

Landscape-scale benefits of protected areas for tropical biodiversity

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52 **The United Nations recently agreed to major expansions of global protected areas**
53 **(PAs) to slow biodiversity declines ¹. But while reserves often reduce habitat loss,**
54 **their efficacy at preserving animal diversity is unclear, as is their influence on**
55 **biodiversity in surrounding unprotected areas ²⁻⁵. Unregulated hunting can empty**
56 **PAs of larger animals ⁶, illegal tree felling can degrade habitat quality ⁷, and parks**
57 **can simply displace disturbances such as logging and hunting to unprotected areas of**
58 **the landscape (‘leakage’) ⁸. Alternatively, well-functioning PAs could enhance animal**
59 **diversity within reserves as well as in nearby unprotected sites (‘spillover’) ⁹. Here**
60 **we test if PAs across mega-diverse Southeast Asia contribute to vertebrate**
61 **conservation inside and outside their boundaries. Reserves increased all facets of**
62 **bird diversity. Large reserves also had substantially enhanced mammal diversity in**
63 **the adjacent unprotected landscape. Rather than PAs generating leakage that**
64 **deteriorated ecological conditions elsewhere, our results are consistent with PAs**
65 **inducing spillover that benefits biodiversity in surrounding areas. These findings**
66 **support the 2030 United Nations goals of achieving 30% PA coverage by**
67 **demonstrating that protected areas are associated with higher vertebrate diversity**
68 **both inside their boundaries and in the broader landscape.**

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70 The establishment of protected areas (PAs) such as national parks and nature reserves is a
71 foundational strategy to slow and reverse the global loss of biodiversity^{3,7} – one of
72 humanity’s greatest challenges. The recent Conference of Parties to the Convention on
73 Biological Diversity (CBD) in Montreal, Canada, committed nations to protecting 30% of
74 their lands and seas by 2030 (“30 × 30 goal”) ¹. But to justify this goal, we need to know
75 that PAs are actually effective at enhancing a range of metrics of biodiversity. Indeed, the
76 conservation outcomes of PAs are highly variable^{3,7,10,11}. Many lack the resources for
77 effective management^{6,12} and are considered “paper parks” (Fig. 1). While others may be
78 successful at maintaining habitat cover^{3,7,13,14} and even alleviating poverty of nearby
79 communities¹⁵, their efficacy at protecting vulnerable elements of biodiversity – such as
80 wildlife – remains uncertain^{2,3,5,16,17}.

81 Prior studies have assessed the efficacy of PAs at enhancing a variety of
82 conservation metrics, often with mixed results. For example, PAs in forested areas tend to
83 experience lower habitat conversion pressures than matched unprotected sites³, and have
84 been reported to contain higher levels of biodiversity^{2,16,18,19}. But in much of the world, PAs
85 were established in relatively remote areas²⁰ because these locations had low societal
86 opportunity costs (i.e., agriculture, logging, and other commercial land uses would have
87 been difficult there). Therefore, any differences in biodiversity levels observed in PAs
88^{16,18,19} or in landscapes with a high proportion of protected area² could simply be due to
89 PAs having been established in inaccessible areas where forest disturbance and extractive
90 pressures were low due to logistical constraints rather than due to the protection status
91 itself. In other words, any effects of PAs on biodiversity are statistically confounded with

92 site accessibility and habitat conditions, both of which directly influence biodiversity and
93 could also have affected the locations of PAs. Such confounding has extremely important
94 implications for the UN 30 × 30 goal. If PAs have enhanced biodiversity simply because
95 they tend to be located in remote areas with undisturbed habitat; it would mean that
96 proposed expansions of PA networks would be unlikely to lead to the desired biodiversity
97 outcomes. New parks are increasingly being designated in disturbed and degraded areas ¹⁷,
98 because there are ever fewer tracts of undisturbed, unprotected habitat remaining in most
99 parts of the world. In sum, then, in order to justify costly ^{21,22} expansions of the global PA
100 estate, we need to ascertain whether protection status itself contributes to positive
101 biodiversity outcomes; we can do this by accounting for (i.e., “de-confounding”) potentially
102 biased PA placement, especially with regards to habitat quality and accessibility.

103 Assessing the efficacy of PAs while accounting for their potentially biased placement
104 can be done using Structural Causal Modeling ^{23,24} to remove the confounding effects of site
105 accessibility and habitat quality, along with statistical matching based on propensity scores
106 ²⁵ to ensure balanced covariate values between sampling sites within versus outside PAs.
107 But such de-confounding has been hindered by a lack of high-resolution, regional-scale
108 metrics of accessibility and forest structure. Thus, while many studies have used statistical
109 matching based on environmental factors like elevation and topography ^{13,16}, none have
110 been able to explicitly account for forest structure and accessibility.

111 New data now allow us to measure habitat quality much more effectively than
112 before. Habitat quality has often been measured with optical (passive) remote sensing
113 products, for example, satellite imagery for monitoring changes in forest cover ²⁶. But
114 emerging research has highlighted the importance of three-dimensional (3D) habitat

115 structure (e.g., vertical complexity, leaf density profiles, or forest height) as a stronger and
116 more nuanced determinant of animal occurrence, composition, and diversity than forest
117 cover ²⁷⁻²⁹. While changes in forest cover can be detected precisely and with high spatial
118 resolution ²⁶, they may not be a suitable proxy for forest vertical structure ^{30,31} and may
119 therefore say relatively little about the state of non-tree biodiversity ³². Measurements
120 from lidar, an active remote sensing technology, offer great promise for monitoring 3D
121 habitat structure and biodiversity ^{28,33}. The recent NASA Global Ecosystem Dynamics
122 Investigation (GEDI) lidar mission ³⁴ provides pantropical 3D canopy structure information
123 ^{33,34}, but these data have not yet been leveraged for large-scale biodiversity conservation
124 assessments.

125 Recent modeling advances also allow us to measure site accessibility in realistic
126 ways and with high resolution. For example, a simple measure of accessibility, the distance
127 from any given location on the landscape to the nearest road or village, was shown to be a
128 strong predictor of vertebrate abundance across the tropics ⁶. This has been expanded to
129 incorporate differences in travel speed on different types of roads and through different
130 off-road areas as a function of topography and land cover ³⁵. Circuit theoretical movement
131 models now allow the high-resolution mapping of accessibility as a function of the location
132 and size of human population centers, the transport infrastructure networks connecting
133 them, and movement speeds through different types of terrain ^{35,36}. Such accessibility
134 metrics are distinct from other metrics of anthropogenic influence such as the “Human
135 Footprint” ³⁷ (see Methods); for example, many areas without agriculture or infrastructure
136 (i.e., that would have a low human footprint score) still have roads leading through them
137 and thus are accessible to hunting, logging, and other extractive activities ³⁸. (In our study,

138 accessibility is only very weakly correlated with Human Footprint – see Methods.) Indeed,
139 such extraction is critical to consider in assessing PA effectiveness. Even if PAs protect
140 against habitat loss ³, this might not translate into positive outcomes for wildlife. Vast
141 regions of the world have structurally intact habitats but are nearly or completely devoid of
142 large animals due to unsustainable hunting and trapping, referred to as defaunation or
143 ‘empty forests’ ^{39,40}. PA assessments, and indeed biodiversity mapping in general, that are
144 based solely on habitat – failing to account for accessibility to hunting and other extraction
145 – can severely bias estimates of species occurrence ⁶, diversity ⁴¹, and even ecosystem
146 function ⁴².

147 Finally, while research (described above) has investigated the effects of PAs on
148 biodiversity inside reserve boundaries, PA influence on biodiversity in the broader
149 landscape remains unclear. On the one hand, reserve establishment could potentially
150 support biodiversity in the surrounding landscapes. This could occur if the wildlife refugia
151 create population sources, such that in-reserve individuals then disperse to adjacent
152 unprotected areas (‘spillover’) ⁴³. Such neighborhood effects could also be generated by
153 outreach and enforcement activities in the vicinity of parks ⁴⁴ reducing hunting and other
154 extractive activities in nearby areas as well. But on the other hand, PAs often simply
155 displace human disturbance from inside the reserve to nearby unprotected areas; indeed,
156 PA establishment has been observed to increase deforestation and animal harvest rates
157 outside the boundaries, a phenomenon termed ‘leakage’ ^{8,45}. There have been few
158 assessments of whether spillover or leakage tends to be the dominant process, so we still
159 know little about how PAs, particularly in hyper-diverse tropical regions, affect animal
160 diversity in the surrounding landscape.

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

183 We assessed these facets of vertebrate diversity across Southeast Asia (Fig. 2;
184 Extended Data) – a region with some of the highest levels of biodiversity and the gravest
185 conservation threats in the world. For mammals, we used 1,365 camera stations (biological
186 replicates; 42.4% inside PAs) in 65 study areas to detect 112 taxa. For birds, we used 1,079
187 eBird sampling locations (20.1% inside PAs) to detect 1,361 bird taxa (Fig. 2). Data were
188 cleaned, filtered, and standardized to ensure comparability across sites with different
189 survey efforts and data structures (see Methods). To de-confound the effects of site
190 accessibility, we accounted for this factor using circuit theoretical models parameterized
191 with human travel speeds across different terrains and the locations of population centers
192 and transportation networks ^{6,35}. Other covariates might mediate how accessibility
193 (effectively a measure of *potential* hunting and other extraction pressures) would translate
194 into *actual* hunting pressure, notably socioeconomic factors such as poverty. We partially
195 accounted for this by including the Human Development Index (HDI; see Methods) and
196 statistical interactions between accessibility and HDI in our models. But we also note that
197 prior work in Malaysian Borneo demonstrated that accessibility alone (i.e., even without
198 socioeconomic covariates) was a strong predictor of hunter detections on camera traps ³⁵.
199 Likewise, as noted, accessibility alone (as measured simply by the distance to the nearest
200 road or town) strongly predicts vertebrate abundance across the tropics ⁶.

201 We assessed 3D forest structure at the biodiversity sampling sites using
202 geostatistical interpolation (kriging; see Methods) of GEDI forest structure data for the
203 study region. We generated the following 3D structure metrics: (i) canopy height (*rh95*; m),
204 (ii) plant area volume density between 0 and 5 meters (*pavd*; m²/m³), selected as a proxy
205 for the density of the forest understory, (iii) cumulative plant area index (PAI) from the

206 ground to the top of canopy (m^2/m^2), (iv) structural complexity measured as foliage height
207 diversity (Shannon's diversity index) of plant area index for 1 m height bins, and (v)
208 proportional cover (0 = completely open, 1 = completely closed canopy). These tended to
209 be highly correlated, so we did not include them all in our models. Univariate analyses
210 showed that canopy height fit the diversity data the best, so we included this and
211 understory density (which was only weakly correlated with canopy height; see Methods) in
212 our models.

213 We found that PAs significantly enhanced all facets of bird diversity. Bird sampling
214 locations inside reserves tended to be less accessible (logistic regression of PA status
215 against accessibility: $\beta = -0.897$, $p < 0.001$) and to have taller forest (PA status against
216 forest height: $\beta = 0.130$, $p < 0.001$) than locations outside reserves, as is commonly
217 observed due to the biased placement of PAs in remote areas²⁰. But using structural causal
218 modeling^{23,24} and propensity score matching²⁵ (see Methods) to de-confound these effects,
219 we still detected strong influence of PA status on bird diversity. Estimated bird SR, FR, and
220 PD were 19.2%, 7.4%, and 13.1% higher, respectively, inside than outside PAs (linear
221 mixed-effects models [LMM]; all $p < 0.01$; Fig. 3; Extended Data Table 1), even after
222 accounting for accessibility and forest structure. The enhanced bird SR that we detected in
223 PAs is nearly double the 10.6% enhancement that Gray et al.¹⁶ found in their global
224 synthesis. Birds detected at PA sites included more large-bodied species ($\beta = 12.492$, $p =$
225 0.001), predators of vertebrate ectotherms ($\beta = 3.454$, $p = 0.004$), species occupying mid-
226 high levels of the forest canopy ($\beta = 4.505$, $p = 0.018$), and fewer scavengers ($\beta = -2.817$, $p =$
227 0.003), than those at unprotected sites.

228 The effects of PAs on mammals were also strong but quite different from those on
229 birds. In contrast to the results for birds, no facet of mammal diversity was significantly
230 different inside versus outside PAs (Extended Data Table 1). This was likely because, even
231 outside of PAs, mammal diversity remained high in nearby unprotected areas, particularly
232 adjacent to large PAs. This enhanced mammal diversity outside large PAs rendered non-
233 significant the pairwise differences in diversity between ‘protected’ and ‘non-protected’
234 sites. Estimated mammal SR, FR, and PD outside of PAs were 25.4%, 193.7%, and 23.8%
235 higher, respectively, when the nearest PA was large (>500 km²) than when it was smaller
236 (all $p < 0.001$; Fig. 4; Extended Data Table 1). Bird FR and PD outside of PAs were also
237 significantly higher near large reserves (9.4% and 9.9% higher, respectively; Fig. 5) but
238 these differences were considerably smaller than those of mammals (Extended Data Table
239 1). For sampling locations outside PAs, distance to the nearest reserve was significantly
240 associated with only one of the six diversity metrics, whereby mammal FR was higher in
241 proximity to PAs than farther away (Extended Data Table 1).

242 Taken together, our results show that the legal designation of PAs, and not just their
243 biased placement, provides strong and significant benefits to Southeast Asian bird
244 diversity. Our findings also show that large PAs are associated with higher diversity of both
245 mammals and birds in surrounding unprotected areas, consistent with spillover rather
246 than leakage being the dominant pattern at the landscape scale. The effects of PAs on birds
247 inside parks and both taxa in the surrounding landscape are likely explained, at least in
248 part, by PAs limiting hunting. We statistically controlled for accessibility in our models –
249 this means that even at sites with equivalent potential hunting pressure inside versus
250 outside PAs, sites at the former had lower realized hunting pressure. Enforcement,

251 community engagement, or other PA management activities ⁴⁴ may be reducing hunting
252 activities even in areas that are logistically accessible to hunters.

253 The potential spillover that we detected may be driven by density dependent
254 dispersal of animals out of source populations inside PAs ⁴³, with bigger reserves being
255 particularly effective by supporting larger source populations. Spillover is frequently
256 reported from marine PAs, supporting fishing in nearby areas ⁴³, but such evidence is far
257 more limited in terrestrial environments. It is important to note that spillover in the marine
258 PA context is measured as the movement of individuals and biomass, with few studies
259 assessing changes in overall diversity. Indeed, our results may be conservative in that they
260 focus on diversity rather than the abundance dynamics of particular species. Hunting and
261 other threats will reduce abundance before they start to cause the outright extirpations (or
262 declines to such low levels that detection is unlikely) that influence richness. The fact that
263 we detected such strong changes in occurrence (measured cumulatively, across species, as
264 changes in SR, FR, and PD) means that any influences of PAs inside (birds) and outside
265 (mammals and birds) their boundaries are strong indeed. But as techniques improve for
266 abundance estimation for multiple species at large spatial scales and high temporal
267 resolutions ⁵¹, biodiversity monitoring in general and PA efficacy assessments in particular
268 will become more powerful. We also note that an alternative mechanism for the patterns
269 we detected is that large reserves may be more effective than smaller ones at attracting
270 investment in conservation interventions such as outreach and enforcement ⁴⁴. Better
271 understanding the mechanisms of biodiversity spillover from tropical PAs may be very
272 important for conservation and the achievement of the UN 30 × 30 goals.

273 We assessed diversity outside PAs as a function of Euclidean distance to the nearest
274 reserve, though it is not entirely surprising that these variables were not significantly
275 related. Straight-line distance does not account for how topography, forest quality, human
276 infrastructure, or hunting might affect animal movement out of protected areas and across
277 the landscape, and so is only a very crude metric of PA proximity. Future work could
278 explore declines in diversity with decreasing PA proximity, a pattern predicted from the
279 ‘spillover’ hypothesis, using circuit theoretical movement models, as we did to estimate site
280 accessibility to humans while accounting for ease-of-movement through different
281 topographies and landscapes ^{35,36}.

282 Based on prior research ^{3,20}, we were able to identify clear confounding variables for
283 our assessment of PA efficacy and to de-confound the resulting analyses using structural
284 causal modeling, propensity score-matching, and newly available data on the confounding
285 variables. Based on this, we suggest that PA designation enhances bird diversity. For the
286 assessment of PA effects outside their boundaries, potential confounding and missing
287 variables were less clear, so we cannot claim that large PAs ‘cause’ (in a metaphysical
288 sense) elevated diversity in the surrounding landscape. But even demonstrating a
289 predictive, probabilistic relationship between PAs and diversity inside and outside their
290 boundaries suggests that expanding the PA network in accordance with 30 × 30 goals
291 should enhance bird and mammal diversity. This argument would be belied, however, if
292 high-diversity areas had been protected first, with newer PAs relegated to areas with
293 successively lower diversity. Such a pattern would imply that further expansions of the PA
294 network would be likely to occur in even lower diversity areas and thus contribute little to
295 conservation. But this scenario is not supported. Protected area ‘year of designation’ was

296 not significantly related to any facet of bird (p value range: 0.235 – 0.933) or mammal (p
297 values: 0.180 – 0.871) diversity. Our predictions of increasing diversity with PA coverage
298 may be inaccurate in terms of how the designation of any one particular new PA will affect
299 diversity; there are just too many contingencies and idiosyncrasies for that level of
300 prediction to be robust. But at broader scales, our results show strong positive effects of
301 PAs on average diversity levels. This supports that if the region develops the numerous
302 new PAs that will be required to meet 30 × 30 commitments, then cumulatively these new
303 areas will contribute to the conservation of bird and mammal diversity.

304

305 Our results can inform and improve implementation of the UN 30 × 30 agreement
306 and the Convention on Biological Diversity’s post-2020 Global Biodiversity Framework
307 with regards to biodiversity monitoring. The vast majority of species are not visible from
308 space; their occurrence, abundance, and diversity must be measured on the ground and
309 then, for spatial and temporal extrapolation, linked to remote sensing data via predictive
310 modelling⁵². The Essential Biodiversity Variables (EBVs) approach was developed by the
311 UN 2030 Agenda for Sustainable Development goals⁵³ to facilitate monitoring biodiversity
312 trends and evaluate management impact³¹. EBVs are intended to integrate on-the-ground
313 biodiversity information with remote sensing data^{54,55}. Our results advance the
314 development, integration, and monitoring of EBVs related to species traits, community
315 composition, and ecosystem structure rather than just distributions of a few target taxa.
316 Furthermore, our results highlight the need to incorporate 3D forest structure and proxies
317 for hunting pressure into spatial biodiversity modelling in order to explain trends in
318 certain EBVs and formulate effective management responses. Accessibility, especially if

319 paired with socioeconomic and cultural mediating factors, can be a very useful proxy for
320 current hunting pressure for certain taxa ^{35,36}. The distribution of other species may be
321 determined by past hunting pressure. Such historical influence is often overlooked, but
322 needs to be incorporated into spatial models, particularly for “refugee species” ⁵⁶; tigers
323 (*Panthera tigris*) in Southeast Asia, for example, are currently relegated to remote, hilly
324 areas because they have been hunted out of their preferred habitat, lowland plains and
325 riparian areas. While regional and global maps are available for most conservation threats,
326 robust regional maps of hunting pressure have only recently emerged ^{35,39}. These maps
327 present new opportunities for biodiversity monitoring and PA efficacy assessment and
328 could be updated dynamically over time, with investments in new technology-based
329 approaches to monitoring hunting (e.g., with acoustics or camera traps). We have made our
330 potential hunting pressure map for Southeast Asia publicly available (See ‘Data
331 availability’), and our circuit theory approach ³⁵ could be applied to nearly any region.

332 PAs have long been the cornerstone of global biodiversity conservation, but our
333 results suggest that reserve designation alone is insufficient for conserving biodiversity.
334 Our findings are consistent with management (rather than simple remoteness) enhancing
335 vertebrate diversity inside and outside PAs. But other studies have demonstrated huge
336 variance in management effectiveness ^{3,5,7,12,16,19}, with many PAs being mere ‘paper parks’.
337 Effective management of hunting is a key opportunity to improve PA effectiveness, as is
338 designating larger PAs that may enhance the spillover of animals (or conservation
339 measures) to surrounding landscapes. The designation of new, large protected areas could
340 include traditional PAs such as national parks, but also the variety of “Other Effective area-
341 based Conservation Measures” that are being explored as de facto means of increasing

342 protected area coverage in accordance with national and international targets ⁵⁷. We echo
343 earlier suggestions that expansion of PAs must be accompanied by substantial investment
344 in initiatives promoting hunting sustainability ^{58,59}, such as capacity building for park staff
345 and the creation of alternative livelihoods for hunters. Investment by way of forest-based
346 carbon financing, with projects adhering to the Climate, Community, and Biodiversity
347 Standards, provides explicit provisions for biodiversity protection and community
348 livelihoods including active control of hunting and encroachment, with such standards
349 assessed during regular audits ⁶⁰. Such measures can help ensure that reserves in less
350 developed countries, and in the myriad areas susceptible to unsustainable hunting, can
351 achieve the same conservation outcomes as those in more developed and less hunted areas.

352

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505

506 **Fig. 1 | Protected area (PA) effectiveness depends on safeguarding multiple facets of**
507 **biodiversity. (a)** PAs such as national parks can reduce habitat loss and degradation
508 (logging) and extractive behaviors such as hunting (shown in red circle), but there are a
509 wide range of real-world outcomes based on management effectiveness. **(b)** PAs aim to
510 safeguard multiple facets of biodiversity, including species richness (SR), functional
511 richness (FR) and phylogenetic diversity (PD). PAs often focus on vertebrate conservation
512 due to their threat-levels and value to humans, including for tourism. Our study focuses on
513 Southeast Asian wildlife, with mammals shown here representing a variation of feeding
514 guilds and sizes. The same approach repeated for birds. **(c)** Wildlife communities inside
515 PAs and in the surrounding landscape may have distinctive levels and types of diversity.
516

517 **Fig. 2 | Site accessibility overlain with bird (triangle) and mammal (circle) sampling**
518 **locations across Southeast Asia.** Variation in the accessibility of locations (e.g., to
519 hunters; yellow-red) is estimated from circuit theoretic movement models. Designated
520 terrestrial protected areas within the study region are shown in green.

521
522 **Fig. 3 | All facets of bird diversity were higher inside than outside protected areas.**
523 Panels **a – c** show violin plots of calculated diversity across sites, including variance in
524 many covariates, and the percent difference in diversity means; points and lines show
525 means and s.d., respectively. Panels **d – f** show estimated diversity (and mean differences
526 between protected and unprotected sites) from spatial mixed-effects regression (two-
527 tailed) on propensity score-matched data; points and lines show means and s.e.m.,
528 respectively. Adjustments were not made for multiple comparisons; n = 1072, 1074, and

529 1073 biologically independent sites for species richness (**a, d**), functional richness (**b, e**),
530 and phylogenetic diversity (**c, f**), respectively.

531

532 **Fig. 4 | All facets of mammal diversity outside of protected areas (PAs) are higher**
533 **near large (>500 km²) than small PAs.** Panels **a – c** show violin plots of calculated
534 diversity across sites, including variance in many covariates, and the percent difference in
535 diversity means; points and lines show means and s.d., respectively. Panels **d – f** show
536 estimated diversity (and mean differences between sites near large versus small PAs) from
537 spatial mixed-effects regression (two-tailed) on propensity score-matched data; points and
538 lines show means and standard errors, respectively. Adjustments were not made for
539 multiple comparisons; n = 1362, 1362, and 1360 biologically independent sites for species
540 richness (**a, d**), functional richness (**b, e**), and phylogenetic diversity (**c, f**), respectively.

541

542 **Fig. 5 | All facets of bird diversity outside of protected areas (PAs) are higher near**
543 **large (>500 km²) than small PAs, but these differences are lower than with mammals**
544 **(Fig. 4).** Panels **a – c** show violin plots of calculated diversity across sites, including
545 variance in many covariates, and the percent difference in diversity means; points and lines
546 show means and s.d., respectively. Panels **d – f** show estimated diversity (and mean
547 differences between sites near large versus small PAs) from spatial mixed-effects
548 regression (two-tailed) on propensity score-matched data; points and lines show means
549 and standard errors, respectively. Adjustments were not made for multiple comparisons; n
550 = 1074, 1072, and 1073 biologically independent sites for species richness (**a, d**), functional
551 richness (**b, e**), and phylogenetic diversity (**c, f**), respectively.

553 METHODS

554 *Species observations, trait data, and phylogeny construction*

555 We assembled camera trap data of mammals from across the region. These data came from
556 different research projects spanning 65 distinct study areas within the region (Fig. 2;
557 Extended Data Table 2). In all cases, cameras were un-baited, active 24 hours per day, and
558 attached to trees at ~0.3 - 0.6 m (depending on topography, vegetation understory, and
559 other factors mediating the camera viewshed), heights capable of obtaining pictures of
560 animals of a wide variety of sizes. Cameras were spaced ~1 km apart in most study areas
561 and ~2.5 km apart in Vietnam. Cameras were active for a median 88 days (SD = 60.5; range
562 = 16 - 439). In 9.3% of the 178,169 total photographic records it was impossible to
563 determine the exact species of *Callosciurus*, *Herpestes* [including *Urva*], *Hystrix*, *Muntiacus*,
564 *Tragulus*, *Tupaia*, or “otter”; we assigned these cases the average functional trait values for
565 each genus (for the FR calculation) and assigned the records to a widespread member of
566 each genus (for the PD calculation). We also lumped unidentified murid rodents and
567 squirrels, assigning them to *Maxomys whiteheadi* and *Callosciurus prevostii*, respectively,
568 for FR and PD calculation. In total, we detected 112 taxa. For sites with multiple years of
569 sampling, we chose the most recent year for analysis.

570 For birds, we used community science records from the eBird database⁶¹; these
571 constitute species lists from surveys, with multiple surveys per location used to estimate
572 diversity. We collected all records from ‘stationary’ or ‘travelling’ survey protocols from
573 January 2015 through August 2021 for the study region (Fig. 2). We followed data cleaning
574 recommendations⁶²⁻⁶⁴ by filtering the data to only include surveys where (i) all species
575 were recorded, (ii) the distance travelled during the observation (for ‘travelling’ protocol)

576 was ≤ 8.1 km, (iii) the sampling duration (for 'stationary' protocol) was ≥ 5 and ≤ 240
577 minutes, (iv) there were no more than 10 observers, and (v) the observation started
578 between 05:00 and 20:00 local time. Sampling locations had a median 23 samples (range =
579 10 – 1,200; SD = 105.6). We removed records of domestic species and those with
580 identifications that were ambiguous as to genus. This resulted in a final dataset of
581 1,345,922 records of 1,361 taxa. Of these taxa, 1,262 were identified to species and the
582 remaining 7.3% assigned to a widespread congener that occurred at the location.

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

591 For the phylogenetic diversity calculations, we constructed consensus phylogenies
592 (including consensus branch lengths) of all detected bird and mammal species from 1000
593 trees for each taxon from the VertLife database⁶⁶. Taxa identified only to genus level were
594 added to the root nodes of their genera. The resulting consensus trees were ultrametric,
595 rooted, and dichotomous. We standardized taxonomic nomenclature between the field
596 data, traits data, and phylogenies.

597

598 *Variables*

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

610 Site accessibility is a proxy for potential hunting pressure, but realized hunting
611 pressure will also be mediated by socioeconomic factors. As a simple metric of
612 socioeconomic level, we included the Human Development Index (HDI) ⁶⁸ of each country
613 both as a main effect and as a statistical interactor with site accessibility. In analyses on the
614 full dataset, we included a binary variable indicating whether or not the site was in a
615 protected area (PA) using the World Database on PAs ⁶⁹. For analyses on the subset of sites
616 inside PAs, we replaced the binary variable with the size of the PA (km^2). For analyses on
617 the subset of sites outside PAs, the binary variable was replaced with the distance (km) to
618 the nearest PA and the size (km^2) of that PA.

619 To assess the role of forest structure, we used five variables (described in the main
620 text) derived from the Global Ecosystem Dynamics Investigation (GEDI) ³⁴ generated using
621 kriging to interpolate the sample-based data to the exact locations of the biodiversity

622 sampling sites. We selected ecologically relevant metrics from the GEDI L2A (Elevation and
623 Height Metrics) and L2B (Canopy Cover and Vertical Profile Metrics) products (version 2;
624 from 2019-04-17 to 2022-04-12). After filtering based on quality and degrade flags, the
625 average sampling density across the study region was 15 points km⁻². We performed the
626 spatial interpolation processes with the *gstat* package ⁷⁰ in R ⁷¹. We first derived separate
627 empirical variograms for each structural variable on each major landmass of the study
628 region. We optimized the model parameters with grid searches and selected the best
629 models based on weighted (with inverse square distance) least squares fit. To determine an
630 estimate of each variable at the exact location of each species observation site, we
631 performed local kriging with a neighborhood of the 5000 closest valid GEDI samples. To
632 map each variable at each pixel across the study region, we performed local kriging at the
633 pixel locations with a neighborhood of the 500 closest GEDI samples ⁷². Rasters of the
634 interpolated, GEDI-derived forest structure metrics are available (see 'Data availability').

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

642

643 *Diversity estimation*

644 For both birds and mammals, the sampling intensity varied across locations and species
645 were detected imperfectly. We accounted for this by using rarefaction-extrapolation
646 techniques, using the *iNEXT* package ⁷³ in R, to determine the estimated diversity for a
647 standardized sampling intensity ‘endpoint’. For mammals, we used a minimum sampling
648 intensity of 15 days, following Kays et al. ⁷⁴, who suggested a minimum of two weeks
649 sampling for camera trap studies, after which time the number of detected species rapidly
650 plateaus. We set the sampling endpoint at three times this number, as diversity
651 extrapolation is not considered reliable beyond triple the reference sample size ^{75,76}. Thus,
652 our mammal diversity estimates should be viewed as the SR, FR, or PD at a given site as
653 detected within a 45-day sampling window. For birds, we set the minimum number of
654 samples at a given location equal to 10, which balanced the need for sufficient sampling to
655 ensure robust diversity estimation with the need to avoid throwing away excessive data
656 (i.e., increasing the minimum number of samples to 15 would have necessitated throwing
657 away 28% of sampling locations, which could have biased results by increasing Type II
658 error). Again, our sampling endpoint was set to three times the minimum sample size, so
659 our bird diversity estimates should be viewed as the SR, FR, or PD at a given site as
660 detected within a 30-day sampling window.

661 For SR, we generated a species × sample matrix populated by incidence data. We
662 calculated the increase in Faith’s phylogenetic diversity (PD) metric ⁵⁰ across successive 5-
663 day sample intervals at each site using the *picante* ⁷⁷ package in R and then used the
664 asymptote of the curve as the estimated PD for that site. We calculated Villéger et al.’s
665 functional richness (FR) metric ⁷⁸ using the *FD* ⁴⁴ package in R; FR values are not
666 necessarily monotonically related to sampling intensity or species diversity, so we used the

667 maximum FR value at each site rather than an asymptotic approximation. Diversity
668 estimates are available ⁷⁹ (see 'Data availability').

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

675

676 *Structural causal modelling*

677 We used Structural Causal Modeling (SCM) to assess PA efficacy while de-confounding the
678 effects of site accessibility and forest structure. SCM also allowed us to produce a set of
679 predictor variables for each analysis that would result in unbiased coefficient estimation –
680 while many variables could potentially affect diversity, adjusting for all of them in
681 analytical models can bias results by introducing, rather than minimizing, conditional
682 associations ⁸⁰. We constructed a directed acyclic graph (Extended Data Fig. 2) showing
683 potential causal pathways among variables and used DAGGITY ⁸¹ to identify the sufficient
684 adjustment sets (i.e., suites of covariates) necessary to include in the models in order to
685 generate unbiased estimates of the effects of exposure variables on outcome variables. We
686 began with a nearest-neighbor matching with logit link function, but this yielded somewhat
687 poor covariate balances. We then used full matching on the propensity score estimated
688 with a probit link function; this yielded much better balances (shown in Extended Data
689 Table 3).

690

691 *Linear mixed effects modelling*

692 We used the variables identified in the SCM in linear mixed-effects models to assess PA
693 efficacy and determine the environmental factors related to bird and mammal diversity.
694 We accounted for spatial autocorrelation in two ways. First, we use mixed-effects models
695 with an exponential correlation structure based on the covariance in pairwise distances
696 among sites, following Hakkenberg & Goetz⁸². Second, we also included (for mammals)
697 *study area* nested within *country* as random effects because the data were highly spatially
698 clustered and to account for the potential for other (un-modelled) national-level
699 anthropogenic factors to affect diversity. For birds, we used *country* alone as a random
700 effect because the sampling locations were not clustered into discrete study areas. The SCM
701 identified 'forest structure' as a critical variable to include in the models in order to de-
702 confound our PA efficacy analysis. We determined which GEDI variable to use to represent
703 forest structure based on univariate analyses, as we could not include all of them in the
704 same model because they were highly correlated. *Canopy height* fit the diversity data better
705 (i.e., had lower AIC values) than the other GEDI variables and we included that variable,
706 along with understory vegetation density (*pavd*, which was not strongly correlated with
707 canopy height: $r = -0.01$) in the linear models. All variables included in the same model had
708 correlation coefficients $r < 0.6$. We checked regression diagnostics to assess linear
709 relationships between residuals and fitted values and normality of the residuals. In a few
710 cases (see Extended Data Table 1) we removed some observations to improve normality of
711 the residuals. We assessed the leverage of each observation using the *hatvalues* function in
712 R. In all models, the highest-leverage observations were well below 2 (maximum values for

713 the different analyses were 0.21 – 0.40 and 0.86 – 0.90 for birds and mammals,
714 respectively).

715 To assess PA efficacy, we ran linear mixed-effects models in a statistically matched
716 framework. Matching was conducted using nearest-neighbor propensity score matching
717 without replacement, estimating the propensity score with logistic regression of the
718 treatment (PA status) on the covariates to achieve the best possible balance of covariate
719 values (except protected status) between sites inside versus outside PAs^{3,25}. We matched
720 the datasets based on canopy height, site accessibility, HDI, and location (UTM easting and
721 northing) using the *MatchIt*⁸³ package in R. We then ran linear mixed-effects models on the
722 matched datasets, ensuring that comparisons between sites inside versus outside PAs were
723 on datasets that were otherwise as similar as possible in forest structure, accessibility, and
724 human influence, while also being as geographically matched as possible. We ran these
725 models in the *nlme*⁸⁴ package in R. We tested whether high-diversity areas had been
726 protected first, with newer PAs relegated to areas with successively lower diversity. We
727 ran mixed-effects linear regressions using the same predictor variables as above but also
728 including PA ‘year of designation’.

729 To assess support for spillover versus leakage patterns, we modeled diversity as a
730 function of the predictor variables described above on the subset of sites outside PAs ($N =$
731 621 and 774 for birds and mammals, respectively). In these models, we replaced the *PA*
732 *status* binary variable with either the size of the nearest PA or (in separate models), the
733 distance to the nearest PA. These data were analyzed propensity score-based statistical
734 matching to achieve covariate balances, using full matching and probit link functions, as
735 described above. Covariate balances are shown in Extended Data Table 3 and model results

736 (standardized beta coefficients and p values) in Extended Data Table 1. The point of
737 propensity score matching is to achieve balanced sets of covariate values between two sets
738 of data – thus the response variables in such analyses are binary. Despite broad consensus
739 that large protected areas are necessary for conserving certain vulnerable elements of
740 biodiversity^{85,86}, and evidence that they provide a higher per-unit return-on-investment
741 than smaller PAs⁸⁷, surprisingly little research allows us to determine size thresholds in PA
742 performance – in other words, to ascertain ‘how large are large PAs?’. A prior assessment
743 of PA effectiveness at conserving natural habitat in other tropical regions suggests that
744 strong habitat disturbance can occur ~12 km into the boundary of PAs⁸⁸. Assuming
745 circular reserves, this would translate to a minimum of ~500 km² for a PA to maintain a
746 core of little-disturbed habitat. Therefore, we used 500 km² as a threshold distinguishing
747 ‘large’ from ‘small’ PAs in our analysis. After establishing that diversity was higher near
748 large than small PAs based on this threshold, we ran sensitivity analyses where we re-ran
749 the models but with different PA size thresholds. Diversity was generally enhanced in large
750 relative to small PAs at alternative thresholds of 400, 600, and 1000 km², particularly for
751 mammals (Extended Data Table 4).

752

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837 AUTHOR CONTRIBUTIONS

838 JFB conceived the study and analyzed the data. JFB, JA-M, CC, ORW, SWT, PW, ES, AN, JM,
839 and MSL led the camera-trapping field work. MCMD generated the potential hunting
840 pressure map, PB processed the GEDI data, and JGCB conducted the interpolation of the
841 GEDI data. JFB wrote the initial manuscript, with input from MSL; all authors contributed to
842 revising and rewriting.

843

844 DATA AVAILABILITY

845 Data used in the mixed-effects modeling analysis are available at
846 <https://doi.org/10.6084/m9.figshare.22527298.v1>. Rasters (1-km resolution) for the
847 study area for the GEDI-derived forest structural covariates and estimated site accessibility
848 are available at https://rcdata.nau.edu/geode_data/SEA Vertebrate Diversity Rasters/.

849

850 CODE AVAILABILITY

851 Analysis codes (in the R programming language) are available at
852 doi.org/10.5281/zenodo.7796347.

853

854 COMPETING INTERESTS

855 Mammal data collection in one study area (out of 65) was funded by Sarawak Energy
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857 reviewed the manuscript before it was submitted.

858

859 ADDITIONAL INFORMATION

860 Supplementary Information is available for this paper.

861

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864

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868

869 EXTENDED DATA FIGURE LEGENDS

870 FIGURE 1. Estimates of sampling completeness – the correspondence between the number
871 of species detected at sampling locations and the number estimated from rarefaction-
872 extrapolation (see Methods) for birds (panel a; Pearson's $r = 0.91$) and mammals (b; $r =$
873 0.79), with 1 : 1 lines shown.

874

875 FIGURE 2. Directed acyclic graph of bird or mammal diversity in relation to exposure
876 variables and covariates. The structure of the graph shows how the influence of protected
877 areas on diversity are de-confounded from the influence of forest structure and site
878 accessibility.

879

880 EXTENDED DATA TABLE LEGENDS

881 TABLE 1. Results from mixed-effects linear regression (two-tailed) for species richness
882 (SR), functional richness (FR), and phylogenetic diversity (PD). Values are the model β
883 coefficients (SE; *p*-value) for the exposure variables in each analysis ('PA', 'PA size', and
884 'Distance to PA') and associated covariates, with conditional R^2 shown. Adjustments were
885 not made for multiple comparisons. PC = Principal Component axis; HDI = Human
886 Development Index (a national-level metric); PA = Protected Area; other variables are
887 explained in the main text. All continuous covariates were standardized prior to analysis.
888 Exposure variable coefficients with *p*-values <0.05 are in bold; covariate coefficients and *p*-
889 values should not be interpreted in propensity score-matched analyses.

890

891 TABLE 2. Locations of the mammal study areas showing mean (SD) latitude, longitude,
892 elevation, topographic position index (TPI), and site accessibility, along with the
893 percentage of camera stations inside protected areas (PAs).

894

895 TABLE 3. Propensity score statistical matching results. UTM = Universal Transverse
896 Mercator; TPI = Topographic Position Index; HDI = Human Development Index (a national-

897 level metric); PC = Principle Component axis; PA = Protected Area; other variables are
898 explained in the main text.

899

900 TABLE 4. Results from mixed-effects linear regression (two-tailed) for species richness
901 (SR), functional richness (FR), and phylogenetic diversity (PD) of birds and mammals as a
902 function of protected area size (binary) across different size thresholds. Adjustments were
903 not made for multiple comparisons. Values are the model β coefficients (*p*-value).

904

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906