Kunming–Montreal Global Biodiversity Framework, the integration of traditional knowledge and practices by Indigenous peoples into biodiversity studies needs to be improved. Previous biodiversity assessments have revealed that information is particularly scarce for IPL[4,5,11] and that a lack of knowledge has prevented a comprehensive understanding of its importance. In addition to the essential and often incomplete data of the distribution of species, information about land management practices applied by IPLs across regions would be invaluable to further explore the effects of land use on biological invasions. Filling these gaps requires engaging with, learning from and co-developing knowledge with Indigenous peoples on the basis of mutual benefits. Ultimately recognizing the rights and agency of Indigenous peoples to manage their lands, including invasive alien species, will be essential if the 2050 vision for biodiversity, 'living in harmony with nature', is to be fulfilled.

Methods

Data

We used the most comprehensive global map of IPLs currently available[6]. This map provides information about terrestrial lands that are managed or owned by Indigenous peoples. Land managed by local and traditional communities but not people who do not currently identify as Indigenous was included in other lands as no spatial layer currently exists for such land. In total, 37.9 million km^2 of IPLs have been identified in 87 countries or administrative entities worldwide.

Alien species were here defined as species introduced through human agency to regions outside their native range where they established new populations. The analysis was based on a recently established dataset of alien species distributions, which contains point-wise occurrence records of alien species worldwide[59]. This dataset was generated by sequentially applying two recently published workflows. The first workflow[60] was applied to standardize and integrate seven major global databases of lists of alien species for countries and islands, creating a cross-taxonomic collection of regional alien species[61]. The coarse spatial resolution of this dataset is a limitation as it impedes an analysis on a finer geographical scale such as most IPLs. Thus, a second workflow[59] was used to downscale the regional information on the basis of species occurrences provided by the GBIF and the Ocean Biodiversity Information System. The downscaling was done by using available checklists of alien species on a regional scale obtained from the first workflow to identify occurrence records of alien species. Through this process, a final database of 35,666,064 coordinate-based occurrence records of alien species populations globally was generated covering 17,424 alien taxa[62]. Most available records were for vascular plants (61%), followed by birds (29%), mammals (3%), fishes (3%) and arthropods (1%). Geographically, most species occurrence data were from Europe (44%), followed by North America (33%), Australasia (14%), Temperate Asia (4%), Tropical Asia (2%), Africa (2%), South America (1%) and the Pacific Islands (0.2%).

To account for potential confounding factors influencing alien species numbers in the analysis, we considered the following additional variables (links and references in Supplementary Table 2).

(1) Habitat structure: this variable provides a general description of the habitat structure and was measured as the proportion of forest, cropland and settlement cover per grid cell.

(2) Ecological intactness: the number of alien species is usually higher in degraded landscapes with reduced densities of native species. As a measure of ecological intactness, we used the mean species abundance index (MSA). The MSA represents a simulated estimate of the actual abundance of species at a site relative to the number of individuals expected in an intact ecosystem[63]. Thus, a higher MSA score indicates a more intact ecological community.

(3) Human population density and wealth: human population density and wealth measured as, for example, gross domestic product, have been found to be important correlates of alien species numbers[21]. As gross domestic product is measured only at the regional or national scale, while our study was conducted for individual grid cells, we used the night-time light index[64]. The night-time light index is based on light emissions during the night and could be generated from satellite images globally. The night-time light index has been shown to represent a reliable proxy for regional prosperity[64] and was thus used here as a measure for human population density and wealth.
(4) Accessibility: many alien species have been introduced through human transportation systems, and thus accessibility of sites by humans facilitates biological invasions[65]. As a proxy for accessibility, we used travel times to nearest cities, which integrated sizes of human infrastructure, such as roads, railways and waterways, and urban areas into a single measure for each grid cell globally[66].
(5) Disturbance: the availability of roads has been found to be a good proxy for anthropogenic disturbance, particularly in remote places, as the disturbance of native ecological communities facilitates the establishment of alien species[67]. Road density as a proxy for disturbance was therefore considered as an additional predictor variable.
(6) Sampling intensity: the intensity of sampling affects the number of recorded species, and intensity varied across regions. We considered the number of records provided by GBIF as a proxy to account for spatial variation in recording intensity.
(7) Biomes: to test for variation between biomes, we included the terrestrial ecoregions of the world[68].
(8) Regions: the number of alien species varied distinctly among countries due to, for example, different capacities to manage alien species. We therefore included administrative regions in the analysis to account for variation among countries. Regions refer mostly to countries, while in cases where sub-national units differ distinctly from the mainland country, these geographic units were considered separately. This applies to many islands, such as Galapagos or La Réunion, and to regions in biogeographically distinct areas, such as Alaska distinguished from the contiguous United States.

All datasets were harmonized and transformed to the equal-area projection Mollweide with a resolution of 50 km × 50 km to avoid the influences of a varying size of grid cells.

Data analyses

To test our hypothesis that fewer alien species are found on IPLs, we conducted a regression analysis using GLMM. This analysis allowed us to test explicitly for differences in alien species numbers on IPLs and other lands while accounting for covariates and possible confounding factors. We applied GLMM as implemented in the package glmmTMB[69] of the statistical software R[70]. The number of alien species per grid cell was used as a response variable. As the response variable represents count data and the model was over-dispersed, we selected a negative binomial distribution. Different combinations of predictor variables (fixed effects) were tested and compared using the Akaike information criterion (AIC). A model was considered prior if the difference in AIC value was >10, which represents a conservative interpretation of AIC[71]. As predictor variables, we used the variables listed in Supplementary Table 2. The number of GBIF records, night-time light index, road density and travel times to the nearest city were log-transformed. All continuous predictor variables were normalized to a mean value of zero and a standard deviation of one to allow a direct comparison of effect sizes. Region was included as a random effect to account for inter-regional variation in data availability. All continuous predictor variables were tested for multicollinearity, which revealed strong correlations ($r >= 0.8$) between road density and travel time as well as proportion of urban areas and night-time light index (Supplementary Fig. 7). We therefore removed the variables urban areas and road density. For the combinations of night-time light index with travel time and travel time with MSA, interaction terms were included in the GLMM to account for detected high correlation of $0.8 > r > 0.7$. To allow a comparison of effect sizes of predictor variables, standardized estimates of regression coefficients were calculated using the R package sjPlot. To distinguish between the influences of the fixed effects and the random effect in the GLMM, the marginal and conditional coefficients of determination (R^2) were calculated using the method by ref. 72 implemented in the R package performance.

To test the robustness of the regression results, a sensitivity analysis was conducted. First, relationships between predictor and response variables might be nonlinear. We therefore applied a generalized additive model using the R package mgcv with the same combination of predictor variables as in the GLMM but now with smoothing terms to allow for nonlinearity. Second, to test for potential effects of spatial autocorrelation on the estimation of regression coefficients, again a generalized additive model was applied with the same combination of predictor variables as used in the GLM (now without smoothing terms) plus a tensor product of longitude and latitude of each grid cell. In this way, the regression coefficients were calculated by explicitly taking potential spatial patterns of the dynamics into account. Third, the total number of grid cells of IPLs was lower than those of other lands. We therefore re-ran the model with a random selection of the same number of grid cells from both lands. Finally, incorporating additional predictor variables such as climatic variables to account for differences associated with broad climatic regimes such as zonobiomes (deserts versus tropical forests) or protected areas did not change the results and did not improve the predictability of the model.

To further explore the influences of individual variables on the number of alien species on land types, we applied a resampling approach, which accounts for the variation in the availability of records on IPLs and other lands. By randomly selecting sites of similar characteristics, this approach allows a fair comparison of alien species numbers, thereby taking the biases inherent in the data such as uneven spatial distributions and different numbers of records into account. In addition, it allows a direct visual representation of the differences and therefore complements the regression analysis. The resampling was done by randomly selecting 500 pairs of grid cells from IPLs and from other lands and comparing the respective alien species numbers. The grid cells were selected either purely randomly or by selecting grid cells of similar land characteristics using the variables listed in Supplementary Table 2. The latter was done by first randomly depicting a grid cell of IPL and subsequently selecting one grid cell of other lands from a pool of cells with similar characteristics as the focal IPL grid cell. This was repeated 500 times to obtain 500 pairs of grid cells with similar characteristics. The resampling procedure was applied for each variable either in isolation or in various combinations. Only combinations of maximal three land characteristics could be run because the number of grid cells available for comparison quickly dropped with the number of simultaneously considered land characteristics.

The similarity of grid cells was determined according to the respective variable. For geographic units such as biomes or regions, only grid cells from the same geographic unit were selected. For continuous variables such as disturbance, accessibility, ecological intactness, human population density and wealth, night-time light index and sampling intensity, a deviation of 10% was considered. For example, to compare grid cells with a similar number of records, first a grid cell on IPL was randomly selected and the sampling intensity determined. Suppose that it has a value of 1,000 GBIF records, then grid cells on other lands within the range of 900 to 1,100 (10% deviation) were considered to form the pool of grid cells, from which sites were randomly drawn. The similarity of land-cover distributions was determined by calculating the Euclidean distance of the proportional cover of forests, arable lands and settlements, and only those grid cells with Euclidean distances below 17.3 were selected, which corresponds to 10% of maximal variation.

To determine hot and cold spots of alien species numbers by taking the land type characteristics into account, the resampling approach was refined in the following way. First, a grid cell on IPL was randomly selected. Then, grid cells outside IPL but within the same region and with similar sampling intensity and land-cover distribution were identified. The similarities of land-cover distribution and sampling intensity were calculated as described in the preceding. Once grid cells with characteristics similar to the randomly selected grid cell on IPL were identified, the quantiles of the number of alien species in these cells were determined. Finally, the randomly selected grid cell on IPL was classified as having a disproportionately large or small number of alien species if it fell above the 95% or below the 5% quantile, respectively.

Reporting summary

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

Data availability

Records of alien species occurrences are freely available online via Zenodo (https://doi.org/10.5281/zenodo.6458083) (ref. 62) as is the workflow to produce such data (https://doi.org/10.5281/zenodo.5841930) (ref. 73). Data of predictor variables other than IPL are freely available online under the addresses provided in Supplementary Table 2. The map of IPLs can be provided by the author S.T.G. on reasonable request (email: stephen.garnett@cdu.edu.au).

Code availability

The R code to run the statistical analysis (Figs. 1 and 2) and the randomized comparison (Fig. 3) is available via figshare at https://doi.org/10.6084/m9.figshare.22303408 (ref. 74).

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Author contributions

H. Seebens, L.A.M. and A.N. conceived the study. H. Seebens conducted the analyses with support by J.A.K. and A.N. H. Seebens and S.T.G. wrote the case study for Australia. H. Seebens, A.N., F.E., S.T.G., J.A.K., Z.M., H. Saeedi and L.A.M. commented on the study design and contributed to the interpretation of results and text writing.

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	No software were used to collect data.
Data analysis	All data required to conduct the analysis is openly available except the map of Indigenous Peoples' lands, which is available upon request as this data set contains sensitive information. The analysis was conducted using the open source language R and the scripts to run the central analysis of the study are publicly available on figshare (see data and code availability statements in the article).

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Data availability statement

Records of alien species occurrences are freely available online (https://doi.org/10.5281/zenodo.6458083) as well as the workflow to produce such data (https://

doi.org/10.5281/zenodo.5841930). Data of predictor variables other than IPL are freely available online under the addresses provided in Table S2. The map of IPL can be provided by the author S.T.G. on reasonable request.

Code availability statement
The R code to run the statistical analysis (Figs. 1, 2) and the randomised comparison (Fig. 3) are available at 10.6084/m9.figshare.22303408.

Human research participants

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Sample size	The data set underlying this analysis was derived from 20.246.698 coordinates of species occurrences available on the open platforms www.gbif.org and www.obis.org. These records have been aggregated to 36.515 grid cells of land areas worldwide, which have been used for conducting the analyses of this study.
Data exclusions	No data were excluded.
Replication	All analyses were done in R and are fully reproducible. When analyses required repeated sampling, we used 500 replicates each time.
Randomization	Randomisation took place to create random subsets of data, which was repeated 500 times to generate robust estimates. This is described in detail in the methods.
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