Article

Landscape-scale benefits of protected areas for tropical biodiversity

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The United Nations recently agreed to major expansions of global protected areas (PAs) to slow biodiversity declines[1]. However, although reserves often reduce habitat loss, their efficacy at preserving animal diversity and their influence on biodiversity in surrounding unprotected areas remain unclear[2–5]. Unregulated hunting can empty PAs of large animals[6], illegal tree felling can degrade habitat quality[7], and parks can simply displace disturbances such as logging and hunting to unprotected areas of the landscape[8] (a phenomenon called leakage). Alternatively, well-functioning PAs could enhance animal diversity within reserves as well as in nearby unprotected sites[9] (an effect called spillover). Here we test whether PAs across mega-diverse Southeast Asia contribute to vertebrate conservation inside and outside their boundaries. Reserves increased all facets of bird diversity. Large reserves were also associated with substantially enhanced mammal diversity in the adjacent unprotected landscape. Rather than PAs generating leakage that deteriorated ecological conditions elsewhere, our results are consistent with PAs inducing spillover that benefits biodiversity in surrounding areas. These findings support the United Nations goal of achieving 30% PA coverage by 2030 by demonstrating that PAs are associated with higher vertebrate diversity both inside their boundaries and in the broader landscape.

The establishment of PAs such as national parks and nature reserves is a foundational strategy to slow and reverse the global loss of biodiversity[3,7]—one of humanity's greatest challenges. The recent Conference of Parties to the Convention on Biological Diversity (CBD) in Montreal, Canada, committed nations to protecting 30% of their lands and seas by 2030[1] (the '30 × 30 goal'). But to justify this goal, we need to know that PAs are actually effective at enhancing a range of metrics of biodiversity. Indeed, the conservation outcomes of PAs are highly variable[3,7,10,11]. Many lack the resources for effective management[6,12] and are considered 'paper parks' (Fig. 1), and whereas others may be successful at maintaining habitat cover[3,7,13,14] and even alleviating poverty of nearby communities[15], their efficacy at protecting vulnerable elements of biodiversity—such as wildlife—remains uncertain[2,3,5,16,17].

Prior studies have assessed the efficacy of PAs at enhancing a variety of conservation metrics, often with mixed results. For example, PAs in forested areas tend to experience lower habitat conversion pressures than matched unprotected sites[3], and have been reported to contain higher levels of biodiversity[2,16,18,19]. But in much of the world, PAs were established in relatively remote areas[20] because these locations had low societal opportunity costs (that is, agriculture, logging and other commercial land uses would have been difficult there). Therefore, any differences in biodiversity levels observed in PAs[16,18,19] or in landscapes with a high proportion of protected area[2] could simply be owing to PAs having been established in inaccessible areas where forest disturbance and extractive pressures were low owing to logistical constraints rather than owing to the protection status itself. In other words, any effects of PAs on biodiversity are statistically confounded with site accessibility

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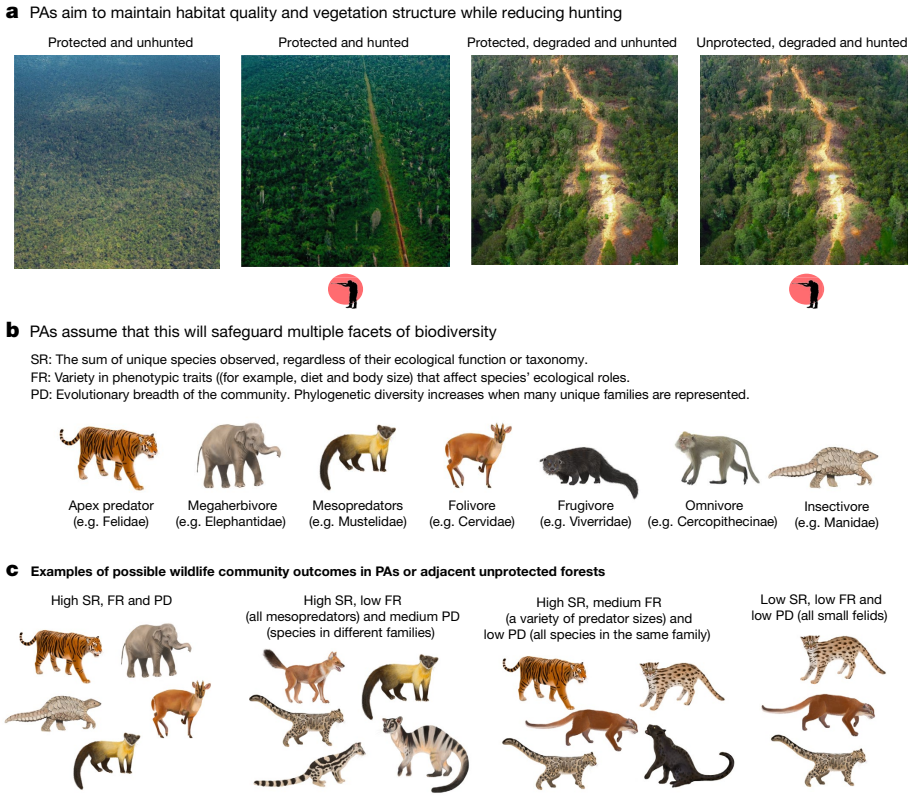

Fig. 1 | The effectiveness of PAs depends on safeguarding multiple facets of biodiversity. a, PAs such as national parks can reduce habitat loss and degradation (from logging) and extractive behaviours such as hunting (shown in red circle), but there are a wide range of real-world outcomes based on management effectiveness. **b**, PAs are aimed at safeguarding multiple facets of biodiversity, including species richness (SR), functional richness (FR) and phylogenetic diversity (PD). PAs often focus on vertebrate conservation, owing to their threat levels and value to humans, including for tourism. Our study focuses on wildlife in Southeast Asia, with mammals shown here representing a variation of feeding guilds and sizes. The same approach is repeated for birds. **c**, Wildlife communities inside PAs and in the surrounding landscape may exhibit distinct levels and types of diversity.

and habitat conditions, both of which directly influence biodiversity and could also have affected the locations of PAs. Such confounding has extremely important implications for the United Nations (UN) 30 × 30 goal. If PAs have enhanced biodiversity simply because they tend to be located in remote areas with undisturbed habitat, it would mean that proposed expansions of PA networks would be unlikely to lead to the desired biodiversity outcomes. New parks are increasingly being designated in disturbed and degraded areas[17] because there are ever fewer tracts of undisturbed, unprotected habitat remaining in most parts of the world. In sum then, to justify costly[21,22] expansions of the global PA estate we need to ascertain whether protection status itself contributes to positive biodiversity outcomes; we can do this by accounting for (that is, de-confounding) potentially biased PA placement, particularly with regards to habitat quality and accessibility.

Assessing the efficacy of PAs while accounting for their potentially biased placement can be done using structural causal modelling[23,24] to remove the confounding effects of site accessibility and habitat quality, along with statistical matching based on propensity scores[25] to ensure balanced covariate values between sampling sites within versus outside PAs. Such de-confounding has been hindered by a lack of high-resolution, regional-scale metrics of accessibility and forest structure. Thus, although many studies have used statistical matching based on environmental factors such as elevation and topography[13,16], none have been able to explicitly account for forest structure and accessibility.

New data now enable us to measure habitat quality much more effectively than before. Habitat quality has often been measured with optical (passive) remote sensing products such as satellite imagery for monitoring changes in forest cover[26]. However, emerging research has highlighted the importance of three-dimensional (3D) habitat structure (for example, vertical complexity, leaf density profiles or forest height) as a stronger and more nuanced determinant of animal occurrence, composition and diversity than forest cover[27–29]. Although changes in forest cover can be detected precisely and with high spatial resolution[26], they may not be a suitable proxy for forest vertical structure[30,31] and may therefore provide relatively little information about the state of non-tree biodiversity[32]. Measurements from lidar, an active remote sensing technology, offer great promise for monitoring 3D habitat structure and biodiversity[28,33]. The recent NASA Global Ecosystem Dynamics Investigation (GEDI) lidar mission[34] provides pantropical 3D canopy structure information[33,34], but these data have not yet been leveraged for large-scale biodiversity conservation assessments.

Recent advances in modelling enable us to measure site accessibility in realistic ways and with high resolution. For example, a simple measure of accessibility—the distance from any given location on the landscape to the nearest road or village—was shown to be a strong predictor of vertebrate abundance across the tropics[6]. This has been expanded to incorporate differences in travel speed on different types of roads and through different off-road areas as a function of topography and land cover[35]. Circuit theoretical movement models now enable the high-resolution mapping of accessibility as a function of the location and size of human population centres, the transport infrastructure networks connecting them, and movement speeds through different types of terrain[35,36]. Such accessibility metrics are distinct from other metrics of anthropogenic influence such as the 'human footprint'[37] (Methods); for example, many areas without agriculture or infrastructure (those that would have a low human footprint score) still have roads leading through them and thus are accessible to hunting, logging and other

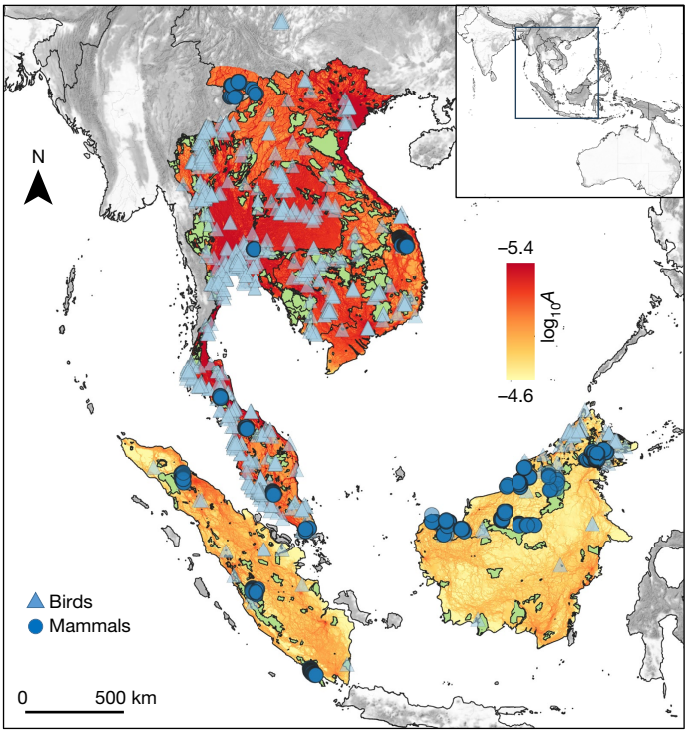

Fig. 2 | Site accessibility across Southeast Asia. The accessibility of locations (for example, to hunters) is estimated from circuit theoretic movement models. This is overlaid on the map with bird (triangle) and mammal (circle) sampling locations. Designated terrestrial PAs within the study region are shown in green. *A*, current flow in amperes in circuit theoretic movement model.

extractive activities[38]. (In our study, accessibility is only very weakly correlated with human footprint (Methods)). Indeed, such extraction is critical to consider in assessing PA effectiveness. Even if PAs protect against habitat loss[3], this might not translate into positive outcomes for wildlife. Vast regions of the world have structurally intact habitats but are nearly or completely devoid of large animals owing to unsustainable hunting and trapping, referred to as defaunation or 'empty forests'[39,40]. PA assessments, and indeed biodiversity mapping in general, that are based solely on habitat—and do not account for accessibility to hunting and other extraction—can severely bias estimates of species occurrence[6], diversity[41] and even ecosystem function[42].

Finally, although research (as described above) has investigated the effects of PAs on biodiversity inside reserve boundaries, the influence of PAs on biodiversity in the broader landscape remains unclear. Reserve establishment could potentially support biodiversity in the surrounding landscapes. This could occur if the wildlife refugia create population sources, such that in-reserve individuals then disperse to adjacent unprotected areas[43] (spillover). Such neighbourhood effects could also be generated by outreach and enforcement activities in the vicinity of parks[44] reducing hunting and other extractive activities in nearby areas as well. Conversely, PAs often simply displace human disturbance from inside the reserve to nearby unprotected areas. Indeed, the establishment of PAs has been observed to increase deforestation and animal harvest rates outside the boundaries, a phenomenon termed 'leakage'[8,45]. There have been few assessments of whether spillover or leakage tends to be the dominant process, so we still know little about how PAs—particularly in hyper-diverse tropical regions—affect animal diversity in the surrounding landscape.

Here we assess the efficacy of terrestrial PAs for conserving tropical mammal and bird diversity while de-confounding the effects of 3D forest structure and accessibility, and while evaluating spillover versus leakage into surrounding unprotected areas. Moreover, we assess how PAs contribute not just to SR but to the functional and phylogenetic diversity of vertebrate communities[4,46] (Fig. 1). Whereas many broad-scale biodiversity assessments rely on relatively crude measures of biodiversity such as species distributions[47] or the coverage of particular ecosystem types (for example, forest[26]), anthropogenic impacts often have cascading effects on both the functional and phylogenetic diversity of taxa[46]. Functional richness (FR) represents the variety of phenotypic traits that are likely to influence how species interact with others around them and with their environment[48]. Although the relationship between functional traits and ecological function is not necessarily straightforward[49], FR can be a proxy for the potential of an assemblage to contribute to important processes such as herbivory or seed dispersal[46]. Phylogenetic diversity (PD) measures the cumulative evolutionary time embodied by a given assemblage[50]. Our study is unique in assessing how PAs contribute to vertebrate conservation while accounting for forest structure and accessibility. Past work[3] used statistical matching to assess the efficacy of PAs at preventing habitat conversion but not explicitly at protecting biodiversity. Other studies have assessed the effects of PA on biodiversity[2,16,18,19], but without de-confounding or statistical matching, or with a population-level focus on a single taxon[5]. Finally, to our knowledge, no other study has assessed PA efficacy at protecting multiple facets of biodiversity and community structure (that is, SR, FR and PD) across multiple taxa, or has evaluated spillover versus leakage patterns for vertebrates outside terrestrial PAs.

We assessed these facets of vertebrate diversity across Southeast Asia (Fig. 2 and Extended Data Fig. 2)—a region with some of the highest levels of biodiversity and gravest conservation threats in the world. For mammals, we used 1,365 camera stations (biological replicates; 42.4% inside PAs) in 65 study areas to detect 112 taxa. For birds, we used 1,079 eBird sampling locations (20.1% inside PAs) to detect 1,361 bird taxa (Fig. 2). Data were cleaned, filtered and standardized to ensure comparability across sites with different survey efforts and data structures (Methods). To de-confound the effects of site accessibility, we accounted for this factor using circuit theoretical models parameterized with human travel speeds across different terrains and the locations of population centres and transportation networks[6,35]. Other covariates might mediate how accessibility (effectively a measure of potential hunting and other extraction pressures) would translate into actual hunting pressure, notably socioeconomic factors such as poverty. We partially accounted for this by including the human development index (HDI) (Methods) in our models. We also note that prior work in Malaysian Borneo demonstrated that accessibility alone (that is, even without socioeconomic covariates) was a strong predictor of hunter detections on camera traps[35]. Similarly, as noted, accessibility alone—as measured simply by the distance to the nearest road or town—strongly predicts vertebrate abundance across the tropics[6].

We assessed 3D forest structure at the biodiversity sampling sites using geostatistical interpolation (kriging; Methods) of GEDI forest structure data for the study region. We generated the following 3D structure metrics: (1) canopy height (as RH95 (relative height at 95%)); (2) plant area volume density between 0 and 5 m (PAVD), selected as a proxy for the density of the forest understory; (3) cumulative plant area index (PAI) from the ground to the top of canopy; (4) structural complexity, measured as foliage height diversity (Shannon's diversity index) of the plant area index for 1-m height bins; and (5) proportional cover (scored as: 0, completely open; 1, completely closed canopy). These tended to be highly correlated, so we did not include them all in our models. Univariate analyses showed that canopy height fit the diversity data the best, so we included this in our models.

We found that PAs significantly enhanced all facets of bird diversity. Bird sampling locations inside reserves tended to be less accessible (logistic regression of PA status against accessibility: $\beta = -0.897$, $P \ll 0.001$) and to have taller forest (PA status against forest height: $\beta = 0.130$, $P \ll 0.001$) than locations outside reserves,

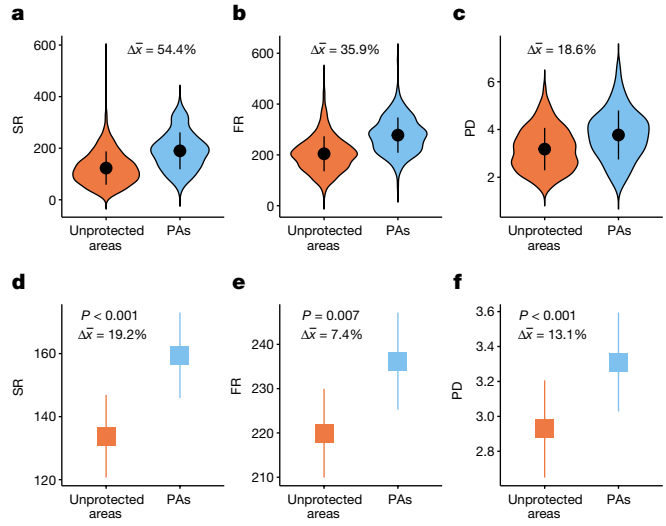

Fig. 3 | All facets of bird diversity are higher inside PAs than outside PAs. **a**–**c**, Violin plots showing calculated SR (**a**), FR (**b**) and PD (**c**) across sites, including variance in many covariates, and the per cent difference in diversity mean ($\Delta\bar{x}$). Points and lines show mean and s.d., respectively. **d**–**f**, Estimated SR (**d**), FR (**e**) and PD (**f**) (and mean difference between protected and unprotected sites) from spatial mixed-effects regression (two-tailed) on propensity score-matched data. Points and lines show mean and s.e.m., respectively. *P* values are shown where significant. Adjustments were not made for multiple comparisons. SR: $n = 1{,}072$; FR: $n = 1{,}074$; and PD: $n = 1{,}073$ biologically independent sites.

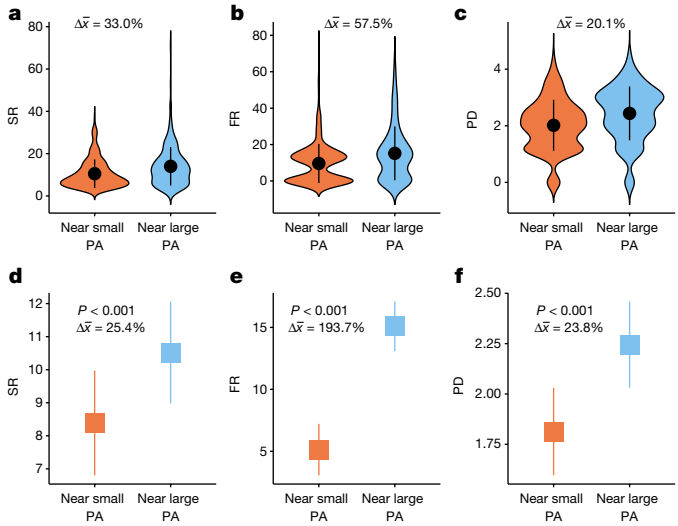

Fig. 4 | All facets of mammal diversity outside PAs are higher near large PAs than near than small PAs. **a**–**c**, Violin plots showing calculated SR (**a**), FR (**b**) and PD (**c**) across sites, including variance in many covariates, and the per cent difference in diversity means. Points and lines show mean and s.d., respectively. **d**–**f**, Estimated SR (**d**), FR (**e**) and PD (**f**) (and mean difference between protected and unprotected sites) from spatial mixed-effects regression (two-tailed) on propensity score-matched data. Points and lines show mean and s.e.m., respectively. *P* values are shown where significant. Adjustments were not made for multiple comparisons. SR: $n = 1{,}362$; FR: $n = 1{,}362$; and PD: $n = 1{,}360$ biologically independent sites. Large PAs are those with area larger than 500 km^2.

as is commonly observed owing to the biased placement of PAs in remote areas[20]. Using structural causal modelling[23,24] and propensity score matching[25] (Methods) to de-confound these effects, we still detected a strong influence of PA status on bird diversity. Estimated bird SR, FR and PD were 19.2%, 7.4% and 13.1% higher, respectively, inside than outside PAs (linear mixed-effects models (LMM); all $P < 0.01$; Fig. 3 and Supplementary Table 1), even after accounting for accessibility and forest structure. The enhanced bird SR that we detected in PAs is nearly double the 10.6% enhancement that Gray et al.[16] found in their global synthesis. Birds detected at PA sites included more large-bodied species ($\beta = 12.492$, $P = 0.001$), more predators of vertebrate ectotherms ($\beta = 3.454$, $P = 0.004$), more species occupying mid-to-high levels of the forest canopy ($\beta = 4.505$, $P = 0.018$) and fewer scavengers ($\beta = -2.817$, $P = 0.003$) than those at unprotected sites.

The effects of PAs on mammals were also strong but quite different from those on birds. In contrast to the results for birds, no facet of mammal diversity was significantly different inside versus outside PAs (Supplementary Table 1). This was probably because even outside PAs, mammal diversity remained high in nearby unprotected areas, particularly adjacent to large PAs. This enhanced mammal diversity outside large PAs rendered non-significant the pairwise differences in diversity between 'protected' and 'non-protected' sites. Estimated mammal SR, FR and PD outside PAs were 25.4%, 193.7% and 23.8% higher, respectively, when the nearest PA was large (more than 500 km^2) than when it was smaller (all $P < 0.001$; Fig. 4 and Supplementary Table 1). Bird FR and PD outside PAs were also significantly higher near large reserves (9.4% and 9.9% higher, respectively; Fig. 5) but these differences were considerably smaller than those of mammals (Supplementary Table 1). For sampling locations outside PAs, distance to the nearest reserve was significantly associated with only one of the six diversity metrics—bird SR was higher in proximity to PAs than farther away (Supplementary Table 1).

In sum, our results show that the legal designation of PAs, and not just their biased placement, provides substantial and significant benefits to Southeast Asian bird diversity. Our findings also show that large PAs are associated with higher diversities of both mammals and birds in surrounding unprotected areas, consistent with spillover rather than leakage being the dominant pattern at the landscape scale. The effects of PAs on birds inside parks and both taxa in the surrounding landscape are probably explained, at least in part, by PAs limiting hunting. We statistically controlled for accessibility in our models—this means that even at sites with equivalent potential hunting pressure inside versus outside PAs, the sites inside the PAs had lower realized hunting pressure. Enforcement, community engagement or other PA management activities[44] may be reducing hunting activities even in areas that are logistically accessible to hunters.

The potential spillover that we detected may be driven by density-dependent dispersal of animals out of source populations inside PAs[43], with larger reserves being particularly effective by supporting larger source populations. Spillover is frequently reported from marine PAs, supporting fishing in nearby areas[43], but such evidence is far more limited in terrestrial environments. It is important to note that spillover in the marine PA context is measured as the movement of individuals and biomass, with few studies assessing changes in overall diversity. Indeed, our results may be conservative in that they focus on diversity rather than the abundance dynamics of particular species. Hunting and other threats will reduce abundance before they start to cause the outright extirpations (or declines to such low levels that detection is unlikely) that influence richness. The fact that we detected such strong changes in occurrence (measured cumulatively, across species, as changes in SR, FR and PD) means that any influences of PAs inside (birds) and outside (mammals and birds) their boundaries are strong. But as techniques improve for abundance estimation for multiple species at large spatial scales and high temporal resolutions[51], biodiversity monitoring in general and PA efficacy assessments in particular will become more powerful. We also note that an alternative mechanism for the patterns that we detected could be that large reserves are more effective than smaller ones at attracting investment in conservation

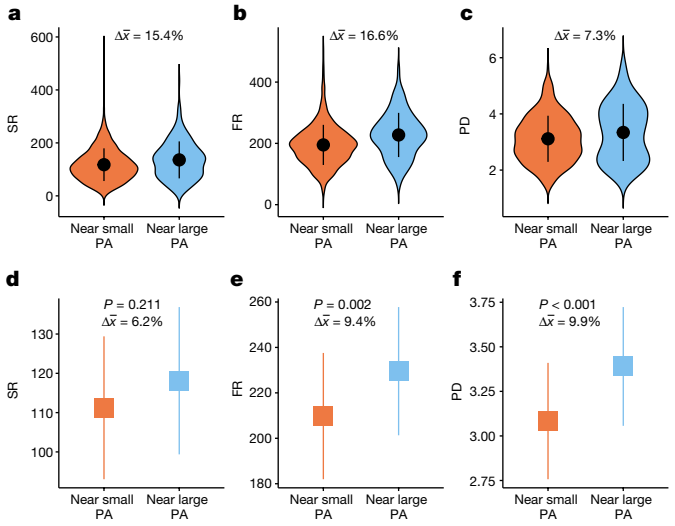

Fig. 5 | All facets of bird diversity outside PAs are higher near large PAs than near small PAs, but these differences are smaller than for mammals. **a**–**c**, Violin plots showing calculated SR (**a**), FR (**b**) and PD (**c**) across sites, including variance in many covariates, and the per cent difference in diversity means. Points and lines show mean and s.d., respectively. **d**–**f**, Estimated SR (**d**), FR (**e**) and PD (**f**) (and mean difference between protected and unprotected sites) from spatial mixed-effects regression (two-tailed) on propensity score-matched data. Points and lines show mean and s.e.m., respectively. *P* values are shown where significant. Adjustments were not made for multiple comparisons. SR: $n = 1{,}074$; FR: $n = 1{,}072$; and $n = 1{,}073$ biologically independent sites. Large PAs are those with area larger than 500 km^2.

interventions such as outreach and enforcement[44]. Better understanding the mechanisms of biodiversity spillover from tropical PAs may be very important for conservation and the achievement of the UN 30 × 30 goals.

We assessed diversity outside PAs as a function of Euclidean distance to the nearest reserve; it is not entirely surprising that these variables were not significantly related. Straight-line distance does not account for how topography, forest quality, human infrastructure or hunting might affect animal movement out of PAs and across the landscape, and it is thus only a very crude metric of PA proximity. Future work could explore declines in diversity with decreasing PA proximity—a pattern predicted from the spillover hypothesis—using circuit theoretical movement models, as we did to estimate site accessibility to humans while accounting for ease of movement through different topographies and landscapes[35,36].

Based on prior research[3,20], we were able to identify clear confounding variables for our assessment of PA efficacy and to de-confound the resulting analyses using structural causal modelling, propensity score matching, and newly available data on the confounding variables. On this basis, we suggest that PA designation enhances bird diversity. For the assessment of PA effects outside their boundaries, potential confounding and missing variables were less clear, so we cannot claim that large PAs cause (in a metaphysical sense) increased diversity in the surrounding landscape. But even demonstrating a predictive, probabilistic relationship between PAs and diversity inside and outside their boundaries suggests that expanding the PA network in accordance with 30 × 30 goals should enhance bird and mammal diversity. This argument would be negated, however, if high-diversity areas had been protected first, with newer PAs relegated to areas with successively lower diversity. Such a pattern would imply that further expansions of the PA network would be likely to occur in even lower diversity areas and thus contribute little to conservation, but this scenario is not supported. The year of designation of a PA was not significantly related to any facet of bird (*P* value range 0.201–0.884) or mammal (*P* value range 0.200–0.877) diversity. Our predictions of increasing diversity with PA coverage may be inaccurate in terms of how the designation of any one particular new PA will affect diversity; there are just too many contingencies and idiosyncrasies for that level of prediction to be robust. However, at broader scales, our results show strong positive effects of PAs on average diversity levels. This supports the notion that if the region develops the many new PAs that will be required to meet the 30 × 30 commitments, then these new areas will contribute cumulatively to the conservation of bird and mammal diversity.

Our results can inform and improve implementation of the UN 30 × 30 agreement and the Convention on Biological Diversity's post-2020 Global Biodiversity Framework with regards to biodiversity monitoring. The vast majority of species are not visible from space—their occurrence, abundance and diversity must be measured on the ground and then, for spatial and temporal extrapolation, linked to remote sensing data via predictive modelling[52]. The essential biodiversity variables (EBVs) approach was developed by the UN 2030 Agenda for Sustainable Development goals[53] to facilitate monitoring biodiversity trends and evaluate management impact[31]. EBVs are intended to integrate on-the-ground biodiversity information with remote sensing data[54,55]. Our results advance the development, integration and monitoring of EBVs related to species traits, community composition and ecosystem structure rather than just distributions of a few target taxa. Furthermore, our results highlight the need to incorporate 3D forest structure and proxies for hunting pressure into spatial biodiversity modelling in order to explain trends in certain EBVs and formulate effective management responses. Accessibility, especially if paired with socio-economic and cultural mediating factors, can be a very useful proxy for current hunting pressure for certain taxa[35,36]. The distribution of other species may be determined by past hunting pressure. Such historical influence is often overlooked, but needs to be incorporated into spatial models, particularly for refugee species[56]—for example, tigers (*Panthera tigris*) in Southeast Asia are currently relegated to remote, hilly areas because they have been hunted out of their preferred habitat, lowland plains and riparian areas. Whereas regional and global maps are available for most conservation threats, robust regional maps of hunting pressure have only recently emerged[35,39]. These maps present new opportunities for biodiversity monitoring and PA efficacy assessment and could be updated dynamically over time, with investments in new technology-based approaches to monitoring hunting (for example, with acoustics or camera traps). We have made our potential hunting pressure map for Southeast Asia publicly available, and our circuit theory approach[35] could be applied to almost any region.

PAs have long been the cornerstone of global biodiversity conservation, but our results suggest that reserve designation alone is insufficient for conserving biodiversity. Our findings are consistent with management (rather than simple remoteness) enhancing vertebrate diversity inside and outside PAs. But other studies have demonstrated huge variance in management effectiveness[3,5,7,12,16,19], with many PAs being mere paper parks. Effective management of hunting presents a key opportunity to improve PA effectiveness, as does designating larger PAs that may enhance the spillover of animals (or conservation measures) to surrounding landscapes. The designation of new, large PAs could include traditional PAs such as national parks, but also the variety of "other effective area-based conservation measures" that are being explored as de facto means of increasing PA coverage in accordance with national and international targets[57]. We echo earlier suggestions that expansion of PAs must be accompanied by substantial investment in initiatives promoting hunting sustainability[58,59], such as capacity building for park staff and the creation of alternative livelihoods for hunters. Investment by way of forest-based carbon financing, with projects adhering to the Climate, Community, and Biodiversity Standards, provides explicit provisions for biodiversity protection and community livelihoods including active control of hunting and encroachment, with such standards assessed during regular audits[60].

Such measures can help ensure that reserves in less developed countries, and in the myriad areas susceptible to unsustainable hunting, can achieve the same conservation outcomes as those in more developed and less hunted areas.

Online content

Any methods, additional references, Nature Portfolio reporting summaries, source data, extended data, supplementary information, acknowledgements, peer review information; details of author contributions and competing interests; and statements of data and code availability are available at https://doi.org/10.1038/s41586-023-06410-z.

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Methods

Species observations, trait data and phylogeny construction

We assembled camera trap data of mammals from across the region. These data came from different research projects spanning 65 distinct study areas within the region (Fig. 2 and Supplementary Table 2). In all cases, cameras were unbaited, active 24 h per day, and attached to trees at ~0.3–0.6 m (depending on topography, vegetation understory and other factors mediating the camera viewshed), heights capable of obtaining pictures of animals of a wide variety of sizes. Cameras were spaced ~1 km apart in most study areas and ~2.5 km apart in Vietnam. Cameras were active for a median 88 days (s.d. = 60.5; range 16–439). In 9.3% of the 178,169 total photographic records it was impossible to determine the exact species of *Callosciurus*, *Herpestes* (including *Urva*), *Hystrix*, *Muntiacus*, *Tragulus*, *Tupaia* or the various species of otters; we assigned these cases the average functional trait values for each genus (for the FR calculation) and assigned the records to a widespread member of each genus (for the PD calculation). We also lumped unidentified murid rodents and squirrels, assigning them to *Maxomys whiteheadi* and *Callosciurus prevostii*, respectively, for FR and PD calculations. In total, we detected 112 taxa. For sites with multiple years of sampling, we chose the most recent year for analysis.

For birds, we used community science records from the eBird database[61]; these constitute species lists from surveys, with multiple surveys per location used to estimate diversity. We collected all records from 'stationary' or 'travelling' survey protocols from January 2015 through August 2021 for the study region (Fig. 2). We followed data cleaning recommendations[62–64] by filtering the data to only include surveys where: (1) all species were recorded; (2) the distance travelled during the observation (for 'travelling' protocol) was ≤8.1 km; (3) the sampling duration (for the 'stationary' protocol) was ≥5 min and ≤240 min; (4) there were no more than 10 observers; and (5) the observation started between 05:00 and 20:00 local time. Sampling locations had a median 23 samples (range 10–1,200; s.d. = 105.6). We removed records of domestic species and those with identifications that were ambiguous as to genus. This resulted in a final dataset of 1,345,922 records of 1,361 taxa. Of these taxa, 1,262 were identified to species and the remaining 7.3% assigned to a widespread congener that occurred at the location.

For the FR calculations, we used data on traits from Wilman et al.[65] that could clearly be related to potential ecological functions. Specifically, for both taxa we used body size, forest stratum preference and the proportion of the diet made up of invertebrates, vertebrate endotherms, vertebrate ectotherms, fish, scavenging, fruit, nectar, seeds, and other plant materials. Variables were standardized to mean = 0, variance = 1 before FR analysis. For the bird genera and the mammal groups listed above that were lumped at the genus or group level, we used genus- or group-level average trait values.

For the PD calculations, we constructed consensus phylogenies (including consensus branch lengths) of all detected bird and mammal species from 1,000 trees for each taxon from the VertLife database[66]. Taxa identified only to genus level were added to the root nodes of their genera. The resulting consensus trees were ultrametric, rooted and dichotomous. We standardized taxonomic nomenclature between the field data, traits data and phylogenies.

Variables

To measure site accessibility, we calculated the circuit-theory-derived accessibility ($\log_{10}$ transformed) of each sampling site to humans, based on multi-modal travel speeds (that is, on foot and by land vehicles) and human population density from specified population centres across different terrains and transportation networks. This is an extension of the map of Deith and Brodie[35] for Malaysian Borneo to the whole study area (Fig. 2). Previous work has shown that this predicts detections of hunters on camera traps in Malaysian Borneo very well[35]. While hunting can be assessed via acoustic monitoring in some systems[67], in much of Asia harvest is done using snares, blowpipes or other silent means and so may be better detected with camera traps. This metric was very weakly correlated with the human footprint index[37] (r = 0.379 and 0.129 for bird and mammal sampling locations, respectively).

Site accessibility is a proxy for potential hunting pressure, but realized hunting pressure will also be mediated by socioeconomic factors. As a simple metric of socioeconomic level, we included the human development index[68] (HDI) of each country. In analyses on the full dataset, we included a binary variable indicating whether or not the site was in a PA using the World Database on PAs[69]. For analyses on the subset of sites inside PAs, we replaced the binary variable with the size of the PA (km^2). For analyses on the subset of sites outside PAs, the binary variable was replaced with the distance (km) to the nearest PA and the size (km^2) of that PA.

To assess the role of forest structure, we used five variables (described in the main text) derived from the GEDI data[34] generated using kriging to interpolate the sample-based data to the exact locations of the biodiversity sampling sites. We selected ecologically relevant metrics from the GEDI L2A (elevation and height metrics) and L2B (canopy cover and vertical profile metrics) products (version 2; from 17 April 2019 to 12 April 2022). After filtering based on quality and degrade flags, the average sampling density across the study region was 15 points km^{-2}. We performed the spatial interpolation processes with the gstat package[70] in R[71]. We first derived separate empirical variograms for each structural variable on each major landmass of the study region. We optimized the model parameters with grid searches and selected the best models based on weighted (with inverse square distance) least squares fit. To determine an estimate of each variable at the exact location of each species observation site, we performed local kriging with a neighbourhood of the 5,000 closest valid GEDI samples. To map each variable at each pixel across the study region, we performed local kriging at the pixel locations with a neighbourhood of the 500 closest GEDI samples[72]. Rasters of the interpolated, GEDI-derived forest structure metrics are available (see 'Data availability').

We excluded sampling locations that had undergone recent (2015–2019) forest loss, from the global forest cover data in Hansen et al.[26]. Field sampling (2015–2021) at some of our sites may have occurred prior to when GEDI data were collected (2018–2021). Excluding recently deforested sites removed the possibility of the field data having come from sites that were forested when field surveyed but then logged prior to the GEDI overpass. All continuous variables were standardized to mean = 0 and variance = 1 before the linear mixed-effects modelling described below.

Diversity estimation

For both birds and mammals, the sampling intensity varied across locations and species were detected imperfectly. We accounted for this by using rarefaction-extrapolation techniques, using the iNEXT package[73] in R, to determine the estimated diversity for a standardized sampling intensity 'endpoint'. For mammals, we used a minimum sampling intensity of 15 days, following Kays et al.[74], who suggested a minimum of two weeks sampling for camera trap studies, after which time the number of detected species rapidly plateaus. We set the sampling endpoint at three times this number, as diversity extrapolation is not considered reliable beyond triple the reference sample size[75,76]. Thus, our mammal diversity estimates should be viewed as the SR, FR, or PD at a given site as detected within a 45-day sampling window. For birds, we set the minimum number of samples at a given location equal to 10, which balanced the need for sufficient sampling to ensure robust diversity estimation with the need to avoid throwing away excessive data (that is, increasing the minimum number of samples to 15 would have necessitated throwing away 28% of sampling locations, which could have biased results by increasing type II error). Again, our

sampling endpoint was set to three times the minimum sample size, so our bird diversity estimates should be viewed as the SR, FR, or PD at a given site as detected within a 30-day sampling window.

For SR, we generated a species × sample matrix populated by incidence data. We calculated the increase in the PD metric[50] across successive five-day sample intervals at each site using the picante[77] package in R and then used the asymptote of the curve as the estimated PD for that site. We calculated the FR metric[78] using the FD[44] package in R; FR values are not necessarily monotonically related to sampling intensity or species diversity, so we used the maximum FR value at each site rather than an asymptotic approximation. Diversity estimates are available[79] (see 'Data availability').

The field sampling was reasonably complete, as evidenced by the correlation (Pearson's $r = 0.91$ and 0.79 for birds and mammals, respectively) and high correspondence (Extended Data Fig. 1) between the number of species detected at sampling locations and the number estimated from rarefaction-extrapolation. The median per cent difference between observed and estimated SR across sampling locations was 23.5%.

Structural causal modelling

We used structural causal modelling (SCM) to assess PA efficacy while de-confounding the effects of site accessibility and forest structure. SCM also allowed us to produce a set of predictor variables for each analysis that would result in unbiased coefficient estimation—while many variables could potentially affect diversity, adjusting for all of them in analytical models can bias results by introducing, rather than minimizing, conditional associations[80]. We constructed a directed acyclic graph (Extended Data Fig. 2) showing potential causal pathways among variables and used DAGGITY[81] to identify the sufficient adjustment sets (that is, suites of covariates) necessary to include in the models in order to generate unbiased estimates of the effects of exposure variables on outcome variables.

Linear mixed-effects modelling and propensity score matching

We used the variables identified in the SCM in linear mixed-effects models to assess PA efficacy and determine the environmental factors related to bird and mammal diversity. We accounted for spatial autocorrelation in two ways. First, we use mixed-effects models with an exponential correlation structure based on the covariance in pairwise distances among sites, following Hakkenberg & Goetz[82]. Second, we also included (for mammals) study area nested within country as random effects because the data were highly spatially clustered and to account for the potential for other (un-modelled) national-level anthropogenic factors to affect diversity. For birds, we used country alone as a random effect because the sampling locations were not clustered into discrete study areas. The SCM identified 'forest structure' as a critical variable to include in the models in order to de-confound our PA efficacy analysis. We determined which GEDI variable to use to represent forest structure based on univariate analyses, as we could not include all of them in the same model because they were highly correlated. Canopy height fit the diversity data better (that is, had lower Aikake information criterion values) than the other GEDI variables and we included that variable in the linear models. All variables included in the same model had correlation coefficients $r < 0.6$. We checked regression diagnostics to assess linear relationships between residuals and fitted values and normality of the residuals. In a few cases (see Supplementary Table 1) we removed some observations to improve normality of the residuals. We assessed the leverage of each observation using the hatvalues function in R. In all models, the highest-leverage observations were well below 2 (maximum values for the different analyses were 0.21–0.40 and 0.86–0.90 for birds and mammals, respectively).

To assess PA efficacy, we ran linear mixed-effects models in a statistically matched framework. Matching was conducted using nearest-neighbour propensity score matching without replacement, estimating the propensity score with logistic regression of the treatment (PA status) on the covariates to achieve the best possible balance of covariate values (except protected status) between sites inside versus outside PAs[3,25]. We matched the datasets based on canopy height, site accessibility, HDI and location (Universal Transverse Mercator (UTM) easting and northing) using the *MatchIt*[83] package in R. We began with a nearest-neighbor matching with logit link function, but this yielded somewhat poor covariate balances. We then used full matching on the propensity score estimated with a probit link function; this yielded much better balances (shown in Supplementary Table 3). We ran linear mixed-effects models on the matched datasets, ensuring that comparisons between sites inside versus outside PAs were on datasets that were otherwise as similar as possible in forest structure, accessibility and human influence, while also being as geographically matched as possible. We ran these models in the nlme[84] package in R. We tested whether high-diversity areas had been protected first, with newer PAs relegated to areas with successively lower diversity. We ran mixed-effects linear regressions using the same predictor variables as above but also including PA 'year of designation'.

To assess support for spillover versus leakage patterns, we modelled diversity as a function of the predictor variables described above on the subset of sites outside PAs ($n = 621$ and 774 for birds and mammals, respectively). In these models, we replaced the PA status binary variable with either the size of the nearest PA or (in separate models), the distance to the nearest PA. These data were analysed using propensity score-based statistical matching to achieve covariate balances, with full matching and probit link functions as described above. Covariate balances are shown in Supplementary Table 3 and model results (standardized beta coefficients and P values) in Supplementary Table 1. The point of propensity score matching is to achieve balanced sets of covariate values between two sets of data—thus the response variables in such analyses are binary. Despite broad consensus that large PAs are necessary for conserving certain vulnerable elements of biodiversity[85,86], and evidence that they provide a higher per-unit return-on-investment than smaller PAs[87], surprisingly little research allows us to determine size thresholds in PA performance – in other words, to ascertain 'how large are large PAs?'. A prior assessment of PA effectiveness at conserving natural habitat in other tropical regions suggests that strong habitat disturbance can occur ~12 km into the boundary of PAs[88]. Assuming circular reserves, this would translate to a minimum of ~500 km^2 for a PA to maintain a core of little-disturbed habitat. Therefore, we used 500 km^2 as a threshold distinguishing 'large' from 'small' PAs in our analysis. After establishing that diversity was higher near large than small PAs based on this threshold, we ran sensitivity analyses where we re-ran the models but with different PA size thresholds. Diversity was generally enhanced in large relative to small PAs at alternative thresholds of 400, 600, and 1,000 km^2, particularly for mammals (Supplementary Table 4).

Reporting summary

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

Data availability

Data used in the mixed-effects modelling analysis are available at https://doi.org/10.6084/m9.figshare.22527298.v1. Rasters (1-km resolution) for the study area for the GEDI-derived forest structural covariates and estimated site accessibility are available at https://rcdata.nau.edu/geode_data/SEA_vertebrate_diversity_rasters/.

Code availability

Codes for analysis (in the R programming language) are available at https://doi.org/10.5281/zenodo.7796347.

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Additional information

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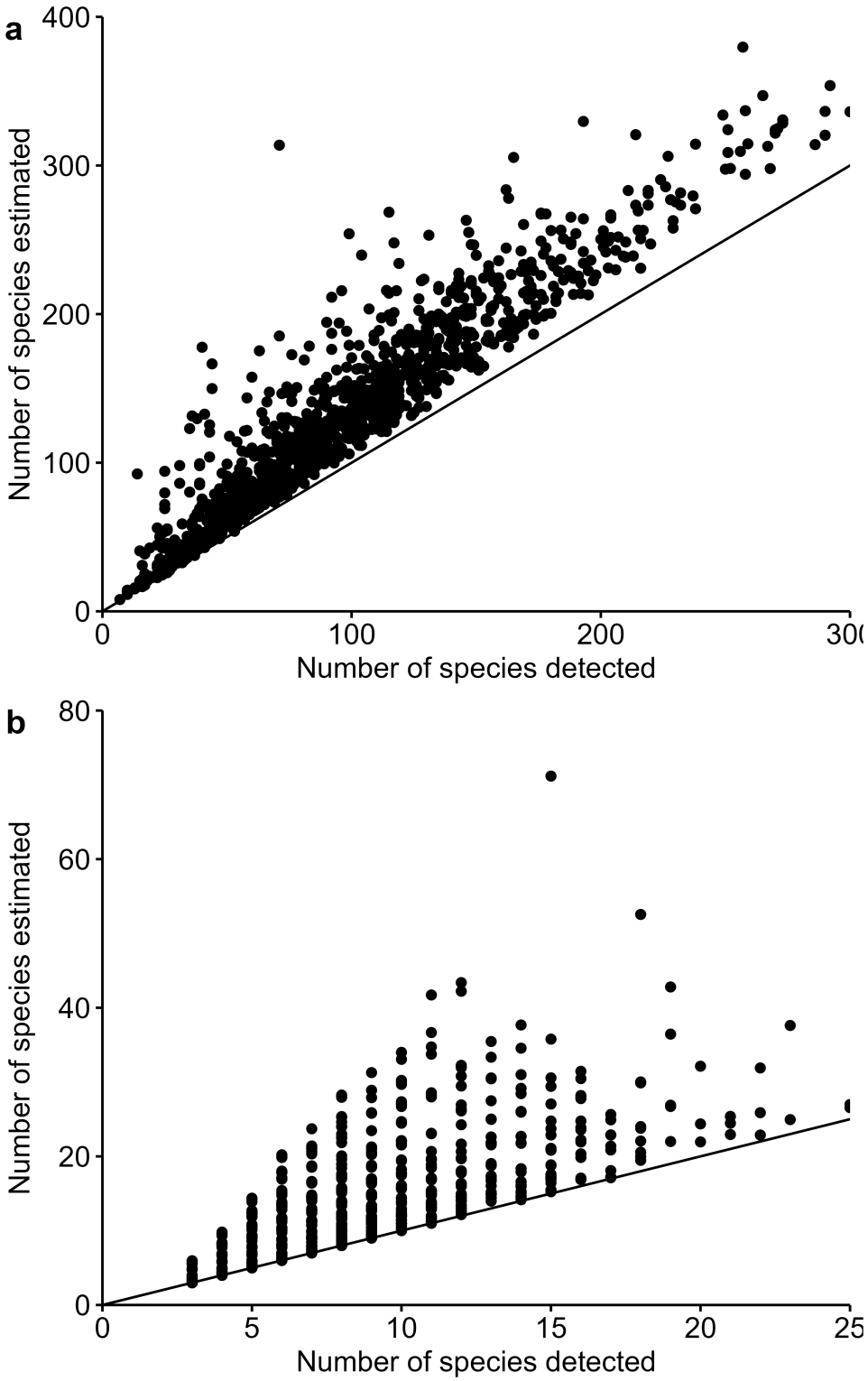
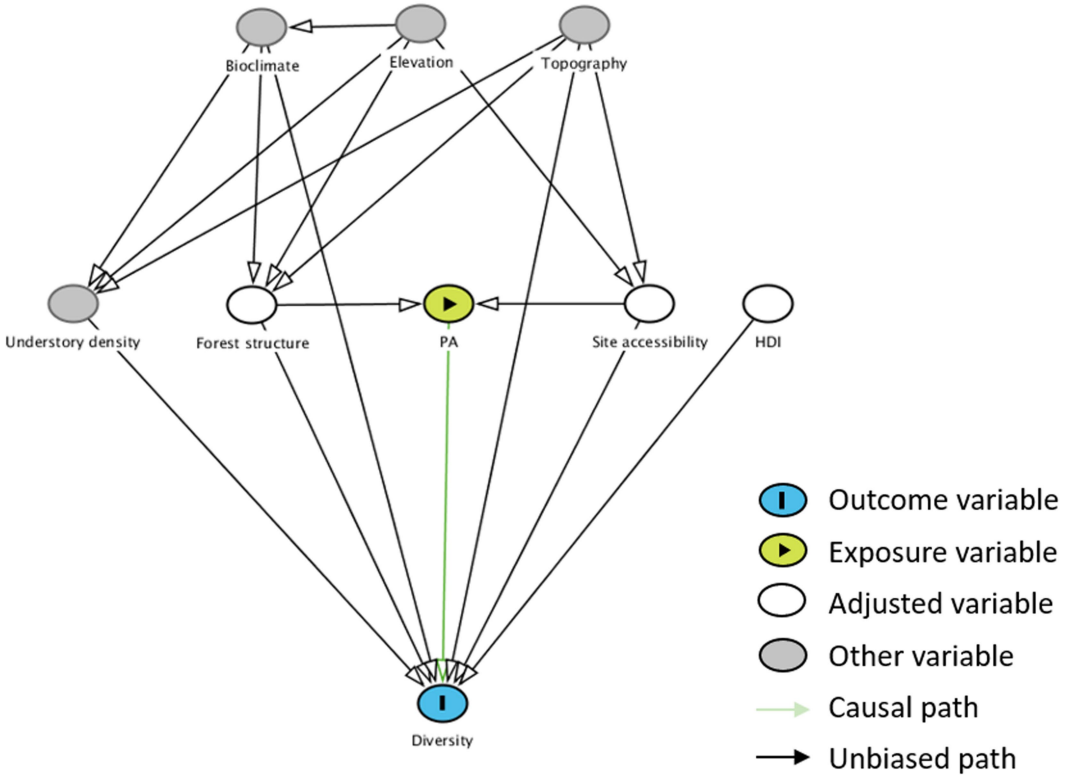
Peer review information *Nature* thanks Robert Bagchi, Erik Meijaard, Hao Tang, Morgan Tingley and the other, anonymous, reviewer(s) for their contribution to the peer review of this work.



Extended Data Fig. 1 | Estimates of sampling completeness – the correspondence between the number of species detected at sampling locations and the number estimated from rarefaction-extrapolation (see Methods) for birds (panel a; Pearson's r = 0.91) and mammals (b; r = 0.79), with 1:1 lines shown.



Extended Data Fig. 2 | Directed acyclic graph of bird or mammal diversity in relation to exposure variables and covariates. The structure of the graph shows how the influence of protected areas on diversity are de-confounded from the influence of forest structure and site accessibility.

nature portfolio

Corresponding author(s): Jedediah Brodie
Double-blind peer review submissions: write DBR and your manuscript number here instead of author names.

Last updated by author(s): 2023-02-10 *YYYY-MM-DD*

Reporting Summary

Nature Portfolio wishes to improve the reproducibility of the work that we publish. This form provides structure for consistency and transparency in reporting. For further information on Nature Portfolio policies, see our Editorial Policies and the Editorial Policy Checklist.

Statistics

For all statistical analyses, confirm that the following items are present in the figure legend, table legend, main text, or Methods section.

n/a	Confirmed	
[ ]	[X]	The exact sample size (*n*) for each experimental group/condition, given as a discrete number and unit of measurement
[X]	[ ]	A statement on whether measurements were taken from distinct samples or whether the same sample was measured repeatedly
[ ]	[X]	The statistical test(s) used AND whether they are one- or two-sided *Only common tests should be described solely by name; describe more complex techniques in the Methods section.*
[ ]	[X]	A description of all covariates tested
[ ]	[X]	A description of any assumptions or corrections, such as tests of normality and adjustment for multiple comparisons
[ ]	[X]	A full description of the statistical parameters including central tendency (e.g. means) or other basic estimates (e.g. regression coefficient) AND variation (e.g. standard deviation) or associated estimates of uncertainty (e.g. confidence intervals)
[ ]	[X]	For null hypothesis testing, the test statistic (e.g. *F*, *t*, *r*) with confidence intervals, effect sizes, degrees of freedom and *P* value noted *Give P values as exact values whenever suitable.*
[X]	[ ]	For Bayesian analysis, information on the choice of priors and Markov chain Monte Carlo settings
[X]	[ ]	For hierarchical and complex designs, identification of the appropriate level for tests and full reporting of outcomes
[ ]	[X]	Estimates of effect sizes (e.g. Cohen's *d*, Pearson's *r*), indicating how they were calculated

Our web collection on statistics for biologists contains articles on many of the points above.

Software and code

Policy information about availability of computer code

Data collection: n/a
Provide a description of all commercial, open source and custom code used to collect the data in this study, specifying the version used OR state that no software was used.

Data analysis: Several R packages were used; these are cited in the text. Our full analysis code will be deposited in FigShare prior to publication

For manuscripts utilizing custom algorithms or software that are central to the research but not yet described in published literature, software must be made available to editors and reviewers. We strongly encourage code deposition in a community repository (e.g. GitHub). See the Nature Portfolio guidelines for submitting code & software for further information.

Data

Policy information about availability of data

All manuscripts must include a data availability statement. This statement should provide the following information, where applicable:

- Accession codes, unique identifiers, or web links for publicly available datasets
- A description of any restrictions on data availability
- For clinical datasets or third party data, please ensure that the statement adheres to our policy

All data will be made publicly available (FigShare) prior to publication

Human research participants n/a

Policy information about studies involving human research participants and Sex and Gender in Research.

Reporting on sex and gender	*Use the terms sex (biological attribute) and gender (shaped by social and cultural circumstances) carefully in order to avoid confusing both terms. Indicate if findings apply to only one sex or gender; describe whether sex and gender were considered in study design whether sex and/or gender was determined based on self-reporting or assigned and methods used. Provide in the source data disaggregated sex and gender data where this information has been collected, and consent has been obtained for sharing of individual-level data; provide overall numbers in this Reporting Summary. Please state if this information has not been collected. Report sex- and gender-based analyses where performed, justify reasons for lack of sex- and gender-based analysis.*
Population characteristics	*Describe the covariate-relevant population characteristics of the human research participants (e.g. age, genotypic information, past and current diagnosis and treatment categories). If you filled out the behavioural & social sciences study design questions and have nothing to add here, write "See above."*
Recruitment	*Describe how participants were recruited. Outline any potential self-selection bias or other biases that may be present and how these are likely to impact results.*
Ethics oversight	*Identify the organization(s) that approved the study protocol.*

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

Field-specific reporting

Please select the one below that is the best fit for your research. If you are not sure, read the appropriate sections before making your selection.

☐ Life sciences ☐ Behavioural & social sciences ☒ Ecological, evolutionary & environmental sciences

For a reference copy of the document with all sections, see nature.com/documents/nr-reporting-summary-flat.pdf

Life sciences study design

All studies must disclose on these points even when the disclosure is negative.

Sample size	*Describe how sample size was determined, detailing any statistical methods used to predetermine sample size OR if no sample-size calculation was performed, describe how sample sizes were chosen and provide a rationale for why these sample sizes are sufficient.*
Data exclusions	*Describe any data exclusions. If no data were excluded from the analyses, state so OR if data were excluded, describe the exclusions and the rationale behind them, indicating whether exclusion criteria were pre-established.*
Replication	*Describe the measures taken to verify the reproducibility of the experimental findings. If all attempts at replication were successful, confirm this OR if there are any findings that were not replicated or cannot be reproduced, note this and describe why.*
Randomization	*Describe how samples/organisms/participants were allocated into experimental groups. If allocation was not random, describe how covariates were controlled OR if this is not relevant to your study, explain why.*
Blinding	*Describe whether the investigators were blinded to group allocation during data collection and/or analysis. If blinding was not possible, describe why OR explain why blinding was not relevant to your study.*

Behavioural & social sciences study design

All studies must disclose on these points even when the disclosure is negative.

Study description	*Briefly describe the study type including whether data are quantitative, qualitative, or mixed-methods (e.g. qualitative cross-sectional, quantitative experimental, mixed-methods case study).*
Research sample	*State the research sample (e.g. Harvard university undergraduates, villagers in rural India) and provide relevant demographic information (e.g. age, sex) and indicate whether the sample is representative. Provide a rationale for the study sample chosen. For studies involving existing datasets, please describe the dataset and source.*
Sampling strategy	*Describe the sampling procedure (e.g. random, snowball, stratified, convenience). Describe the statistical methods that were used to predetermine sample size OR if no sample-size calculation was performed, describe how sample sizes were chosen and provide a rationale for why these sample sizes are sufficient. For qualitative data, please indicate whether data saturation was considered, and what criteria were used to decide that no further sampling was needed.*

Data collection	*Provide details about the data collection procedure, including the instruments or devices used to record the data (e.g. pen and paper, computer, eye tracker, video or audio equipment) whether anyone was present besides the participant(s) and the researcher, and whether the researcher was blind to experimental condition and/or the study hypothesis during data collection.*
Timing	*Indicate the start and stop dates of data collection. If there is a gap between collection periods, state the dates for each sample cohort.*
Data exclusions	*If no data were excluded from the analyses, state so OR if data were excluded, provide the exact number of exclusions and the rationale behind them, indicating whether exclusion criteria were pre-established.*
Non-participation	*State how many participants dropped out/declined participation and the reason(s) given OR provide response rate OR state that no participants dropped out/declined participation.*
Randomization	*If participants were not allocated into experimental groups, state so OR describe how participants were allocated to groups, and if allocation was not random, describe how covariates were controlled.*

Ecological, evolutionary & environmental sciences study design

All studies must disclose on these points even when the disclosure is negative.

Study description	Data on bird observations from 1079 sampling locations plus data on mammal detections on camera traps from 1365 sampling locations
Research sample	All species detected at each sampling location (excluding domestic species and those with ambiguous taxonomic identification)
Sampling strategy	All records were used, except as noted above
Data collection	Bird data were downloaded from eBird website; mammal data were collected by individual authors
Timing and spatial scale	Data restricted to 2014-2022. The spatial scale was Southeast Asia as shown in our Fig. 2
Data exclusions	All species detected at each sampling location (excluding domestic species and those with ambiguous taxonomic identification)
Reproducibility	Non-experimental
Randomization	Non-experimental
Blinding	n/a

Did the study involve field work? ☐ Yes ☒ No

The study consolidated a database of previously-collected field data. No new data were collected in the field for this study

Field work, collection and transport

Field conditions	*Describe the study conditions for field work, providing relevant parameters (e.g. temperature, rainfall).*
Location	*State the location of the sampling or experiment, providing relevant parameters (e.g. latitude and longitude, elevation, water depth).*
Access & import/export	*Describe the efforts you have made to access habitats and to collect and import/export your samples in a responsible manner and in compliance with local, national and international laws, noting any permits that were obtained (give the name of the issuing authority, the date of issue, and any identifying information).*
Disturbance	*Describe any disturbance caused by the study and how it was minimized.*

Reporting for specific materials, systems and methods

We require information from authors about some types of materials, experimental systems and methods used in many studies. Here, indicate whether each material, system or method listed is relevant to your study. If you are not sure if a list item applies to your research, read the appropriate section before selecting a response.

Materials & experimental systems

n/a	Involved in the study
[X]	[ ] Antibodies
[X]	[ ] Eukaryotic cell lines
[X]	[ ] Palaeontology and archaeology
[ ]	[X] Animals and other organisms
[X]	[ ] Clinical data
[X]	[ ] Dual use research of concern

Methods

n/a	Involved in the study
[X]	[ ] ChIP-seq
[X]	[ ] Flow cytometry
[X]	[ ] MRI-based neuroimaging

Antibodies

Antibodies used: *Describe all antibodies used in the study; as applicable, provide supplier name, catalog number, clone name, and lot number.*

Validation: *Describe the validation of each primary antibody for the species and application, noting any validation statements on the manufacturer's website, relevant citations, antibody profiles in online databases, or data provided in the manuscript.*

Eukaryotic cell lines

Policy information about cell lines and Sex and Gender in Research

Cell line source(s): *State the source of each cell line used and the sex of all primary cell lines and cells derived from human participants or vertebrate models.*

Authentication: *Describe the authentication procedures for each cell line used OR declare that none of the cell lines used were authenticated.*

Mycoplasma contamination: *Confirm that all cell lines tested negative for mycoplasma contamination OR describe the results of the testing for mycoplasma contamination OR declare that the cell lines were not tested for mycoplasma contamination.*

Commonly misidentified lines (See ICLAC register): *Name any commonly misidentified cell lines used in the study and provide a rationale for their use.*

Palaeontology and Archaeology

Specimen provenance: *Provide provenance information for specimens and describe permits that were obtained for the work (including the name of the issuing authority, the date of issue, and any identifying information). Permits should encompass collection and, where applicable, export.*

Specimen deposition: *Indicate where the specimens have been deposited to permit free access by other researchers.*

Dating methods: *If new dates are provided, describe how they were obtained (e.g. collection, storage, sample pretreatment and measurement), where they were obtained (i.e. lab name), the calibration program and the protocol for quality assurance OR state that no new dates are provided.*

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

Ethics oversight: *Identify the organization(s) that approved or provided guidance on the study protocol, OR state that no ethical approval or guidance was required and explain why not.*

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: *For laboratory animals, report species, strain and age OR state that the study did not involve laboratory animals.* n/a

Wild animals	Animals were observed non-invasively. No animals were handled, caught, or harmed.
Reporting on sex	n/a
Field-collected samples	n/a
Ethics oversight	ethical oversight not required for compilation of previously collected (non-invasive) data

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	*Provide the trial registration number from ClinicalTrials.gov or an equivalent agency.*
Study protocol	*Note where the full trial protocol can be accessed OR if not available, explain why.*
Data collection	*Describe the settings and locales of data collection, noting the time periods of recruitment and data collection.*
Outcomes	*Describe how you pre-defined primary and secondary outcome measures and how you assessed these measures.*

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	
☐	☐	Public health
☐	☐	National security
☐	☐	Crops and/or livestock
☐	☐	Ecosystems
☐	☐	Any other significant area

Experiments of concern

Does the work involve any of these experiments of concern:

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

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 *May remain private before publication.*	*For "Initial submission" or "Revised version" documents, provide reviewer access links. For your "Final submission" document, provide a link to the deposited data.*
Files in database submission	*Provide a list of all files available in the database submission.*
Genome browser session (e.g. UCSC)	*Provide a link to an anonymized genome browser session for "Initial submission" and "Revised version" documents only, to enable peer review. Write "no longer applicable" for "Final submission" documents.*

Methodology

Replicates	*Describe the experimental replicates, specifying number, type and replicate agreement.*
Sequencing depth	*Describe the sequencing depth for each experiment, providing the total number of reads, uniquely mapped reads, length of reads and whether they were paired- or single-end.*
Antibodies	*Describe the antibodies used for the ChIP-seq experiments; as applicable, provide supplier name, catalog number, clone name, and lot number.*
Peak calling parameters	*Specify the command line program and parameters used for read mapping and peak calling, including the ChIP, control and index files used.*
Data quality	*Describe the methods used to ensure data quality in full detail, including how many peaks are at FDR 5% and above 5-fold enrichment.*
Software	*Describe the software used to collect and analyze the ChIP-seq data. For custom code that has been deposited into a community repository, provide accession details.*

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 preparation	*Describe the sample preparation, detailing the biological source of the cells and any tissue processing steps used.*
Instrument	*Identify the instrument used for data collection, specifying make and model number.*
Software	*Describe the software used to collect and analyze the flow cytometry data. For custom code that has been deposited into a community repository, provide accession details.*
Cell population abundance	*Describe the abundance of the relevant cell populations within post-sort fractions, providing details on the purity of the samples and how it was determined.*
Gating strategy	*Describe the gating strategy used for all relevant experiments, specifying the preliminary FSC/SSC gates of the starting cell population, indicating where boundaries between "positive" and "negative" staining cell populations are defined.*

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

Magnetic resonance imaging

Experimental design

Design type	*Indicate task or resting state; event-related or block design.*

Design specifications

Specify the number of blocks, trials or experimental units per session and/or subject, and specify the length of each trial or block (if trials are blocked) and interval between trials.

Behavioral performance measures

State number and/or type of variables recorded (e.g. correct button press, response time) and what statistics were used to establish that the subjects were performing the task as expected (e.g. mean, range, and/or standard deviation across subjects).

Acquisition

Imaging type(s)

Specify: functional, structural, diffusion, perfusion.

Field strength

Specify in Tesla

Sequence & imaging parameters

Specify the pulse sequence type (gradient echo, spin echo, etc.), imaging type (EPI, spiral, etc.), field of view, matrix size, slice thickness, orientation and TE/TR/flip angle.

Area of acquisition

State whether a whole brain scan was used OR define the area of acquisition, describing how the region was determined.

Diffusion MRI ☐ Used ☐ Not used

Preprocessing

Preprocessing software

Provide detail on software version and revision number and on specific parameters (model/functions, brain extraction, segmentation, smoothing kernel size, etc.).

Normalization

If data were normalized/standardized, describe the approach(es): specify linear or non-linear and define image types used for transformation OR indicate that data were not normalized and explain rationale for lack of normalization.

Normalization template

Describe the template used for normalization/transformation, specifying subject space or group standardized space (e.g. original Talairach, MNI305, ICBM152) OR indicate that the data were not normalized.

Noise and artifact removal

Describe your procedure(s) for artifact and structured noise removal, specifying motion parameters, tissue signals and physiological signals (heart rate, respiration).

Volume censoring

Define your software and/or method and criteria for volume censoring, and state the extent of such censoring.

Statistical modeling & inference

Model type and settings

Specify type (mass univariate, multivariate, RSA, predictive, etc.) and describe essential details of the model at the first and second levels (e.g. fixed, random or mixed effects; drift or auto-correlation).

Effect(s) tested

Define precise effect in terms of the task or stimulus conditions instead of psychological concepts and indicate whether ANOVA or factorial designs were used.

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

Statistic type for inference
(See Eklund et al. 2016)

Specify voxel-wise or cluster-wise and report all relevant parameters for cluster-wise methods.

Correction

Describe the type of correction and how it is obtained for multiple comparisons (e.g. FWE, FDR, permutation or Monte Carlo).

Models & analysis

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

Functional and/or effective connectivity

Report the measures of dependence used and the model details (e.g. Pearson correlation, partial correlation, mutual information).

Graph analysis

Report the dependent variable and connectivity measure, specifying weighted graph or binarized graph, subject- or group-level, and the global and/or node summaries used (e.g. clustering coefficient, efficiency, etc.).

Multivariate modeling and predictive analysis

Specify independent variables, features extraction and dimension reduction, model, training and evaluation metrics.