

42 **Title: Using a large-scale biodiversity monitoring dataset to test the effectiveness of**  
 43 **protected areas ~~inat~~ conserving North-American breeding birds**

44  
 45  
 46 **Authors:** Victor Cazalis\*<sup>1</sup>, Soumaya Belghali<sup>1</sup>, Ana S.L. Rodrigues<sup>1</sup>

47 \* Corresponding author: [victor.cazalis@laposte.net](mailto:victor.cazalis@laposte.net)

48 <sup>1</sup>: Centre d'Ecologie Fonctionnelle et Evolutive, ~~CEFE-UMR 5175, CNRS~~, Univ. de  
 49 Montpellier – [CNRS](#) – Univ. Paul-Valéry Montpellier – EPHE – CNRS, Montpellier, France.

50  
 51  
 52 **Abstract:**

53 Protected areas currently cover about 15% of the global land area, and constitute one of the  
 54 main tools in biodiversity conservation. Quantifying their effectiveness at protecting species  
 55 from local decline ~~and local~~ extinction involves comparing protected with counterfactual  
 56 unprotected sites representing “what would have happened to protected sites ~~if had~~ they ~~had~~ not  
 57 been protected”. Most studies are based on pairwise comparisons, using ~~as counterfactuals~~  
 58 neighbour sites to protected areas as counterfactuals, but this choice is often subjective and may  
 59 be prone to biases. An alternative is to use large-scale biodiversity monitoring datasets, ~~which~~  
 60 whereby the effect of protected areas is analysed statistically by controlling for landscape  
 61 differences between protected and unprotected sites, allowing a more targeted and clearly  
 62 defined measure of the protected areas effect. Here we use the North American Breeding Bird  
 63 Survey dataset as a case study to investigate ~~protected areas the~~ effectiveness ~~in of protected~~  
 64 areas at conserving bird assemblages. We analysed the effect of protected areas on  
 65 ~~species-species~~ richness, on assemblage-level abundance, and on the abundance of individual  
 66 species by modelling how these metrics relate to the proportion of each site that is protected,  
 67 while controlling for ~~site~~local habitat, altitude, productivity and for spatial autocorrelation. At  
 68 the assemblage level, we found almost no relationship between protection and species richness  
 69 or overall abundance. At the species level, we found that ~~species that avoid human activities~~  
 70 ~~tend to be favoured by protected areas are the one avoiding human activities. Moreover, we~~  
 71 ~~found that~~ forest ~~protected areas presented~~ species are present in significantly higher abundances  
 72 of within protected forest sites, compared with unprotected forests, with the opposite effect for  
 73 species, making the assemblage that favour open habitats. Hence, even though protected forest  
 74 assemblages are not richer than those of unprotected forests, they are more typical of this  
 75 habitat. We ~~did not find that~~ also found some evidence that species that avoid human activities  
 76 tend to be favoured by protection, but found no such effect for regionally declining species ~~were~~  
 77 particularly favoured by protected areas. Our results highlight the complexity of answering the  
 78 question of assessing protected areas effectiveness, and the necessity ~~to define of~~ clearly defining  
 79 the metrics measured of effectiveness and the controls used in such assessments.

80  
 81 **Acknowledgments:** We thank Jean-Yves Barnagaud for his insightful comments and  
 82 suggestions concerning the analyses. We are grateful to all BBS birders the thousands of U.S.

83 and ~~coordinators for the high quality data they have collected~~Canadian participants who  
84 annually perform and coordinate the Breeding Bird Survey.

85

86 **Keywords:** biodiversity conservation; biodiversity monitoring; protected areas effectiveness;  
87 birds; North-~~America BBS~~American Breeding Bird Survey; conservation effectiveness.

## Introduction

The increasing human footprint on natural ecosystems is leading to major declines in species' populations (McRae et al., 2016) and has already resulted in thousands of extinctions (IUCN, 2018), to such an extent that Ceballos et al. (2017) characterised current times as a period of "biodiversity annihilation". Habitat loss and degradation are the most important pressures on biodiversity (Vié et al., 2009; Balmford and Bond, 2005), as a result of anthropogenic activities such as agriculture, urbanisation, industry, transport and recreation (Foley et al., 2005). The most evident response to these threats is to establish areas with restricted, or even no human activities, *i.e.*, to create protected areas (PAs). Modern PAs have their origins in the 19<sup>th</sup> century and currently represent the most important conservation tool, with about 15% of the global land area already protected to some extent, and coverage planned to reach 17% by 2020 (UNEP-WCMC IUCN, 2016).

Understanding the extent to which PAs are ~~being~~ effective as biodiversity conservation tools is ~~thus~~ fundamental for guiding future conservation efforts. Accordingly, there is a substantial ~~and~~ ~~large~~ literature on PA effectiveness: as of the 1<sup>st</sup> October 2018, 260 publications in the Web of Science included in their title "protected AND area\* AND effective\*". However, within this literature there are disparate approaches to the concept of "effectiveness".

A first set of studies questions whether PAs are effective at representing species or ecosystems, using gap analyses for measuring the overlap between PAs and the distributions of species or ~~ecosystem types (e.g., Rodrigues et al., 2004; Brooks et al., 2004). These studies do not directly quantify the effectiveness of PAs at conserving biodiversity, but the extent to which species or ecosystems are buffered from human impacts under the assumption that PAs are highly effective in doing so. A second set of studies focuses on the means employed locally by PA managers in order to protect biodiversity, for example in terms of staff or money (e.g., Leverington et al., 2010). These analyses do not directly measure PA effectiveness in reducing human impacts, but rather the resources allocated to this purpose. A third type of studies quantifies the effectiveness of PAs at preventing the conversion of natural ecosystems, typically by comparing land use change (e.g., deforestation rates) in protected versus unprotected areas (Nelson and Chomitz, 2009; Andam et al., 2008). These studies quantify PA effects at the habitat or ecosystem level, rather than at the species level. Finally, a set of analyses focuses on measuring the effect of PAs on species themselves, either on the diversity of assemblages or on the abundance of individual species, typically by contrasting protected versus unprotected sites (e.g. Coetzee et al., 2014; Gray et al., 2016; Devictor et al., 2007, discussed below).of ecosystem types (e.g., Rodrigues et al., 2004; Brooks et al., 2004). These studies do not directly quantify the effectiveness of PAs at conserving biodiversity, but the extent to which species or ecosystems are buffered from human impacts under the assumption that PAs are highly effective in doing so. A second set of studies focuses on the means employed locally by PA managers in order to protect biodiversity, for example in terms of staff or money (e.g., Leverington et al., 2010). These analyses do not directly measure PA effectiveness in reducing human impacts, but rather the resources allocated to this purpose. A third type of studies quantifies the effectiveness of PAs at preventing the conversion of natural ecosystems, typically by comparing land use change (e.g., deforestation~~

131 rates) in protected versus unprotected areas (e.g., Nelson and Chomitz, 2009; Andam et al.,  
132 2008). These studies quantify PA effects at the habitat or ecosystem level, rather than at the  
133 species level. Finally, a set of analyses focuses on measuring the effect of PAs on species  
134 themselves, either on the diversity of assemblages or on the abundance of individual species,  
135 typically by contrasting protected versus unprotected sites. This fourth approach to PA  
136 effectiveness is the focus of the present study.

137  
138 ~~Assessing the effectiveness of PAs in conserving species can be implemented by comparing~~  
139 ~~population trends (e.g. Gamero et al., 2017; Devictor et al., 2007; Pellissier et al., 2013).~~  
140 ~~Indeed, if PAs are effective, populations in them are expected to be better buffered from threats~~  
141 ~~and thus decline less, or even to increase more, than those outside. Trends however can be~~  
142 ~~misleading, because they are calculated in relation to a reference date (that seldom precedes all~~  
143 ~~anthropogenic impacts) and because they are measured as percentages (which emphasise~~  
144 ~~changes in small numbers). Hence, for example, given a species in three sites: one where it~~  
145 ~~remained stable at 1000 individuals; a second where it initially declined from 1000 to 10 and~~  
146 ~~recently increased to 20; and a third where it first declined from 1000 to 800 and recently~~  
147 ~~recovered to 1000. In terms of recent trends, the second site appears by far the most effective,~~  
148 ~~even though it has the most depleted population, and even though in absolute numbers the~~  
149 ~~population increase in the third site is 20 times more important. In this study, we focus instead~~  
150 ~~on measures of PA effectiveness that assess current state, namely by contrasting population~~  
151 ~~abundances and species diversity (e.g. Coetzee et al., 2014; Kerbiriou et al., 2018; Devictor et~~  
152 ~~al., 2007). Indeed, if PAs have been effective in conserving species, we expect that over time~~  
153 ~~that translates into higher absolute population abundances than in counterfactual areas, as well~~  
154 ~~(if local extinctions have been prevented) in species diversity.~~

155  
156 The effectiveness of PAs at conserving species can be assessed by comparing population trends  
157 inside and outside PAs (e.g. Gamero et al., 2017; Devictor et al., 2007; Pellissier et al., 2013).  
158 Indeed, if PAs are effective, populations inside these areas are expected to be better buffered  
159 from threats and thus to decline less, or even to increase more, than those outside. Trends  
160 however can be misleading, because they are calculated in relation to a reference date (that  
161 seldom precedes all anthropogenic impacts) and because they are measured as percentages  
162 (which emphasise changes in small numbers). In this study, we focus instead on measures of  
163 PA effectiveness that assess current state, namely by contrasting population abundances and  
164 species diversity inside versus outside PAs (e.g. Coetzee et al., 2014; Kerbiriou et al., 2018;  
165 Devictor et al., 2007). These measures combine two types of effects: the effectiveness at  
166 selecting as PAs sites of higher-than-average conservation interest (i.e. differences that existed  
167 at the time of PA designation); and effectiveness at maintaining species richness and abundance  
168 within existing PAs (i.e. differences established subsequently to PA designation).

169  
170 Three recent ~~studies~~ meta-analyses investigated the effects of PAs on the state of species  
171 abundance and/or diversity, ~~through meta-analyses of~~ by synthesising studies that made  
172 pairwise comparisons between protected and unprotected sites (~~Geldmann et al., 2013; Coetzee~~  
173 ~~et al., 2014; Gray et al., 2016).~~ (Geldmann et al., 2013; Coetzee et al., 2014; Gray et al., 2016).  
174 The underlying studies used in these meta-analyses did not necessarily aim to measure PA

175 effectiveness; more often they investigated the effects of anthropogenic pressure, using PAs as  
176 benchmarks (e.g. Sinclair et al., 2002; Bihn et al., 2008; Wunderle et al., 2006, all used in  
177 Coetzee meta-analysis). The meta-analyses considered that unprotected sites acts (e.g. Sinclair  
178 et al., 2002; Bihn et al., 2008; Wunderle et al., 2006, all integrated in Coetzee meta-analysis).  
179 In the meta-analyses, unprotected sites were treated as counterfactuals to the protected sites  
180 (i.e., by assuming that the latter would be in a similar condition to the former if it had not  
181 been protected), measuring the effect of protection as the observed difference between the two.  
182 Pairwise These pairwise comparisons often compare contrast neighbouring sites, which presents  
183 the advantage of ensuring that both have broadly similar environmental characteristics (e.g.  
184 same climate), but). However, they do not necessarily take into account the fact that PAs tend  
185 to be biased in their location towards higher altitudes and lower productivity areas (Joppa and  
186 Pfaff, 2009)(Joppa and Pfaff, 2009). To account for this reduce these biases, Gray et al. (2016)  
187 controlled for the differences in altitude, slope and agricultural suitability. Controlling for these  
188 factors means that their results are less influenced by PAs' location biases and, therefore, that  
189 they reflect more strongly the effects of protection itself. Another potential bias resulting  
190 from confounding effect in pairwise comparisons of neighbouring sites arises from the leakage  
191 effect, whereby the human activities that would have taken place inside a PA are displaced to  
192 areas around it, artificially inflating the perceived effectiveness of PAs (Ewers and Rodrigues,  
193 2008). This effect is difficult to control for, but should be reduced if the counterfactual sites are  
194 not immediately adjacent to the PAs.

195  
196 An important decision when choosing a suitable spatial counterfactual to a PA, one that strongly  
197 affects the definition and thus the measure of PA effectiveness, is whether to control for habitat  
198 type or not. Indeed On the one hand, not considering it could controlling for habitat can lead to  
199 comparing sites that are not expected to have similar biodiversity regardless of their protection  
200 status (e.g. protected grassland grasslands vs unprotected forest), while not considering it  
201 overlooks the effect forests). On the other hand, controlling for habitat type can result in an  
202 overlooking of the effects that PAs through have on biodiversity by preventing habitat changes  
203 (e.g. deforestation or urbanization). For instance, given a hypothetical PA covering a natural  
204 grassland, possible counterfactuals include an unprotected site of similar habitat (i.e., natural  
205 grassland (same habitat, but), an unprotected), as well as a diversity of unprotected sites site  
206 with a different habitats, for example an type of natural habitat (e.g., forest, wetland), or an  
207 unprotected site with human-modified habitat (e.g., extensive pasture (same vegetation  
208 structure, but with relatively low level anthropogenic use), an herbaceous cropland (same  
209 vegetation structure but highly transformed), or an urbanised, urban area (a wholly different  
210 ecosystem). This). The choice of counterfactual is certain to have a major impact on the  
211 differences observed, and thus on the measure of PA effectiveness, but it is not necessarily  
212 obvious what which option is the best counterfactual should be. In theory, it is the site that best  
213 represents "what would have happened to the PA in the absence of protection"; in practice, this  
214 is not necessarily easily determined. All three meta-analyses (Geldmann et al., 2013; Coetzee  
215 et al., 2014; Gray et al., 2016) include comparisons where habitat has not been controlled for,  
216 meaning that the counterfactual's habitat may be different or similar to the protected site's  
217 habitat. Additionally, a subset of Gray et al. (2016)'s analyses focuses on comparisons between  
218 protected and unprotected sites with matched habitats. In this the latter, the measure of PA

219 effectiveness concerns protection from habitat degradation rather than protection from habitat  
220 conversion.

221

222 Another key consideration in analysing PA effectiveness is the biodiversity metrics ~~of~~  
223 ~~interest applied to comparing protected and unprotected sites.~~ The three meta-analyses  
224 ~~applied/employed~~ a diversity of metrics, some at the level of species' assemblages, some  
225 focused on individual species. Gray et al. (2016) used only assemblage-level metrics and found  
226 higher species richness and overall abundance inside PAs than outside, but no difference in  
227 rarefaction-based richness (i.e. number of species for a given number of individuals) nor in the  
228 proportion of endemic species. When matching sites with similar habitats, species richness was  
229 only higher in young and small PAs than in unprotected sites (no difference between other  
230 protected and unprotected sites), suggesting that the effect of PAs ~~on~~ in preventing habitat  
231 degradation was light. Conversely, Geldmann et al. (2013) considered only species-level  
232 metrics (presence, abundance, nest survival) and found contrasted but mainly positive effects  
233 of PAs. Finally, Coetzee et al. ~~(2014)~~ (2014) considered both levels; at the assemblage level,  
234 they found higher species richness and overall abundance in protected than in unprotected sites;  
235 at the species level, they found that individual species abundances were typically higher inside  
236 PAs.

237

238 ~~In this study, we use a different approach for quantifying PA effectiveness, one which is not~~  
239 ~~based on pairwise comparisons, but instead takes advantage of a large dataset compiling bird~~  
240 ~~counts across a near continental area: the North American Breeding Bird Survey (Pardieck et~~  
241 ~~al., 2017). This approach has already been used in other geographical areas, with other datasets~~  
242 ~~(e.g. Devictor et al., 2007 with French birds; Kerbiriou et al., 2018 with French bats; Duckworth~~  
243 ~~and Altwegg, 2018 with South African birds) with heterogeneous results but mainly showing~~  
244 ~~positive effects of PAs. In this approach, instead of pairing sites, the effect of PAs is quantified~~  
245 ~~through~~ An alternative to measuring PA effectiveness through pairwise comparisons is to use  
246 statistical models in which covariates control for differences between protected and unprotected  
247 sites. This removes the subjectivity in the choice of counterfactuals, by making it clear which  
248 variables are controlled for, and the measure of effectiveness being investigated. In our study,  
249 we control for altitude and productivity in order to reduce the effect of PA location biases. We  
250 estimate This approach requires access to a large dataset on the spatial distribution of  
251 biodiversity, but reduces the subjectivity in the choice of counterfactuals, by making explicit  
252 which variables are controlled for, and the measure of effectiveness being investigated. For  
253 example, Devictor et al. (2007) applied this approach to survey data on common birds across  
254 France to find a positive effect of PAs on bird abundances for half of the species investigated,  
255 especially declining species. Duckworth and Altwegg (2018), working on bird abundance data  
256 collected across South Africa, found that PA coverage was positively correlated with occupancy  
257 of frugivorous, insectivorous, vegivores and predator species, and negatively correlated with  
258 occupancy of granivorous species.

259

260 In the present study, we quantify the effectiveness of Protected Areas at protecting birds by  
261 taking advantage of a large dataset of bird counts across a near-continental area – the North  
262 American Breeding Bird Survey (Pardieck et al., 2017). Controlling statistically for altitude and

263 productivity in order to reduce the effect of PA location biases, we estimated PA effectiveness  
264 on two levels of biodiversity: on species' assemblages, through indices of richness and summed  
265 abundance; and on individual common species, by estimating the effect of PAs on species'  
266 abundance ~~for the most common species.~~ At the assemblage level, we ~~expect~~expected to find  
267 higher species diversity and abundance inside PAs. Indeed, as human activities are causing  
268 species population declines and local extinctions (Ceballos et al., 2017), and as PAs are  
269 expected to buffer against these activities, this should predictably lead to overall higher species  
270 richness and higher total abundance inside PAs, as found by Coetzee et al. ~~(2014)~~(2014) and  
271 Gray et al. (2016). At the individual species level, we ~~expect individual species'~~expected higher  
272 abundances ~~to be higher in~~within PAs. However, given differences in species' habitat  
273 requirements, this result cannot be expected to hold universally (*i.e.*, species are not all expected  
274 to be more abundant in all PAs). For example, we ~~expect~~expected protected forests to have a  
275 positive effect on forest species, but not on grassland species. ~~To take this into account~~Hence,  
276 we ~~control~~controlled in our analyses for broad vegetation structure (forest, shrub, herbaceous),  
277 by investigating separately the effects of PAs dominated by a particular vegetation structure on  
278 species with different habitat requirements. Additionally, we ~~expect~~expected species with  
279 overall declining populations (thus more affected by anthropogenic activities), and species that  
280 avoid human presence (more sensitive to human disturbance) to present higher abundances  
281 inside PAs.

## Methods

As stated in the introduction, in this study, we will use the term PAs “PA effectiveness as” to refer to the difference in species diversity or abundance between protected and unprotected sites, acknowledging that it includes both effectiveness to select. This difference combines the effects of PA site selection (i.e., differences existing prior to the most interesting implementation of PA, for example if they are implemented in sites for conservation when implementing PAs with higher-than-average richness or abundances) and the effectiveness in create more positive or less negative biodiversity trends inside PAs. effects of protection itself (i.e., difference that arise after PA designation, if PAs effectively reduce population depletions and species local extinctions).

### Bird data

We used data from the North-American Breeding Bird Survey (BBS), a long-term volunteer-based monitoring scheme in Canada, the USA, and Mexico (Pardieck et al., 2017). Here we studied only (Pardieck et al., 2017). Our study region encompasses solely Canada and the USA, as few Mexican routes are monitored. This program is based on the annual monitoring of 25–30 thousand routes, each approximately 40 km long, during the bird breeding season. Each route is split into 50 stops; at each stop, the observer counts every bird heard or seen during three minutes, before moving to the next stop.

Given the length of BBS routes, they often intersect multiple land use types (e.g. forested, urban, agriculture; each with different bird assemblages), and they are rarely wholly contained within protected sites (most of the routes that cross PAs do so only in small fractions of their length). As a result, whole BBS routes are not particularly suited sampling units for investigating how PAs affect bird species. We chose instead to focus on small sections of BBS routes – sequences of five stops, covering about 2.5 miles 4 km – in order to obtain field-sampling units that are less heterogeneous more homogeneous in terms of land type use types and for which there is a stronger correspondence between the presence or PAs and the whose bird assemblages detected can be more directly linked to local landscape characteristics, especially protection. For each route, we only used the first sequence of five stops, because the only precisely georeferenced point we had access to was the starting first stop of each route. Indeed, even if in principle additional stops are spaced about 0.5 miles 8 km from each other, in practice this distance can vary, making the location of additional stops in each route progressively more imprecise. Henceforth, and for simplicity, we use the term “routes” to refer to these initial sections of five stops rather than to entire BBS routes.

We excluded bird-aquatic and nocturnal taxa that, which are not well detected by this diurnal road-based monitoring scheme (aquatic and nocturnal birds), those that correspond to, as well as hybrid individuals. We also excluded seven non-indigenous native species, and hybrids. Overall, as they are not the focus of conservation efforts. The main dataset we analysed included 400 species in total. To test if removing non-native species can bias analyses (e.g. because they replace native species) we also ran analyses including these species (results presented in Appendix S6).



368 ~~We focused on routes sampled at least 5 years between 2007 and 2016, obtaining a set of 3,427~~  
369 ~~routes analysed. For routes sampled more than five years, we analysed only five (randomly~~  
370 ~~selected) years of data, thus ensuring a consistent sampling effort across all routes. For each~~  
371 ~~species, the abundances were summed across the five points and the five years, giving a single~~  
372 ~~value per species per route. We winsorized the abundances of each species (i.e., values above~~  
373 ~~95% quantiles were reduced to the 95% quantile value) to limit the impact of extreme values.~~  
374 ~~Following Kendall et al. (1996)'s recommendations, we removed from the dataset the first year~~  
375 ~~of participation of each BBS observer, to reduce bias due to differences in observer experience.~~  
376 ~~To do so, we extracted the observers' identifying number from the "weather" table of the dataset~~  
377 ~~and calculated for each observer the first year of data collection reported in the dataset. We then~~  
378 ~~removed every observation made by this observer this given year. We also removed double~~  
379 ~~counts, which can be either due to the presence of two observers or an observer sampling several~~  
380 ~~times in one year, by excluding observations for which the 'RPID' code (i.e. Run Protocol type)~~  
381 ~~was 102, 103, 104, 203 or 502. We then focused on routes sampled at least 5 years between~~  
382 ~~2007 and 2016, obtaining a set of 3,046 routes. For routes sampled more than five years, we~~  
383 ~~analysed only five (randomly selected) years of data, thus ensuring a consistent sampling effort~~  
384 ~~across all routes. We fixed this arbitrary threshold of five years as a trade-off between obtaining~~  
385 ~~high data quantity (number of routes analysed) and data quality (number of species detected per~~  
386 ~~route, which increases with the number of years sampled). For each species, counts were~~  
387 ~~summed across the five points and the five years, to obtain a single value per species per route,~~  
388 ~~which we used as a measure of abundance. We acknowledge that these values correspond only~~  
389 ~~to detected birds rather than true abundances. Detection is known to vary between habitats,~~  
390 ~~depending on vegetation structure (Pacifi et al., 2008). This could lead to a difference of~~  
391 ~~detection probability (and thus of perceived abundance) between protected and unprotected~~  
392 ~~sites if vegetation structure differs; controlling for vegetation structure in our analyses reduces~~  
393 ~~this bias.~~

#### 395 Landscape data

396 For each route, we analysed the properties of the landscape within a 500 m buffer around the  
397 route's ~~2.5-mile~~4 km track (total area ca. ~~6 km<sup>2</sup>~~, which ~~5 km<sup>2</sup>~~). Given that 500 m corresponds  
398 broadly to the bird detection radius of the BBS (Sauer et al., 2017), we considered ~~as this~~ a  
399 suitable description of the environment affecting the composition of birds detected by the BBS  
400 ~~and which corresponds broadly to the bird detection radius of the BBS.~~ Small et al. (2012)  
401 ~~showed~~found that the immediate landscape composition (buffer of 0.4 km) of BBS routes was  
402 similar to ~~the~~ large-scale landscape composition (buffer of 10 km), so ~~we do not expect~~ this  
403 choice ~~is not expected~~ to strongly affect the results.

404  
405 ~~Protected area is defined by the IUCN as "a clearly defined geographical space, recognised,~~  
406 ~~dedicated and managed, through legal or other effective means, to achieve the long term~~  
407 ~~conservation of nature with associated ecosystem services and cultural values". They are~~  
408 ~~categorised by the IUCN within seven categories based on their protection level from Ia "strictly~~  
409 ~~protected areas set aside to protect biodiversity [...], where human visitation, use and impacts~~  
410 ~~are strictly controlled and limited to ensure protection of the conservation values." to VI which~~

411 ~~“conserve ecosystems and habitats together with associated cultural values and traditional~~  
412 ~~natural resource management systems. They are generally large, with most of the area in a~~  
413 ~~natural condition, where a proportion is under sustainable natural resource management and~~  
414 ~~where low-level non-industrial use of natural resources compatible with nature conservation is~~  
415 ~~seen as one of the main aims of the area” (UNEP-WCMC and IUCN, 2018). We used the PAs’~~  
416 ~~shapefile, including both locations and IUCN categories of PAs, which was provided by the~~  
417 ~~World Database on Protected Areas (UNEP-WCMC and IUCN, 2018). We calculated the~~  
418 ~~proportion of area inside each route’s buffer that falls within a PA (all IUCN categories~~  
419 ~~combined, and dissolved to avoid double-counting of areas under multiple PA designations).~~  
420 ~~We have also run analyses considering stricter PAs only (categories I-IV), as the effectiveness~~  
421 ~~can vary with protection level.~~

422  
423 For each route, we obtained values according to four environmental variables: A Protected Area  
424 is defined by the IUCN as “a clearly defined geographical space, recognised, dedicated and  
425 managed, through legal or other effective means, to achieve the long term conservation of  
426 nature with associated ecosystem services and cultural values” (UNEP-WCMC IUCN, 2016).  
427 PAs are categorised by the IUCN within seven categories based on their protection level. At  
428 one extreme, Ia PAs are “strictly protected areas set aside to protect biodiversity [...], where  
429 human visitation, use and impacts are strictly controlled and limited to ensure protection of the  
430 conservation values”. At the other extreme, VI PAs “conserve ecosystems and habitats together  
431 with associated cultural values and traditional natural resource management systems [and] are  
432 generally large, with most of the area in a natural condition, where a proportion is under  
433 sustainable natural resource management and where low-level non-industrial use of natural  
434 resources compatible with nature conservation is seen as one of the main aims of the area”  
435 (UNEP-WCMC and IUCN, 2018). We used data on locations (polygon shapefile) and IUCN  
436 categories of PAs collated in the World Database on Protected Areas (UNEP-WCMC and  
437 IUCN, 2018). According to the Word Database of Protected Areas methodology to calculate  
438 area covered by PAs (UNEP-WCMC and IUCN, 2019), we excluded “Man and Biosphere”  
439 reserves and PAs for which implementation was not finalised, keeping only PAs with a status  
440 “designated”, “inscribed” or “established”. In addition, we also removed PAs that were not  
441 spatialized (no polygon associated). Using QGis (QGIS Development Team, 2017), we  
442 calculated the proportion of area inside each route’s buffer that falls within a PA (all IUCN-  
443 categories combined, and dissolved to avoid double-counting of areas under multiple PA  
444 designations). We have also run analyses considering stricter PAs only (categories I-IV), as the  
445 effectiveness can vary with protection level (Gray et al., 2016; Coetzee et al., 2014).

446  
447 We characterised each route according to four additional landscape variables, using QGis  
448 (QGIS Development Team, 2017): net primary productivity, altitude, human footprint, and type  
449 of vegetation structure. The first three are continuous variables, available as raster files, and we  
450 obtained a value per route by calculating the mean valuesvalue across all pixels that overlap the  
451 respective buffer. We calculated net primary productivity as the mean during spring months  
452 (~~Mars~~March to June) between 2004 and 2015 according to the monthly Net Primary  
453 Productivity Terra/Modis (NASA, 2017)(NASA, 2017; resolution 0.1 degree, about 62 km<sup>2</sup> at  
454 45°N); ~~altitude using~~). Altitude was obtained from the GLOBE Digital Elevation Model

455 ~~(National Geophysical Data Center, 1999)~~(National Geophysical Data Center, 1999; resolution  
456 0.008 degree, about 0.40 km<sup>2</sup> at 45°N); ~~human~~). Human footprint was derived from the 2009  
457 Global terrestrial Human Footprint map (Venter et al., 2016; resolution 0.01\*~~x~~ 0.008 degrees,  
458 about 0.50 km<sup>2</sup> at 45°N). We defined the vegetation structure as a categorical variable with  
459 three types: forest, shrub and herbaceous. We ~~started by reclassifying~~used the Climate Change  
460 Initiative – Land Cover layer, using 2011 values as this is the central year of our sampling period  
461 (ESA, 2015, resolution 300m) and reclassified the land cover classes ~~in the Global Land Cover~~  
462 ~~2000 layer (Bartholomé and Belward, 2005; resolution 0.009 degree, about 0.50 km<sup>2</sup> at 45°N)~~  
463 into the three vegetation structure types: forest from land cover classes 50-90 and 160-170  
464 (N=1-9 (N=1,749,282 routes); shrub, 11-12120-122 (N=409298); herbaceous, 13-16130-153  
465 (which includes croplands; N=1,140214). We then obtained the main vegetation structure type  
466 for each route as the dominant one in the buffer. Routes ~~which were~~ dominated by other land  
467 use classes (~~burned trees, 10; mosaic, 17-18; [30-40, 100-110 and 180]; bare areas, 19; [200-~~  
468 ~~202]; water areas 20-21; artificial, 22)bodies [210]; urban [190], other [220]) were not analysed~~  
469 because they were too scarce. ~~Routes~~The 2,794 routes used in analyses are mapped in Appendix  
470 S1.

471

#### 472 Statistical analyses

473 We estimated the effect of PAs on each of two assemblage-level indices (species richness and  
474 summed abundance) and on the abundance of individual species using General Additive Models  
475 (GAMs). Models all had identical structures, with the response variable modelled as function  
476 of the proportion of PAs inside the buffer, interacting with vegetation structure type. We added  
477 smoothed terms controlling for productivity and altitude, as ~~PAs are globally biased towards~~  
478 ~~high altitude and low productivity areas (Joppa and Pfaff, 2009), as well as longitude and~~  
479 ~~latitude in order to correct for spatial autocorrelation~~well as longitude and latitude in order to  
480 correct for spatial autocorrelation. The general structure of the GAMs was:

481 Response ~ PA \* vegetation + s(productivity, altitude, longitude, latitude)

#### 482 Assemblage-level analyses

483 For each route, and across all 400 bird species analysed, we calculated two assemblage indices,  
484 in each case using the cumulative number of species or individuals seen across the 5 stops, over  
485 5 years: species richness ( $\mu = 28.65 \pm 9.54$  species); summed bird abundance across all species  
486 ( $\mu = 249 \pm 88248 \pm 90$  individuals). We then used a GAM to model each of these two assemblage  
487 variables against the above-mentioned covariates, assuming a Gaussian distribution for richness  
488 and a negative binomial distribution for abundance.

#### 489 Species-level analyses

490 We excluded the rarest species from this analysis in order to have enough statistical power,  
491 keeping only the 149133 species observed on more than 100 in at least 150 routes, in order to  
492 have enough statistical power. Under this threshold, numerous species were too rarely detected  
493 within protected routes, leading to aberrant estimates of PA effectiveness (either highly positive  
494 or highly negative). For each species, we only analysed routes that fall within the species'  
495 distribution within our study area. We ~~obtained an approximation of~~defined this distribution by  
496 delimitingas the 90 % spatial kernel of the routes where the species was observed, obtained

497 using the 'adehabitat' R package (Calenge, 2006). We treated all routes inside the kernel where  
498 the species was not observed as having zero abundance.

499  
500 We modelled each species' abundance using a GAM as mentioned above, with a  
501 [Poisson-negative binomial](#) distribution. We then calculated for each species a "PA effect" (PAE),  
502 measured as the difference in predicted abundance between a fully protected ([i.e. 100 %](#)  
503 [protected](#)) and an unprotected route ([i.e. 0 % protected](#)) with all control variables fixed to their  
504 median values. We calculated PAE separately for each of the three types of vegetation structure,  
505 to obtain for each species a value of PAE<sub>For</sub> for routes dominated by forest, PAE<sub>Shrub</sub> for shrub  
506 routes, and PAE<sub>Herb</sub> for herbaceous routes.

507  
508 For each type of vegetation structure, we studied PAE values in order to understand the factors  
509 explaining which species are favoured or not by PAs. To do so, we used a linear model ([LM](#))  
510 and ~~two~~ phylogenetic linear ~~models (phyBM and phyL, see below)~~ [model](#) with [similar](#)  
511 [structures using](#) species-level covariates. We considered three covariates: species' habitat  
512 preference, population trend, and human-affinity. ~~We extracted from Del Hoyo et al. (2013)~~  
513 ~~species' main habitat (11 categories; see Fig.2).~~ [We used species' main habitat compiled in 11](#)  
514 [classes by Barnagaud et al. \(2017, see Fig.2\).](#) We used species' population trends in North  
515 America between 1966 and 2015, calculated for each species by [Sauer et al. \(2017\) from the](#)  
516 ~~BBS data (negative number~~ [Sauer et al. \(2017\) from the BBS data \(negative numbers](#) for  
517 declining species, positive for increasing species). We winsorized these values, folding down  
518 the 2.5% extreme values on each side, bringing estimates to a Gaussian distribution. Finally,  
519 we estimated for each species a human-affinity index, as the median human footprint of the  
520 routes where the species was observed, weighted by species' abundance on the route. [This index](#)  
521 [was calculated across all 3,046 routes prior to the exclusion of routes based on habitat types](#)  
522 [\(i.e. also including routes dominated by mosaic, bare areas, water bodies and urban land cover\)](#)  
523 [to be more representative of the diversity of habitats where species are present.](#)

524  
525 ~~The two~~ [To account for](#) phylogenetic ~~models used are the~~ [autocorrelation, we ran a](#) Brownian  
526 motion model ~~(phyBM) and the Lambda model (phyL), both~~ implemented in the 'phyloilm' R  
527 package ~~(Tung Ho and Ané, 2014).~~ [\(Tung Ho and Ané, 2014\).](#) To obtain the bird phylogeny,  
528 we selected randomly 100 phylogenetic [Hackett backbone](#) trees over 10,000 from Jetz et al.  
529 (2012) and calculated a maximum clade credibility tree using *Tree Annotator* from *Mr Bayes*  
530 (Drummond et al., 2012) with no burnin, and node heights calculated with the median.

531 Confidence intervals of the phylogenetic model were estimated with the *'phylolm'* function,  
532 using a bootstrap with 100 bootstrap replicates.

575  
576  
577  
578  
579  
580  
581  
582  
583  
584  
585  
586  
587  
588  
589  
590  
591  
592  
593  
594  
595  
596  
597  
598  
599  
600  
601  
602  
603  
604  
605  
606  
607  
608  
609  
610  
611  
612  
613  
614  
615  
616

## Results

### Assemblage-level analyses

At the assemblage level, species richness and summed abundance differed ~~very~~ significantly between vegetation structure types (respectively  $P < 0.013$ ,  $P = 4.10^{-16}$ ,  $P = 1.10^{-6}$ ), underlying the importance of accounting for habitat differences when studying ~~PAs effect~~ PA effects.

~~However, neither~~ Neither species richness, nor summed abundance were significantly affected by the proportion of PAs in ~~the buffer~~ models that did not control for vegetation structure (respectively  $c = -0.1315$ ,  $P = 0.13$ ), ~~or its interaction with vegetation structure type~~ (respectively  $c = -0.20046$ ,  $P = 0.29$ ). ~~This lack of significance between assemblage indices and the proportion of PAs in the buffer was also true when not~~ 143). In models controlling for vegetation structure ~~(respectively, species richness did not vary significantly with protection within forest or within shrub routes~~ (respectively  $c = -1.39$ ,  $P = 0.68121$ ;  $c = -0.305$ ,  $P = 0.847$ ) but increased with protection for herbaceous routes ( $c = 4.353$ ,  $P = 0.022$ ). Summed abundance lightly decreased with protection within forest routes ( $c = -0.084$ ,  $P = 0.058030$ ) but did not vary with protection within shrub or within herbaceous routes (respectively  $c = 0.082$ ,  $P = 0.232$ ;  $c = 0.084$ ,  $P = 0.307$ ).

### Species-level analyses

According to the linear model, values of  $PAE_{For}$  – the predicted difference in a given species' abundance between fully protected *versus* unprotected forest routes – differed significantly depending on the species' main habitat, ~~under both LM and phyL models but not under phyBM model~~. Hence, ~~the first two models indicate that within forest routes, species with any type of that have~~ forest as their main habitat ~~(showed higher abundances in protected than unprotected forests (Table 1, Fig.2). This difference was significant for the three main forest habitat preferences (i.e. mixed, deciduous, conifer) but not for the general forest, conifer; Table 1 and Fig.2) are predicted to have~~ category, which only represented five species (Table 1). Species favouring open habitats were significantly higher abundances when routes are protected, less abundant in protected forests than in unprotected forests (Table 1, Fig.2). We found no significant PA effect within forest routes for species favouring other habitat types.

~~In all models, species'~~ Species' population trends between 1966 and 2015 did not significantly explain  $PAE_{For}$  (Table 1). In contrast, species' human-affinity ~~was significantly tended to be~~ negatively correlated with  $PAE_{For}$  (*i.e.*, we found higher effects of PAs for species with lower affinity to humans ~~had higher effects of PAs in forested routes; Table 1, Fig.3~~). This ~~effect~~ trend was ~~also significant still present~~ when we considered only forest species ~~were considered, but was not significant either~~ (green dots in Fig.3; see Supporting Information in Appendix S2 for additional test).

None of these effect was significant in the phylogenetic model (Table 1 and Fig.2), which presented large confidence intervals.

Mis en f

648 The effect of PAs within shrub routes ( $PAE_{Shrub}$ ) ~~and within herbaceous routes ( $PAE_{Herb}$ )~~ was  
 649 not affected by species' main habitat ~~under any of the models and was only significantly~~  
 650 ~~negatively correlated with human-affinity.  $PAE_{Herb}$  was only significantly affected by habitat~~  
 651 ~~preferences, being negative for conifer-forest species~~ (Supporting information, Appendix S3).  
 652  ~~$PAE_{Shrub}$  decreased significantly with species' trend under all models (i.e., declining species~~  
 653 ~~had higher effects of PAs in shrub routes), whereas it decreased with human-affinity only under~~  
 654 ~~model phyBM.  $PAE_{Herb}$  was not significantly correlated with any of the three covariates.~~

655  
 656 These results, however, need to be interpreted taking into account that shrub or herbaceous  
 657 protected routes were rare in our dataset: on average, each species' kernel included only ~~1013~~  
 658 shrub and ~~79~~ herbaceous routes protected by 50% or more, ~~contrasted in contrast~~ with ~~6050~~  
 659 protected forest routes (Fig.1; see Appendix ~~S1 and S4~~ in Supporting Information). ~~The lack of~~  
 660 ~~significance in models with  $PAE_{Shrub}$  and  $PAE_{Herb}$  might thus be due to the limited number of~~  
 661 ~~protected routes in the sample, whereas the significant correlations between  $PAE_{Shrub}$  and both~~  
 662 ~~species' trends and human-affinity might not be robust.~~

663  
 664 Results, both at the assemblage and at the species levels, were similar but less significant when  
 665 we considered only PAs of stricter management, as defined by IUCN categories I-IV (~~Dudley,~~  
 666 ~~2008~~(Dudley, 2008; see Supporting Information, Appendix ~~S6S7~~). For shrub and herbaceous  
 667 routes, the number of protected routes was even smaller than when all PAs were considered,  
 668 leading to aberrant results. ~~Considering non-native species had little effect on results at the~~  
 669 ~~assembly level, the only difference being that the effect of protection within herbaceous routes~~  
 670 ~~became no longer significant (Appendix S6). At the species level, adding the three non-native~~  
 671 ~~species detected on more than 150 routes did not change the species results (Appendix S6).~~

672  
 673 Table 1: Model summaries regarding the estimated effect of ~~PAs Protected Areas~~ on species within forest routes  
 674 ( $PAE_{For}$ ): linear model (~~LM~~), and phylogenetic linear model with Brownian motion model (~~phyBM~~), ~~phylogenetic~~  
 675 ~~linear model with Lambda model (phyL). The top part gives estimates and P-values for all covariates, the bottom~~  
 676 ~~part gives estimates and P-values for all species' habitat preferences, with trend and human-affinity fixed to zero.~~  
 677 N corresponds to the number of species in each case.

678 \* P-values for the habitat variable as a whole could not be obtained, as Anova tables are not implemented in the 'phylolm' package.

	Linear model LM		PhyBMPhylogenetic model		PhyL	
	Estimate	P	Estimate	P	E	P
Habitat	-	<u>24.10</u> 86	-	NA*	-	N
Trend	<u>0.0272</u> 0 <sup>-3</sup>	<u>0.6029</u> 88	<u>0.0390</u>	<u>0.5449</u> 20	0	0

Mis en f  
 Tableau  
 Cellules  
 Mis en f  
 Mis en f  
 Mis en f  
 Mis en f  
 Mis en f  
 Mis en f

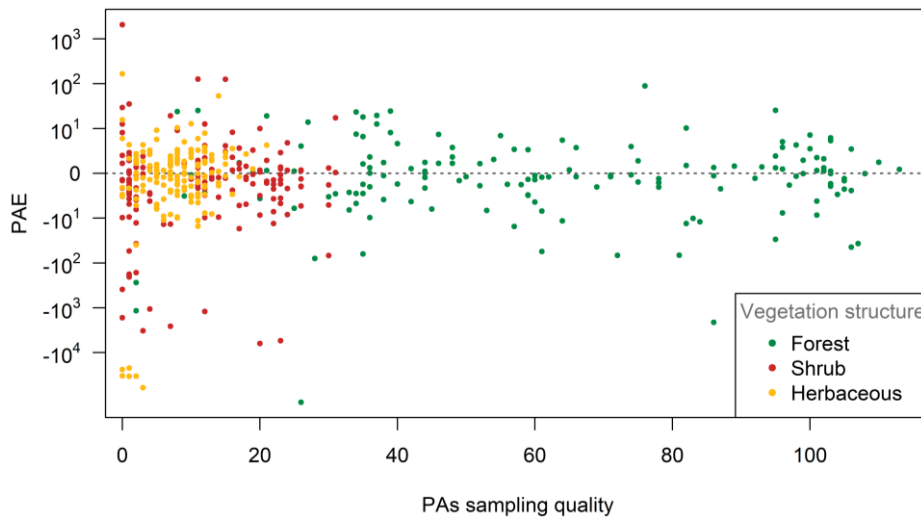




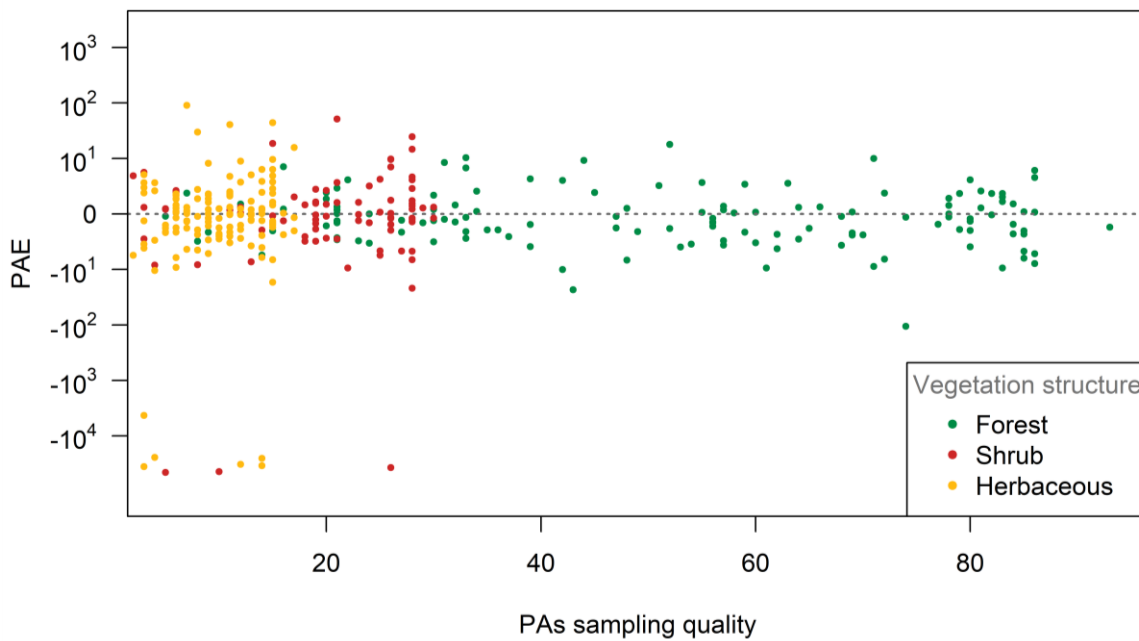
Open (N=1411)	-	<u>0.1300</u>	<u>-0.362.14</u>	<u>0.75238</u>	2
	<u>0.411.76</u>	<u>04</u>			9
					0
					1
					4
					3
Urban (N=1)	<u>-0.8760</u>	<u>0.2766</u>	<u>-0.951.72</u>	<u>0.69642</u>	0
		<u>0</u>			1
					2
					9
					5
					1

Mis en f  
 Mis en f  
 Mis en f  
 Mis en f

685



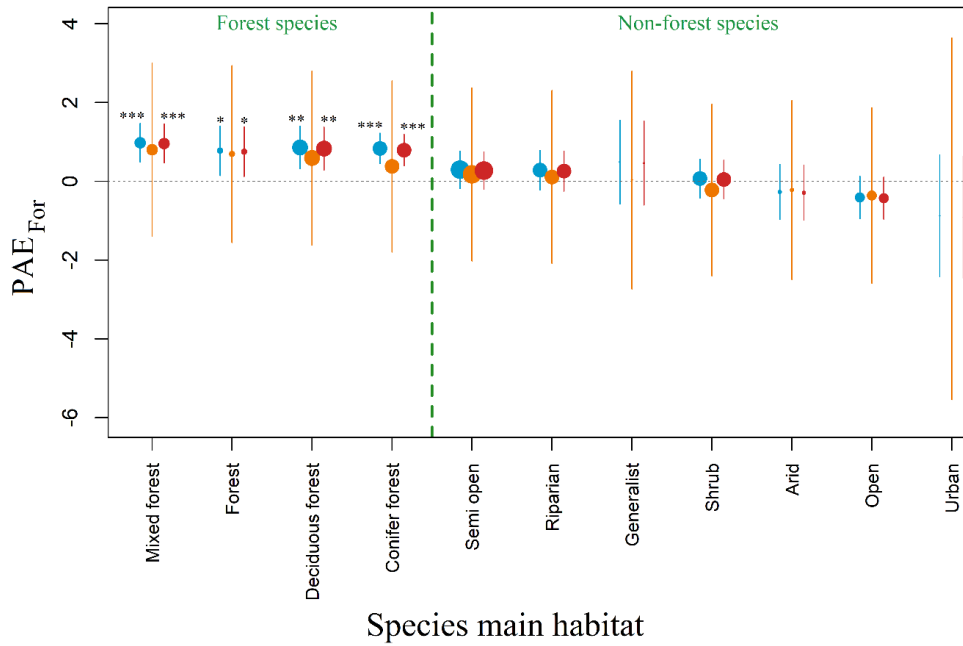
686



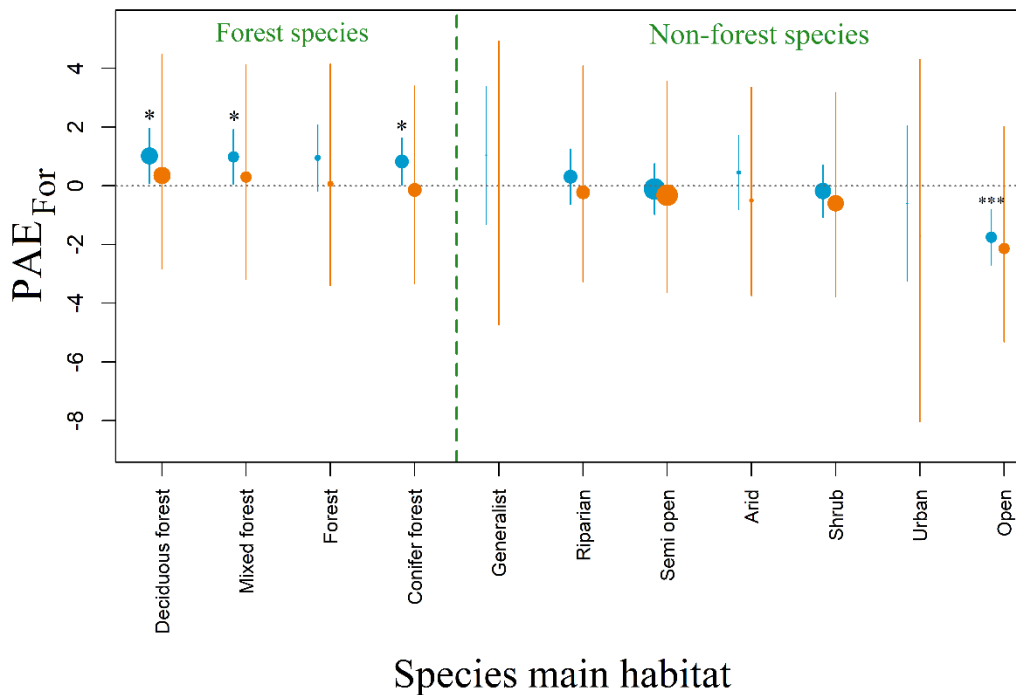
687

688 Figure 1: Estimated Protected Areas effect per species (PAE) (represented on a log scale in both negative and  
 689 positive values), against PAs sampling quality, per vegetation structure type of the routes. PAs sampling quality  
 690 was quantified as the number of routes within the species' kernel with at least 50% of the buffer area covered by

691 [PAs Protected Areas](#). Each point in the plot corresponds to a species, and each species can be represented [by](#) up to  
 692 three [timespoints](#), one for each vegetation structure type.



693

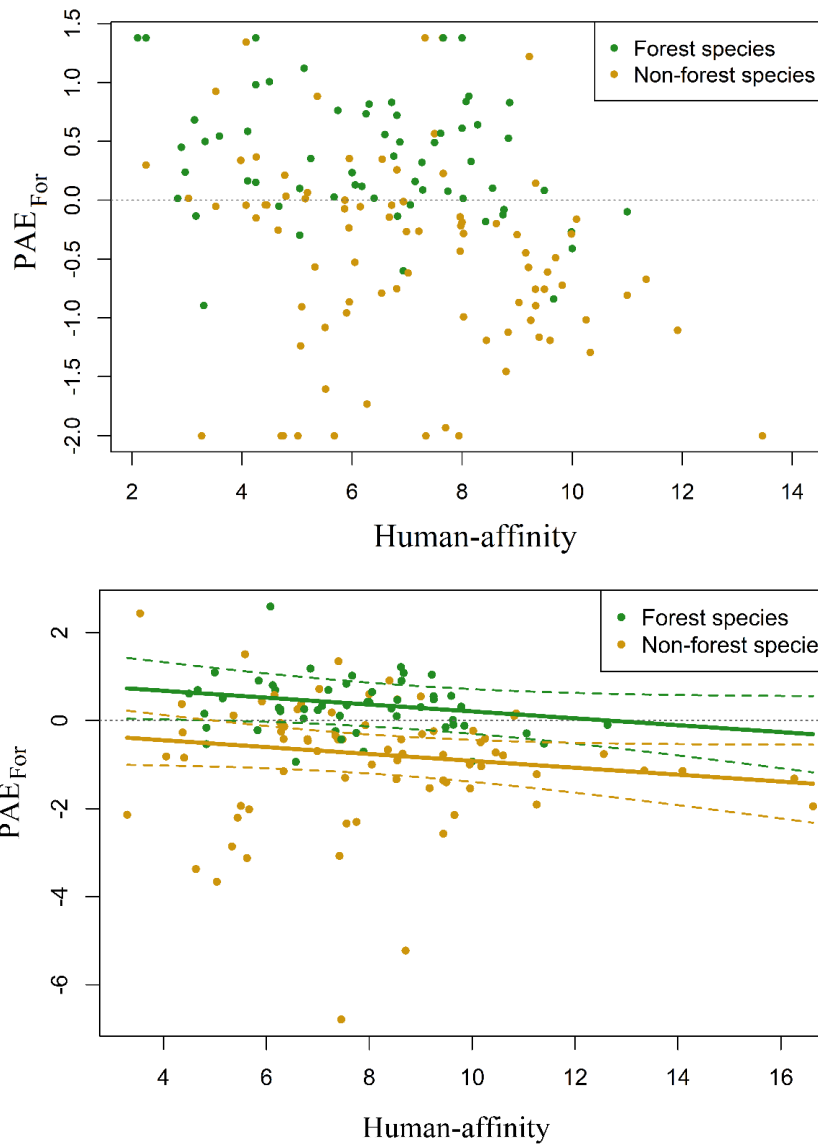


694

695 Figure 2: Estimated effect of [PAs Protected Areas](#) on species within [BBS-forest routes](#) ( $PAE_{For}$ ) per species' main  
 696 habitat ([Del Hoyo et al., 2013](#)), estimated with [three models](#): a linear model ([LM](#), blue), and a phylogenetic linear  
 697 linear model with Brownian motion model ([phyBM](#), orange), and phylogenetic linear model with Lambda model ([phyL](#),  
 698 red). Estimates were all calculated with species' population trend and human-affinity fixed to zero. Error bars  
 699 represent 95% CI; [dots](#) sizes are proportional to the number of species in each habitat group. Stars indicate  
 700 significant effects for the particular model, for the particular species' main habitat ( $P: 0.05 < * < 0.01 < ** < 0.001$ )

713 < \*\*\*). Habitat types are ordered from the highest to the lowest  $PAE_{For}$  values under [phyBM](#) the phylogenetic  
714 model.

715



716

717

718 Figure 3: Species' human-affinity (higher for species found preferably in areas of higher human footprint) against  
719 the estimated effect of [PAs](#) Protected Areas on species within [BBS](#) forest routes ( $PAE_{For}$ , [high above zero](#) for species  
720 whose abundance in forest routes is higher in protected rather than in unprotected areas). Forest species (green) are  
721 species whose main habitat is "forest", "conifer forest", "mixed forest" or "deciduous forest"; non-forest species  
722 (brown) are all other species. [Lines correspond to the effect of human-affinity on  \$PAE\_{For}\$  for deciduous forest  
723 species \(green\) and semi-open species \(brown\), predicted by the linear model and their 95% confidence intervals  
724 in dashed lines.](#)

Mis en f

## Discussion

We compared the effect of PA coverage on bird species diversity, using assemblage indices (species richness, summed abundance) and individual species' abundances.

~~At the assemblage level, we did not find significant differences in species richness or summed abundance between protected and unprotected sites, irrespective of whether vegetation structure was taken into account or not. In one sense, this is not surprising, particularly when it comes to species richness: according to the intermediate disturbance hypothesis, an area with low human-induced disturbance can have higher species richness than a pristine area.~~ At the assemblage level, we found very little effect of protection, only a small increase in richness in herbaceous routes and a small decrease in overall abundance in protected routes. In one sense, this is not surprising, as several large-scale studies found that assemblage metrics – particularly species richness – are relatively resilient to disturbance through species substitution (Dornelas et al., 2014; Supp and Ernest, 2014). Moreover, areas with low human-induced disturbance can have higher species richness than a pristine area, as predicted by the intermediate disturbance hypothesis (Roxburgh et al., 2004). Accordingly, Hiley et al., (2016) found lower alpha avian diversity in Mexican PAs than in unprotected areas. However, our results contrast with previous studies investigating this question such as Coetzee et al. (2014)(2014) or Gray et al. (2016), ~~which~~ who found a positive effect of PAs on species richness and on summed abundance, including in North America (~~Coetzee et al., 2014~~)(Coetzee et al., 2014). These two studies being meta-analyses, it is possible that a publication bias against studies showing negative or null effects of PAs (~~discussed by Coetzee et al., 2014~~)(discussed by Coetzee et al., 2014) artificially increased the difference they measured. This is even more so ~~the case~~ given that the underlying studies of the meta-analyses were often designed to measure the effect of anthropogenic pressures, using PAs as benchmarks, rather than ~~measuring to measure~~ the effectiveness of PAs (e.g. Sinclair et al., 2002; Bihn et al., 2008; Wunderle et al., 2006, all used in Coetzee meta-analysis)(e.g. Sinclair et al., 2002; Bihn et al., 2008; Wunderle et al., 2006, all used in Coetzee meta-analysis), and may thus have focused on particularly intact protected sites and/or in highly degraded non-protected sites. Conversely, our ~~study may not be representative of studies at a global scale~~ results are not necessarily generalizable to other regions or other taxa, for example if North American birds are less sensitive to human activities than other taxa in North America ~~and/or~~ than birds in other regions, or if there is less contrast in human impacts in protected *versus* unprotected areas in North America than elsewhere. In ~~addition~~ our study, the observed lack of difference between protected and unprotected sites in terms of richness and abundance ~~could~~ may also ~~potentially~~ be explained by a difference ~~an artefact of differences~~ in species' detectability (Boulinier et al., 1998), if PAs protect mainly species that are difficult to detect. This detection problem should not affect our result at the species level.

Even ~~if~~ when overall species richness and abundance are similar, PAs may nonetheless have an effect on avian assemblages if different species respond differently to protection. ~~We found that~~ We were only able to investigate this in depth for routes whose vegetation ~~is~~ was dominated by ~~forests, forest, for which there was adequate sampling quality in~~ PAs ~~seem to~~ (Fig. 1). ~~We found that among forest routes, PAs~~ have an overall positive effect on species' abundance, but only

812 for those species with forest as their main habitat. In contrast, abundances of species favouring  
813 open habitats are negatively correlated with protection in forests. Forest PAs thus seem to  
814 maintain a more forest-typical bird assemblage than comparable unprotected forests. This effect  
815 was These effects were significant with the linear model, and with one (phyL), but not the other  
816 (phyBM) of the two phylogenetic linear models. model. This suggests that much of the effect  
817 attributed to habitat preferences under the linear model can actually be considered as relies on  
818 phylogenetic difference relatedness among species, which is not surprising as bird habitat  
819 preferences and phylogeny are correlated. Phylogenetic models could theoretically allow us to  
820 measure the effectiveness of PAs in protecting species across phylogeny, and to check if some  
821 taxa were not effectively protected (e.g., they could highlight that a given family is not protected  
822 by PAs). However, to draw such conclusions

823  
824 Contrary to our prediction, we would need to know how species are affected by PAs in each  
825 vegetation structure types, which is not the case here. Therefore, phylogenetic models give little  
826 information here, only highlighting that the difference in PAE<sub>For</sub> between species habitat  
827 preferences is correlated with phylogeny. Moreover, all models indicated did not find that species  
828 with low human-affinity (*i.e.*, species that avoid human-impacted areas) are more significantly  
829 favoured by forest PAs. This highlights that forest PAs protect species that are the most sensitive  
830 to human pressure, while species with high human affinity, often benefiting from human  
831 presence, showed lower abundances inside PAs. Contrary, even if there was as non-significant  
832 positive effect. Also contrary to our expectation, and to previous results for common French  
833 birds (Devictor et al., 2007), we found no correlation between species' population trends over  
834 the past 50 years and PAE<sub>For</sub>. This may reflect the fact that our model included only relatively  
835 common species (*i.e.*, observed on at least 100 routes in the studied years). It is thus possible  
836 that the most human-averse and endangered species are favoured by PAs, but that we could not  
837 measure it.

838  
839 Our models suggested results suggest that PAs in shrub herbaceous areas have a  
840 beneficial/negative impact on declining conifer-forest species and on those with low human-  
841 affinity, whereas we did not find significant results for herbaceous areas the effect of PAs in  
842 shrub routes was negatively correlated with human-affinity. Given the scarcity of protected  
843 routes within both of these vegetation structure types, we do not consider these results  
844 particularly robust or informative of the effectiveness of PAs, but they nonetheless emphasise  
845 the biases of BBS routes against shrub areas and herbaceous PAs (Appendix S4).

846  
847 Given that PAs located in forests are not expected to favour the same species as PAs located in  
848 grasslands or shrub lands, we controlled for vegetation structure in our analyses of PA effects.  
849 However, this control masked the effect PAs may have had in preventing changes in vegetation  
850 structure (and associated changed changes in bird assemblages). For instance, given the  
851 vegetation structure categorisation we applied, the counterfactual for a protected forest was an  
852 unprotected forest, which does not take into account the possibility that the PA may have  
853 prevented the forest from being cleared. In other words, our approach does not measure the  
854 effect PAs can have on species diversity by preventing habitat destruction (that modifies  
855 vegetation structure type), only the effects PAs can have in preventing habitat degradation (not

856 modifying the vegetation structure type), for example from natural forest to exploited forest, or  
857 from natural grassland to croplands.

858

859 Pairwise comparisons of protected *versus* unprotected sites, and thus the meta analyses ~~from~~  
860 Geldmann et al. (2013), Coetzee et al. (2014) and Gray et al. (2014) and Gray et al. (2016), can  
861 ~~take into account~~ integrate the combined effects of habitat destruction and habitat degradation  
862 on species diversity, given that the counterfactual chosen may ~~well~~ have a different habitat  
863 structure ~~than~~ from the protected site (e.g., a protected forest compared with an unprotected  
864 cropland). Nonetheless, ~~defining the effectiveness measured in because~~ these meta-analyses  
865 ~~build from underlying studies with a diversity of criteria in the choice of the counterfactuals, it~~  
866 is not straightforward, ~~as it depends heavily on the choice of counterfactuals in underlying~~  
867 ~~studies, which are defined directly by authors depending on their objectives. to interpret the~~  
868 ~~effectiveness values obtained.~~ For instance, as discussed before, numerous ~~underlying~~ studies  
869 ~~used in the meta-analyses compare~~ compared a highly degraded site with a protected site used  
870 as benchmark, ~~in order to estimate~~ with the purpose of estimating the impact of anthropogenic  
871 degradation, which can lead to an overestimate of PA effectiveness. Other studies aimed ~~to~~  
872 ~~estimate~~ at estimating PA effectiveness directly (e.g. Wasiolka and Blaum, 2011; Lee et al.,  
873 2007)(e.g. Wasiolka and Blaum, 2011; Lee et al., 2007), but their choice of counterfactual was  
874 subjectively based on what authors considered likely to have happened to the protected site had  
875 it not been protected (Coetzee et al., 2014).(Coetzee et al., 2014). Finally, some other studies  
876 used in meta-analyses were not particularly interested in differences between protected and  
877 unprotected sites, ~~with~~ protection was used only ~~used~~ as a covariate ~~explaining~~ to potentially  
878 ~~some noise~~ explain variation around the signal the authors were interested in (e.g. Naidoo, 2004;  
879 McCarthy et al., 2010)(e.g. Naidoo, 2004; McCarthy et al., 2010). ~~Because of the diversity of~~  
880 ~~approaches used in these meta-analyses, it is difficult to define precisely what has been~~  
881 ~~measured as PA effectiveness. Although~~ So even though our approach does not allow us to  
882 measure the full effects of PAs, the ~~difference~~ differences we measured between protected and  
883 unprotected sites ~~is~~ are defined statistically depending on the covariates included, which  
884 ~~allows~~ allowed to ~~understand~~ define more clearly ~~what is being included in~~ how we measured  
885 ~~effects of~~ PA effectiveness. A main advantage of ~~using~~ large biodiversity monitoring datasets  
886 (such as ~~breeding~~ bird monitoring schemes) ~~in relation to~~ rather than pairwise comparisons is  
887 thus the possibility of applying a well-defined and repeatable control.

888

889 More broadly, our results ~~highlight~~ emphasise that ~~it is impossible to~~ clearly ~~measuring~~  
890 ~~PA~~ measure the effectiveness of PAs in conserving species diversity ~~is impossible~~ without  
891 defining precisely what is expected ~~from~~ of them. In this study, we measured PAs effectiveness  
892 as the difference in ~~abundance or richness~~ bird diversity between protected and unprotected  
893 sites, ~~controlling for main landscape differences.~~ This definition ~~assumes that PAs are expected~~  
894 ~~to protect globally species diversity, and therefore gathers our~~ combines conservation ability to  
895 protect richest areas and to reduce ~~effectively~~ human ~~impacts on biodiversity~~ pressures in these  
896 areas. If PAs are expected to present higher diversity in terms of assemblage metrics (species  
897 richness or summed abundance), then we found no evidence in our analyses that PAs are  
898 effective. If PAs are expected to protect all species' populations, then we did not find they were  
899 effective either, as for about half of the 149133 species studied here we found a negative effect

900 of ~~PAs in~~ forest PAs. However, our results show that North-American forest PAs present higher  
901 abundances in forest species when compared with unprotected forest sites ~~(especially for, and~~  
902 ~~lower abundances of~~ species ~~with low affinity to human activities)~~ favouring open habitats.  
903 That this result holds even though we found no significant difference in total abundance  
904 suggests that bird assemblages in protected forests are more forest-typical than those in  
905 unprotected forests. Our results thus indicate that forest PAs in North-AmericanAmerica are  
906 contributing to prevent forest habitat degradation, and associated losses in the abundance of  
907 forest specialist species. BBS routes do not currently cover sufficiently well other habitats  
908 besides forest to allow us to investigate whether the same result applies to PAs with a different  
909 vegetation structure, but datasets with a bigger proportion of sampling points inside PAs, across  
910 all habitats, would ~~help investigating~~ bring further light into this question.

911  
912 ~~Overall, our results emphasize the complexity of resolving a question that seemed so~~  
913 ~~straightforward, and whose answer seemed so intuitive. In practice, understanding whether PAs~~  
914 ~~are effective or not, and quantifying such effects, involves defining clearly what effect is being~~  
915 ~~tested, on which facet of species diversity, and how to obtain appropriate counterfactuals.~~





954  
955  
956  
957  
958  
959

### Data accessibility statement:

All data used in the study (~~birds~~[bird abundances](#), [bird traits](#) and landscape covariates) are [publicly available](#), and ~~accessible to anybody~~. ~~All~~[can be obtained from the](#) sources ~~are given with~~[listed in the](#) references.

960

### References:

961  
962  
963  
964  
965  
966  
967  
968  
969  
970  
971  
972  
973  
974  
975  
976  
977  
978  
979  
980  
981  
982  
983  
984  
985  
986  
987  
988  
989  
990

~~Andam, K.S., Ferraro, P.J., Pfaff, A., Sanchez-Azofeifa, G.A., and Robalino, J.A. (2008). Measuring the effectiveness of protected area networks in reducing deforestation. Proc. Natl. Acad. Sci. 105, 16089–16094.~~

Balmford, A., and Bond, W. (2005). Trends in the state of nature and their implications for human well-being: Trends in the state of nature. Ecol. Lett. 8, 1218–1234.

~~Bartholomé, E., and Belward, A.S. (2005). GLC2000: a new approach to global land cover mapping from Earth observation data. Int. J. Remote Sens. 26, 1959–1977.~~

~~Barnagaud, J.-Y., Gaüzère, P., Zuckerberg, B., Princé, K., and Svenning, J.-C. (2017). Temporal changes in bird functional diversity across the United States. Oecologia 185, 737–748.~~

~~Bihn, J.H., Verhaagh, M., Brändle, M., and Brandl, R. (2008). Do secondary forests act as refuges for old growth forest animals? Recovery of ant diversity in the Atlantic forest of Brazil. Biol. Conserv. 141, 733–743.~~

Boulinier, T., Nichols, J.D., Sauer, J.R., Hines, J.E., and Pollock, K.H. (1998). Estimating species richness: the importance of heterogeneity in species detectability. Ecology 79, 1018–1028.

~~Brooks, T.M., Bakarr, M.I., Boucher, T., Da Fonseca, G.A.B., Hilton-Taylor, C., Hoekstra, J.M., Moritz, T., Olivieri, S., Parrish, J., Pressey, R.L., et al. (2004). Coverage ~~Provided~~[provided](#) by the ~~Global Protected Area System: Is It Enough~~[global protected-area system: is it enough](#)? BioScience 54, 1081.~~

Calenge, C. (2006). The package “adehabitat” for the R software: A tool for the analysis of space and habitat use by animals. Ecol. Model. 197, 516–519.

Ceballos, G., Ehrlich, P.R., and Dirzo, R. (2017). Biological annihilation via the ongoing sixth mass extinction signaled by vertebrate population losses and declines. Proc. Natl. Acad. Sci. 201704949.

~~Coetzee, B.W.T., Gaston, K.J., and Chown, S.L. (2014). Local ~~Scale Comparisons~~[scale comparisons](#) of ~~Biodiversity~~[biodiversity](#) as a ~~Test~~[test](#) for ~~Global Protected Area Ecological Performance: A Meta-Analysis~~[global protected area ecological performance: a meta-analysis](#). PLOS ONE 9, e105824.~~

~~Del Hoyo, J., Elliott, A., and Sargatal, J. (2013). Handbook of the birds of the World (Barcelona, Spain).~~

Mis en f

Mis en f

Mis en f

Mis en f

Mis en f

Mis en f

Mis en f

Mis en f

1029 [Devictor, V., Godet, L., Julliard, R., Couvet, D., and Jiguet, F. \(2007\). Can common species benefit from](#)  
1030 [protected areas? Biol. Conserv. 139, 29–36.](#)

1031 [Dornelas, M., Gotelli, N.J., McGill, B., Shimadzu, H., Moyes, F., Sievers, C., and Magurran, A.E. \(2014\).](#)  
1032 [Assemblage time series reveal biodiversity change but not systematic loss. Science 344, 296–299.](#)

1033 [Drummond, A.J., Suchard, M.A., Xie, D., and Rambaut, A. \(2012\). Bayesian Phylogenetics with BEAUti](#)  
1034 [and the BEAST 1.7. Mol. Biol. Evol. 29, 1969–1973.](#)

1035 Duckworth, G.D., and Altwegg, R. (2018). Effectiveness of protected areas for bird conservation  
1036 depends on guild. Divers. Distrib. [24, 1083–1091.](#)

1037 Dudley, N. (2008). Guidelines for applying protected area management categories ([IUCN](#)). [Gland,](#)  
1038 [Switzerland: International Union for Conservation of Nature\).](#)

1039 [ESA \(2015\). Climate Change Initiative - Land cover project map v2.0.7.](#)  
1040 [<http://maps.elie.ucl.ac.be/CCI/viewer/index.php>.](#)

1041 Ewers, R.M., and Rodrigues, A.S.L. (2008). Estimates of reserve effectiveness are confounded by  
1042 leakage. Trends Ecol. Evol. 23, 113–116.

1043 Foley, J.A., DeFries, R., Asner, G.P., Barford, C., Bonan, G., Carpenter, S.R., Chapin, F.S., Coe, M.T.,  
1044 Daily, G.C., Gibbs, H.K., et al. (2005). Global [Consequences](#) [consequences](#) of [Land Use](#) [land use](#).  
1045 Science 309, 570–574.

1046 Gamero, A., Brotons, L., Brunner, A., Foppen, R., Fornasari, L., Gregory, R.D., Herrando, S., Hořák, D.,  
1047 Jiguet, F., Kmecl, P., et al. (2017). Tracking [Progress Toward](#) [progress toward](#) EU [Biodiversity](#)  
1048 [Strategy Targets](#) [biodiversity strategy targets](#): EU [Policy Effects](#) [policy effects](#) in  
1049 [Preserving](#) [preserving](#) its [Common Farmland Birds](#) [common farmland birds](#). Conserv. Lett. 10, 395–  
1050 402.

1051 Geldmann, J., Barnes, M., Coad, L., Craigie, I.D., Hockings, M., and Burgess, N.D. (2013). Effectiveness  
1052 of terrestrial protected areas in reducing habitat loss and population declines. Biol. Conserv. 161,  
1053 230–238.

1054 Gray, C.L., Hill, S.L.L., Newbold, T., Hudson, L.N., Börger, L., Contu, S., Hoskins, A.J., Ferrier, S., Purvis,  
1055 A., and Scharlemann, J.P.W. (2016). Local biodiversity is higher inside than outside terrestrial  
1056 protected areas worldwide. Nat. Commun. 7, 12306.

1057 Hiley, J.R., Bradbury, R.B., and Thomas, C.D. (2016). Impacts of habitat change and protected areas  
1058 on alpha and beta diversity of Mexican birds. Divers. Distrib. 22, 1245–1254.

1059 IUCN (2018). IUCN Red List of [Threatened Species](#). [Versio](#) [threatened species](#). [Version](#) 2018.1.  
1060 [<http://iucnredlist.org>.](#)

1061 Jetz, W., Thomas, G.H., Joy, J.B., Hartmann, K., and Mooers, A.O. (2012). The global diversity of birds  
1062 in space and time. Nature 491, 444–448.

1063 Joppa, L.N., and Pfaff, A. (2009). High and [Far: Biases](#) [far: biases](#) in the [Location](#) [location](#) of  
1064 [Protected Areas](#). [PLoS One](#) [protected areas](#). PLOS ONE 4.

1065 [Kendall, W.L., Peterjohn, B.G., and Sauer, J.R. \(1996\). First-time observer effects in the North](#)  
1066 [American breeding bird survey. The Auk 113, 823–829.](#)

Mis en f

Mis en f

Mis en f

Mis en f

Mis en f

Mis en f

Mis en f

Mis en f

Mis en f

Mis en f

Mis en f

Mis en f

Mis en f

Mis en f

Mis en f

Mis en f

Mis en f

- 1106 Kerbiriou, C., Azam, C., Touroult, J., Marmet, J., Julien, J.-F., and Pellissier, V. (2018). Common bats  
1107 are more abundant within Natura 2000 areas. *Biol. Conserv.* 217, 66–74.
- 1108 Lee, T.M., Sodhi, N.S., and Prawiradilaga, D.M. (2007). [THE IMPORTANCE OF PROTECTED  
1109 AREAS FOR THE FOREST AND ENDEMIC AVIFAUNA OF SULAWESI  
1110 \(INDONESIA\)-The importance of protected areas for the forest and endemic avifauna of Sulawesi  
1111 \(Indonesia\)](#). *Ecol. Appl.* 17, 1727–1741.
- 1112 Leverington, F., Costa, K.L., Pavese, H., Lisle, A., and Hockings, M. (2010). [A Global Analysis of  
1113 Protected Area Management Effectiveness-A global analysis of protected area management  
1114 effectiveness](#). *Environ. Manage.* 46, 685–698.
- 1115 McCarthy, J.L., McCarthy, K.P., Fuller, T.K., and McCarthy, T.M. (2010). Assessing [Variationvariation  
1116 in Wildlife Biodiversitywildlife biodiversity](#) in the Tien Shan [Mountainsmountains](#) of Kyrgyzstan  
1117 [Using Ancillary Camerausing ancillary camera-trap Photosphotos](#). *Mt. Res. Dev.* 30, 295–301.
- 1118 McRae, L., Freeman, R., and Marconi, V. (2016). “The Living Planet index” in: Living Planet Report  
1119 2016: Risk and resilience in a new era (ed. Oerlemans N). (Gland, Switzerland).
- 1120 Naidoo, R. (2004). Species richness and community composition of songbirds in a tropical forest-  
1121 agricultural landscape. *Anim. Conserv.* 7, 93–105.
- 1122 NASA (2017). Net Primary Productivity (Terra/Modis) NASA Earth Observations (monthly data 2004-  
1123 2015). [\[downloaded 08.03.2017\]](#)  
1124 [https://neo.sci.gsfc.nasa.gov/view.php?datasetId=MOD17A2\\_M\\_PSN](https://neo.sci.gsfc.nasa.gov/view.php?datasetId=MOD17A2_M_PSN).
- 1125 National Geophysical Data Center (1999). Global Land One-kilometer Base Elevation (GLOBE), version  
1126 1. <https://www.ngdc.noaa.gov/mgg/topo/gltiles.html>.
- 1127 Nelson, A., and Chomitz, K.M. (2009). Protected [Area Effectivenessarea effectiveness](#) in [Reducing  
1128 Tropical Deforestationreducing tropical deforestation](#) (Washington DC, USA: Independent  
1129 Evaluation Group, The World Bank).
- 1130 [Pacifici, K., Simons, T.R., and Pollock, K.H. \(2008\). Effects of vegetation and background noise on the  
1131 detection process in auditory avian point-count surveys. The Auk 125, 600–607.](#)
- 1132 [Pardieck, K.L., Ziolkowski, D.J., Lutmerding, M., Campbell, K., and Hudson, M.-A.R. \(2017\). North  
1133 American Breeding Bird Survey Dataset 1966 - 2016, version 2016.0. U.S. Geological Survey, Patuxent  
1134 Wildlife Research Center. <https://www.pwrc.usgs.gov/bbs/RawData/>; doi:10.5066/F7W0944J.](#)
- 1135 Pellissier, V., Touroult, J., Julliard, R., Sibley, J.P., and Jiguet, F. (2013). Assessing the Natura 2000  
1136 network with a common breeding birds survey: Assessing Natura 2000 with a common breeding  
1137 birds survey. *Anim. Conserv.* 16, 566–574.
- 1138 [QGIS Development Team \(2017\). QGIS Geographic Information System. Open Source Geospatial  
1139 Foundation Project. http://qgis.osgeo.org.](#)
- 1140 [Rodrigues, A.S.L., Andelman, S.J., Bakarr, M.I., Boitani, L., Brooks, T.M., Cowling, R.M., Fishpool,  
1141 L.D.C., da Fonseca, G.A.B., Gaston, K.J., Hoffmann, M., et al. \(2004\). Effectiveness of the global  
1142 protected area network in representing species diversity. Nature 428, 640–643.](#)
- 1143 Roxburgh, S.H., Shea, K., and Wilson, J.B. (2004). The intermediate disturbance hypothesis: patch  
1144 dynamics and mechanisms of species coexistence. *Ecology* 85, 359–371.

Mis en f

Mis en f

Mis en f

Mis en f

Mis en f

Mis en f

Mis en f

Mis en f

Mis en f

Mis en f

Mis en f

Mis en f

Mis en f

Mis en f

Mis en f

1180 Sauer, J.R., Niven, D.K., Hines, J.E., Ziolkowski, D.J.J., Pardieck, K.L., Fallon, J.E., and Link, W.A. (2017).  
 1181 The North American ~~Breeding Bird Survey, Results~~[breeding bird survey, results](#) and  
 1182 ~~Analysis~~[analysis](#), 1966 - 2015. Version 2.07.2017 (Laurel, MD: USGS Patuxent Wildlife Research  
 1183 Center).

1184 Sinclair, A.R.E., Mduma, S.A.R., and Arcese, P. (2002). Protected areas as biodiversity benchmarks for  
 1185 human impact: agriculture and the Serengeti avifauna. *Proc. R. Soc. Lond. Ser. B-Biol. Sci.* 269, 2401–  
 1186 2405.

1187 Small, M.F., Veech, J.A., and Jensen, J.L.R. (2012). Local landscape composition and configuration  
 1188 around North American Breeding Bird Survey routes: *Ecological Archives* E093-215. *Ecology* 93,  
 1189 2298–2298.

1190 ~~Supp, S.R., and Ernest, S.K.M. (2014). Species-level and community-level responses to disturbance: a~~  
 1191 ~~cross-community analysis. Ecology 95, 1717–1723.~~

1192 ~~Tung Ho, L. si, and Ané, C. (2014). A Linear-Time Algorithm~~[A linear-time algorithm](#), for Gaussian  
 1193 and ~~Nonnon~~-Gaussian ~~Trait Evolution Model~~[trait evolution models](#), *Syst. Biol.* 63, 397–408.

1194 UNEP-WCMC, and IUCN (2018). Protected Planet: [WDPA-shapefile-polygons; The World Database  
 1195 on Protected Areas (WDPA)/The Global Database on Protected Areas Management Effectiveness  
 1196 (GD-PAME)] [On-line, downloaded 02/10/2018], Cambridge, UK: ~~UNEP-WCMC and IUCN.~~  
 1197 ~~Available at: <www.protectedplanet.net>~~

1198 ~~UNEP-WCMC, and IUCN (2019). Calculating protected area coverage. [On-line, consulted~~  
 1199 ~~06/02/2019]. <www.protectedplanet.net/c/calculating-protected-area-coverage>~~

1200 ~~UNEP-WCMC IUCN (2016). Protected Planet Report (Cambridge UK and Gland, Switzerland: UNEP-~~  
 1201 ~~WCMC and IUCN).~~

1202 Venter, O., Sanderson, E.W., Magrath, A., Allan, J.R., Beher, J., Jones, K.R., Possingham, H.P.,  
 1203 Laurance, W.F., Wood, P., Fekete, B.M., et al. (2016). Global terrestrial Human Footprint maps for  
 1204 1993 and 2009. *Sci. Data* 3, 160067.

1205 Vié, J.-C., Hilton-Taylor, C., and Stuart, S.N. (2009). *Wildlife in a changing world: an analysis of the*  
 1206 *2008 IUCN red list of threatened species* (Gland, Switzerland : Barcelona, Spain: IUCN ; Lynx Edicions).

1207 Wasiolka, B., and Blaum, N. (2011). Comparing biodiversity between protected savanna and adjacent  
 1208 non-protected farmland in the southern Kalahari. *J. Arid Environ.* 75, 836–841.

1209 Wunderle, J.M., Henriques, L.M.P., and Willig, M.R. (2006). Short-~~Term Responses~~[term responses](#) of  
 1210 ~~Birds~~[birds](#) to ~~Forest Gaps~~[forest gaps](#) and ~~Understory: An Assessment~~[understory: an assessment](#)  
 1211 of ~~Reduced Impact Logging~~[reduced-impact logging](#) in a ~~Lowland Amazon Forest~~<sup>†</sup>: ~~Reduced-~~  
 1212 ~~Impact Logging Effects~~[lowland amazon forest: reduced-impact logging effects](#) on ~~Amazon~~  
 1213 ~~Birds~~[amazon birds](#). *Biotropica* 38, 235–255.

1214

Mis en f

Mis en f

Mis en f

Mis en f

Mis en f

Mis en f

Mis en f

Mis en f

Mis en f

Mis en f

Mis en f

Mis en f

Mis en f

Mis en f

Mis en f

Mis en f

Mis en f

Mis en f