

1 **The jaguar's patches: viability of jaguar populations in fragmented landscapes**

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15

16 **Abstract**

17 Habitat loss and fragmentation have serious consequences for long-term population
18 persistence, thus we investigated the effects of these processes on jaguars (*Panthera onca*)
19 across the species' distribution range. We employed theoretical simulations of population
20 dynamics, making use of real and hypothetical landscapes to understand how landscape
21 patterning affects the long-term persistence of species, and investigated the isolated and
22 synergistic effects of habitat loss and fragmentation. Jaguar persistence probability was
23 related both to the amount and pattern of landscape subdivision, but with a strong tolerance
24 for habitat loss because the amount habitat could be between 230 to 5841 km². In contrast, the
25 persistence probability of smaller jaguar populations decreased dramatically in fragmented
26 landscapes, indicating that fragmentation is a greater threat to jaguar long-term viability than
27 habitat loss. Only two of the 28 populations included in our study were deemed viable in the
28 long-term. Given the increase in habitat fragmentation and the current threat status of the
29 jaguar, we discuss the best strategies for their conservation.

30

31 **Keywords**

32 Critical threshold, habitat loss, habitat fragmentation, *Panthera onca*, population viability
33 analyses

34 **Introduction**

35 Human land use and habitat conversion are a central topic in conservation biology
36 because they are largely responsible for the current and alarming biodiversity extinction rate
37 (Foley et al., 2005). The conversion of native vegetation into anthropogenic cover alters
38 landscapes, fragmenting habitats while simultaneously reducing their extent (Fahrig, 2003).
39 Thus, habitat loss and fragmentation are simultaneous processes arising from human-induced
40 landscape changes (Andrén, 1994; Fahrig, 2003). Nevertheless, habitat loss and fragmentation
41 can be considered different processes, since habitat loss infers a decrease in available habitat
42 while fragmentation refers to habitat subdivision into smaller patches (Andrén, 1994; Fahrig,
43 2003). Despite inherent difficulties, it is critical to understand the differing effects of each
44 process in order to better guide wildlife management strategies, permitting a more efficient
45 use of limited conservation resources (Lindenmayer & Fischer, 2007; Smith et al. 2009).
46 Therefore, to generate a broad picture of the consequences of habitat loss and fragmentation,
47 studies should understand the synergistic effects of both process, as well as their isolated
48 effects.

49 Landscape metrics provide an excellent tool to enable the study of synergistic and
50 isolated effects of habitat loss and fragmentation (McGarigal & Cushman, 2002). Currently,
51 hundreds of metrics have been described and these are frequently used to capture landscape
52 patterns resulting from complex interactions between habitat loss and fragmentation in real
53 landscapes (McGarigal & Marks, 1994). However, they are also able to represent simple
54 patterns. Habitat area reductions in time or space are a measure of habitat loss (Fahrig, 2003),
55 and the total habitat or proportion of habitat in a landscape can represent this process.
56 Similarly, the number of patches and their relative size are metrics commonly used to quantify
57 fragmentation (Fahrig, 2003). Thus, total habitat area and the number of patches are a good
58 representation of the isolated effects of these processes.

59 Even with the development of landscape metrics, it is difficult make general
60 predictions about the effects of habitat conversion because it may be perceived different by
61 species (Lindenmayer & Fischer, 2007), so a species-specific approach is essential to measure
62 the effects of habitat loss and fragmentation. Population viability analysis (PVA) has become
63 a useful tool because it facilitates the evaluation of individual species' responses to a variety
64 of environmental threat scenarios, generating an estimate of persistence probability (Brook et
65 al., 2002). Therefore, the combination of PVA and landscape metrics should be an efficient
66 approach to investigate individual species' responses to landscape patterns.

67 The goal of our study was to investigate the synergistic and isolated effects of habitat
68 loss and fragmentation to understand how landscape patterning affects the long-term
69 persistence of species. For this, we selected the jaguar (*Panthera onca*, Linnaeus 1758) as a
70 focal species, because jaguars occupy less than 60% of their former geographic range
71 (Morrison et al, 2007). The jaguar is ranked 15th among the large-bodied mammals with the
72 greatest geographic range contraction in the last 500 years due to anthropogenic effects
73 (Morrison et al., 2007). Today, the jaguar is listed as Near Threatened (IUCN, 2013), but this
74 status may soon be revised to reflect further declining populations (IUCN, 2013).

75 To achieve our objectives, we first investigated the synergistic effect of habitat loss
76 and fragmentation. The present-day habitat configuration can be considered as a pattern
77 generated by the effects of both processes because it is a result of past habitat loss and
78 fragmentation (Villard & Metzger, 2013). Therefore, we used real landscapes where the
79 species is present to investigate how the landscape configuration could determine jaguar
80 persistence probability. To better understand the consequences of habitat configuration on
81 species persistence, we created hypothetical landscapes based on the simplest landscape
82 features, i.e. the total habitat area and the number of patches. For that, we modeled jaguar
83 population dynamics in landscape scenarios for (i) a controlled number of patches while

84 reducing the total habitat area, and (ii) a controlled total habitat area while increasing the
85 number of patches. The generation of the hypothetical landscapes mirrored the processes that
86 produce real landscapes, which allowed us to better comprehend habitat configurations, but
87 also allowed us to disentangle the effects of habitat loss and fragmentation on populations and
88 to determine which effect is the greatest threat to jaguars.

89 Each step of our study resulted in an applied outcome, which can inform jaguar
90 conservation and management strategies. The evaluation of jaguar population dynamics in
91 real landscapes permitted us to map threatened populations and to highlight those that need
92 urgent intervention to persist in the long-term. The hypothetical landscapes helped us to
93 identify the amount of habitat necessary to maintain viable populations and the extent of
94 habitat fragmentation a jaguar population can support while maintaining a high persistence
95 probability. Thus, they helped in determining the best management strategies, and provided
96 general insight into the importance of increasing total habitat area and connecting isolated
97 fragments to ensure the long-term persistence of jaguar populations across its range.

98

99 **Methods**

100

101 *Study Area*

102 To conduct our investigation, we selected jaguar populations where density estimates
103 were available. We used the review of Maffei et al. (2011) as our primary source for study
104 areas, where authors reported jaguar densities for 49 study areas distributed across 14
105 countries. However, the studies considered in that review used different density estimation
106 methods and sampling designs, so we selected sites where densities were estimated by the
107 same method to ensure consistency, capture-recapture using two camera-traps at each
108 sampling station as the census technique. Among the evaluated studies, 28 fulfilled the

109 prerequisites and were selected for our investigation. These studies correspond to areas
110 located throughout nine countries, with density estimations varying from 1.12 to 11.56
111 jaguars/100 km² (Supplementary Material A).

112

113 *Landscape scenarios*

114 The real landscapes were delimited by establishing a 10,000 km² buffer around the
115 central point where the density studies were conducted. We used the GlobCover map (ESA,
116 2011) to define the land use across landscapes, and converted GlobCover classification into a
117 binary map to approximate a jaguar's perception of the landscape: we categorized native
118 vegetation cover as suitable for jaguars and anthropogenic landcover as unsuitable. This level
119 of generalization was adopted because jaguars show significant environmental plasticity in
120 terms of their use of vegetation types (Colchero et al., 2011), and although it is known that
121 jaguars occupy anthropogenic vegetation (Colchero et al., 2011), it may be that they simply
122 traverse these areas rather than occupy them. Additionally, jaguar mortality probably
123 increases in anthropogenic vegetation (Inskip & Zimmermann, 2009), justifying our
124 classification of it as unsuitable for jaguars. The number and size of habitat patches were
125 estimated for each landscape in the jaguar habitat map. Patches larger than 100 km² were
126 included in our PVA because we considered that these patches adequately function as
127 stepping stones and since it is a reasonable size for a jaguar home range (Cavalcanti & Gese,
128 2010; Cullen Jr., 2006).

129 The hypothetical landscapes were designed with a controlled structure to measure the
130 effects of habitat area and subdivision. The simulations started considering a landscape with
131 the maximum of structural integrity, i.e. a patch of 10,000 km². In order to model the effects
132 of habitat loss, the total area was reduced gradually, by blocks of 1,000 km², until only 1,000
133 km² remained, and then to 500 km² and finally to 100 km². In order to model the effects of

134 habitat fragmentation, the total area of habitat was kept constant (i.e. the same amount of
135 habitat used in the habitat loss simulations), but it was divided into a number of scenarios
136 where we gradually increased the number of patches. The first scenario had two patches, the
137 second had four patches of equal size, continuing progressively by steps of four up to 28
138 patches. The patches were of equal area without reducing the total area, and so each patch had
139 equivalent relevance to population persistence.

140

141 *Population Viability Analysis*

142 The software VORTEX version 9.99 (Lacy, 2012) was used to simulate the
143 population dynamics of jaguars and estimate persistence probability for 200 years. VORTEX
144 is a Monte Carlo simulation that considers a set of factors affecting a population, including:
145 deterministic forces (e.g. trends in carrying capacity); demographic, environmental and
146 genetic stochasticity; and catastrophes (Lacy, 2000). We chose VORTEX due to its spatially-
147 implicit approach, which was necessary for our study because the literature concerning the
148 jaguar lacks information about dispersal rates and mortality in different landcover types and
149 areas.

150 Most of the life history data were obtained from the ‘Brazilian Action Plan for
151 Jaguars’ because it compiles the most up-to-date biological data on the species (de Paula et
152 al., 2010) (Table 1). These data represent an actual, but non-specified, jaguar population (de
153 Paula et al., 2010), so the population might be derived from anywhere within the species
154 distribution. We used the same life history data to all populations modeled in our study, thus
155 the differences among populations regarded landscapes proprieties where they are located.
156 Due to the spatially-implicit approach, the total habitat area and the number of patches were
157 integrated into the PVA indirectly; the number of patches was used as a surrogate for the
158 number of populations and the total amount of suitable habitat was a surrogate for population

159 size. The total area of the patches multiplied by the jaguar density determined initial
160 population size.

161 We assumed that carrying capacity was equal to the initial population size, which
162 was a conservative approach because there is no information about the temporal change in
163 carrying capacities of these studies areas. There is also no information about jaguar dispersal
164 rates or mortality in the different landcover types. Therefore, we chose a generalized
165 approach, whereby the movement of migrants between fragments was considered symmetric,
166 i.e. individuals could move in either direction between patches at the same rate. The total
167 number of migrants was estimated as a function of the number of subadults in the population
168 because, typically, at this life-history stage, felines are looking to establish a territory
169 (Funston et al., 2003). The proportion of subadults was determined as a proportion of the
170 dynamic sites (*sensu* Gotelli, 1991) that can be occupied in the metapopulation. Since a
171 subadult competitively excludes another individual from its *site*, the excluded jaguar (which
172 can be an adult or another subadult) can compete for another *site* in the metapopulation.
173 Therefore, the number of subadults defined the proportion of dispersers, but the dispersers
174 could be any jaguar in the population.

175 Of the estimated life-history parameters for jaguars, the percentage of males in the
176 breeding pool and mortality were those having the greatest degree of uncertainty. The
177 percentage of males in the breeding pool is difficult to estimate. An accurate estimate would
178 require long-term demographic study, using expensive techniques, such as genetic analysis
179 and GPS monitoring. Mortality too is a complex parameter that varies according to sex, age
180 and location (Ferrerias et al., 2004), as well as anthropogenic factors (Inskip & Zimmermann,
181 2009). We modeled PVAs based on the best preserved landscape in our study area (jaguar
182 density of 11.56 jaguars/100 km² and 10,000 km² of available habitat; Miller & Miller
183 unpublished data; to review, see Maffei et al. 2011), with different values for the percentage

184 of males in the breeding pool and jaguar mortality to take into account the uncertainty of these
185 parameters. The proportions of males in the breeding pool used in the models were 100%,
186 80% and 70% while, for mortality rates, we used 10%, 30% and 50% (for both sexes and
187 every age class). These values were attributed randomly into the 500 PVA models.

188

189 *Statistical Analysis*

190 To investigate the synergistic effects of habitat loss and fragmentation on jaguar
191 population viability, we used landscape metrics as a measure of landscape configuration. We
192 calculated landscape metrics using the Fragstats software program (McGarigal & Marks,
193 1994) on a landcover map (Bontemps et al., 2011), with our classification of
194 suitable/unsuitable habitat for jaguars. The selected metrics included: the proportion of native
195 cover in the landscape (PLand); largest patch index (LPI); landscape shape index (LSI); patch
196 number (PN); cohesion; mean size of patches (Area-MN); and the standard deviation of patch
197 area (Area-SD) (Table2). These various landscape metrics might capture the same process,
198 resulting in over-parameterization of the statistical analysis. Thus, we conducted a principal
199 components analysis (PCA) to remove redundant parameters (Legendre & Legendre, 1998),
200 and the associated principal component scores were used to represent the landscape
201 configuration.

202 The real landscapes studied could be spatially structured throughout the jaguars'
203 distribution and may depict spatial autocorrelation, so we adopted the use of spatial filters as a
204 covariable to address this problem. Spatial filters consist of synthetic variables added into
205 analyses with the objective of expressing the geographic relationships among landscapes
206 (Dray, 2011; Patuelli et al, 2010). They capture orthogonal variation in spatial structure at
207 different scales without inserting redundant parameters (Diniz-Filho & Bini, 2005). Spatial

208 filters are eigenvectors from a principal coordinates analysis of neighbor matrices (Borcard &
209 Legendre, 2002), calculated through the truncated distance matrix W

$$W = (w_{ij}) = \begin{cases} 0 \rightarrow i = j \\ 0 \rightarrow d_{ij} > t \\ \left[1 - (d_{ij} / 4t)^2\right] \rightarrow d_{ij} \leq t \end{cases}$$

210

211 where w_{ij} is each one of the elements and t is the truncation distance. The spatial filters were
212 generated by the Spatial Analysis Macroecology software (SAM) (Rangel et al., 2010) based
213 on the geographical distance between landscape centroids.

214 Model selection was performed to evaluate the best model explaining the relationship
215 between persistence probability, landscape configuration and spatial filters. This was
216 accomplished through the use of the Akaike Information Criterion corrected for small sample
217 size (AICc) (Burnham & Anderson, 2004), which permits a hierarchical ordination of models
218 according to their descriptive power and complexity (Burnham & Anderson, 2004). We
219 expected to generate a non-linear pattern of species responses to habitat loss and
220 fragmentation (Swift & Hannon, 2010), so we used a logistic adjustment for our models to be
221 more consistent with theory. We also included a model composed only of a linear coefficient
222 to evaluate if a random solution explained the persistence probability better than the proposed
223 variables. We considered models with AICc values lower than two as complementary
224 explanations of pattern (Burnham & Anderson, 2004), since the null model was not among
225 the best solutions.

226 To measure the amount of habitat necessary to maintain a viable population of
227 jaguars, and the extent of fragmentation a jaguar population can support while maintaining its
228 viability, we performed a piecewise linear regression with the hypothetical landscape data.
229 Piecewise analysis estimates the tipping point at which system alteration generates qualitative
230 changes in population persistence probability, i.e. from viable to nonviable. This tipping point
231 is known as the critical threshold and it is defined as an abrupt and non-linear alteration in a

232 given variable occasioned by small changes in the original system (Fahrig, 2001; Scheffer et
233 al., 2009). Mathematically, piecewise analysis adjusts more than one regression line through
234 data variation, and the “breakpoint” (or the place where the lines converge) is considered the
235 critical threshold (Toms & Lesperance, 2003). We calculated the critical threshold using the
236 *SiZer* package (Sonderegger, 2011) in R software (R Core Team, 2013).

237 The sensitivity of our base population viability model was investigated using a
238 regression tree (Cutler et al., 2007; Harper et al., 2011), which permits the evaluation of
239 multiple uncertain parameters and their nonlinear interaction (Harper et al., 2011). The
240 regression tree structures data through hierarchical and binary partitions (splits) to create
241 groups (nodes) of higher homogeneity, reflecting parameter importance, up to an undivided
242 group of populations (leaves) (Rejwan et al., 1999). The evaluation of node numbers in the
243 regression tree was accomplished by a cross-validation procedure, which calculates the true
244 prediction error in the addition of nodes (Breiman, 2001). A random forest was performed to
245 evaluate the relative importance of each parameter in the PVA estimations (Cutler et al.,
246 2007), which indicated the variable that needed to be more accurately estimated (Harper et al.,
247 2011). The random forest analysis was carried out using 1000 random trees through bootstrap
248 sampling (Breiman, 2001). We used the *rpart* (Therneau et al., 2011) and *randomForest*
249 (Liaw & Wiener, 2002) packages to conduct the regression tree and random forest analyses in
250 R software (R Core Team, 2013).

251

252 **Results**

253 The studies areas had a large proportion of suitable habitat (Average P_{Land} =
254 77.7%), which could be divided from one to five patches larger than 100 km² (Supplementary
255 material A). However, we observed that the landscapes composed of habitat aggregated into
256 one single patch had a larger proportion of suitable habitat than landscapes with two or more

257 patches (\bar{X} P_{Land}_{2-5patches}=65%; \bar{X} P_{Land}_{1patch}=87%; t-value = 2.18; DF = 26; p = 0.04). Even
258 same with this difference, the landscape metrics used to calculate the configurations of real
259 landscapes were correlated. Therefore, we selected only the first principal component of the
260 PCA according to a broke-stick method, which described 58% of the landscape metrics
261 variation. The variables P_{Land}, LPI, Area-MN, Area-SD and cohesion were positively
262 correlated with the principal component, while PN and LSI were negatively correlated.

263 Two out of the 64 competitive models were considered the best (i.e. AICc < 2) in
264 explaining the persistence probability of jaguars in the landscapes, the null model not being
265 amongst them (Table 3 and Supplementary Material B). The principal component condensing
266 the landscape configuration appeared in both models (Table 3), evidencing the homogenous
267 effect of landscape configuration, which could be observed due to the low variance in the
268 coefficient value and the low standard error of the competitive models (Figure 1). Spatial
269 filters three and five also appeared in the best models, but had large standard errors associated
270 with them, obscuring their importance in predicting persistence probability (Table 3).
271 Therefore, we considered only the principal component summarizing landscape configuration
272 as an efficient predictor of jaguar persistence probability.

273 The habitat loss critical thresholds varied widely among jaguar populations, attaining
274 values ranging from 230 km² to 5,841 km² (Figure 2 B). These values were strongly
275 correlated with jaguar density (Figure 3 A) due to the direct effects of initial population size
276 on persistence probability. Variation in the order of decimal degrees generated changes of
277 more than 100 km² in the critical threshold. However, the fragmentation critical threshold was
278 more sensitive to changes in the landscape than the habitat loss critical threshold. The
279 tolerance of jaguar populations to fragmentation was not sufficient to determine fragmentation
280 critical thresholds; the piecewise linear regression calculated the critical thresholds when the
281 metapopulation had a persistence probability close to zero (tipping points have a negative

282 slope). In only a few cases did the populations have a high persistence probability after the
283 first subdivision, even in landscapes with 10,000 km² of suitable habitat (Figure 4).

284 As a complementary result, we calculated a habitat critical threshold with a 97.5%
285 confidence interval, to have a conservative estimate of ensuring long-term jaguar persistence.
286 When populations had a density greater than 4.13 jaguars/100 km², jaguar population viability
287 suffered an abrupt and stable change following a small reduction of habitat, which resulted in
288 almost uniform residuals and an inadequate fit of the piecewise-regression to bootstrap
289 samples. This mathematical artifact generated a relationship between density and the critical
290 threshold similar to a parabola, in which the estimated density decreases to 4.13 jaguars/100
291 km² and thereafter starts to increase (Figure 3 B). Of course, there is no biological sense to
292 this pattern since the area needed to maintain a jaguar population must decrease with higher
293 density. Thus we considered it acceptable, from a conservation perspective, to consider the
294 threshold estimated at 4.13 jaguars/100 km² for populations with greater densities. Based on
295 that, the jaguar habitat critical threshold with a 97.5% varied from 3,000 km² to 7,000 km²
296 (Supplementary Material A).

297 The real landscapes evaluated were able to support a jaguar population only in two
298 out of the 28 sites investigated (Figure 2 B; Supplementary Material A), based on 95%
299 persistence probability after 200 years (Table 1). Both of these viable populations are located
300 in Guatemala and exhibit high jaguar density and a landscape with almost 100% native
301 vegetation. Many other high density populations were nonviable (Figure 2 B and
302 Supplementary Material A). These landscapes frequently had a total area that was larger than
303 the habitat loss critical threshold, but the area was divided into a number of patches that were
304 also larger than the fragmentation critical threshold, which resulted in nonviable populations.
305 Therefore, the main threat to the long-term persistence of the jaguar populations studied
306 seemed to be habitat fragmentation.

307 The sensitivity analysis showed that 82% of the predictors' variance could be
308 explained by random forest. The regression tree was composed of six nodes, all defined by
309 female mortality (Figure 5). Therefore, the PVA model was sensitive to poorly-estimated
310 parameters, especially adult female mortality (Figure 6). The final node showed the
311 populations with higher persistence probability, which were those with a female mortality rate
312 lower than 20% from birth to sexual maturity (i.e. three years of age) (Figure 5). Thus, low
313 mortality in female jaguars may be seen as a surrogate of population persistence probability.

314

315 **Discussion**

316 Jaguar persistence probability is linked to landscape configuration in an ecologically
317 complex and interesting way. The proportion of suitable habitat in the real landscapes
318 predicted jaguar persistence probabilities - it being greater when the habitat is aggregated in
319 one single patch, which was reinforced by the simulations on hypothetical landscapes.
320 However, although we have shown that a high proportion of habitat could guarantee long-
321 term jaguar persistence, we have also shown that habitat subdivision dramatically reduces
322 their persistence probability, even in landscapes with a large proportion of suitable habitat and
323 a high jaguar density. Therefore, we can confirm that fragmentation is more detrimental than
324 habitat loss to jaguar populations.

325 The correlation among metrics of the real landscapes is a product of the large amount
326 of suitable jaguar habitat. Landscapes comprising an amount of suitable habitat greater than
327 65% are structurally connected and display low structural complexity (Bascompte & Solé,
328 1996; With, 1997), which is the case for the majority of our study areas. Therefore, habitat
329 loss and fragmentation are processes that can homogenize landscape configurations. Based on
330 that, we could also expect that the landscapes composed of habitat aggregated into one single
331 patch had tended to have a larger proportion of suitable habitat than landscapes comprised of

332 two or more patches, and this was supported by the real landscapes analyzed in the current
333 study. Therefore, the relationship we found between total habitat availability and persistence
334 probability expresses more than a simple metric for the predictability of an ecological process.
335 The increase in availability of suitable habitat acts directly on landscape connectivity, thereby
336 altering population structure (Bascompte & Solé, 1996).

337 The low persistence probability of jaguar populations in fragmented landscapes is
338 probably linked to an increase in overall mortality, arising by impediments to dispersal. We
339 established a stable proportion of migrants and survivors between patches in our models, so
340 total mortality increased with an increase in the number of patches. The effects of mortality
341 were reinforced by our sensitivity analysis, especially for female mortality, since the PVA
342 estimates were sensitive to this parameter. Jaguar mortality can vary widely among
343 populations because it is strongly influenced by extrinsic factors (Azevedo, 2008; Polisar et
344 al., 2003). However, it seems reasonable that female mortality at the reproductive stage is
345 important because a relationship between the total number of females in the reproductive pool
346 and growth rate is expected for a polygenic species. Even though this parameter is quite
347 relevant for jaguar ecological studies, there is no information about the variability and
348 intensity of jaguar mortality in terms of sex, age or matrix type. This resulted in persistence
349 probabilities that were sensitive to poorly-estimated parameters. However, an increase in
350 mortality during dispersal in a fragmented landscape can be expected, as we assumed in our
351 models even with the different rates we used. Thus, while our results might vary in intensity
352 with better model parameterization, the overall findings would not change.

353

354 *Conservation implications*

355 Our approach permitted us not only to summarize the effects of habitat loss and
356 fragmentation on jaguar persistence probability, but also to generate a diagnostic of jaguar

357 conservation status because all the results discussed here have strong applicability from a
358 conservation perspective. According to our results, we can predict that jaguar conservation is
359 in a dangerous situation, given that only two of the 28 evaluated populations had a high
360 probability of persistence. Over recent years, the species has become more dependent on
361 protected areas (Riley, 2006), but currently few such areas can support demographically-
362 viable jaguar populations (Sollmann et al., 2008). Thus, our results provide an important
363 contribution to jaguar conservation because the habitat loss critical thresholds can be used to
364 predict the necessary size of protected areas (Traill et al., 2007; 2010).

365 Even with our growing dependence on protected areas for species conservation,
366 many are not fulfilling their conservation function because they do not support long-term
367 viable populations (Sollmann et al., 2008). We can highlight Iguazu National Park (INP) and
368 its surrounding areas as a significant example because it supports one of the few remaining
369 southern jaguar populations located in an area with large suitable habitat fragments (Altrichter
370 et al., 2006; Mazzolli, 2009). However, the jaguar population in this landscape is highly
371 vulnerable to extinction (Persistence Probability < 0.01, Mean time to extinction = 58.7
372 years), even though the landscape comprises 9,200 km² of native vegetation cover in a
373 practically single and large patch. The unviability of this population might be due to the low
374 number of individuals it harbors, since it had the lowest density of all the locations evaluated
375 in this study. Due to the time lag of species' responses to environmental alterations, especially
376 those species of significant longevity (Krauss et al., 2010) such as jaguars, the mean time to
377 extinction can be higher than those estimated. Nevertheless, INP still has one of the most
378 threatened jaguar populations. The areas surrounding INP suffer from severe hunting
379 pressures (Azevedo, 2008), which decrease jaguar population density both directly by
380 poaching and indirectly by prey reduction.

381 Currently, the implementation of dispersal corridors is the main strategy
382 recommended by researchers and conservation managers to bolster threatened jaguar
383 populations and to connect protected areas (e.g. Rabinowitz & Zeller, 2010; Rodríguez-Soto
384 et al., 2013). Our study provides theoretical evidence for low jaguar persistence probabilities
385 under metapopulation dynamics (Figure 4). Thus, the establishment of dispersal corridors
386 needs to be carefully planned, given that the negative consequences of fragmented
387 metapopulation dynamics could be worse than those for populations that remain isolated
388 (Brito & Fernandez, 2002). A corridor can force species to cross less-suitable habitats
389 (Franklin & Lindenmayer, 2009). For top-predators such as jaguars, this can exacerbate
390 retaliatory hunting in response to the intensification of jaguar predation on domestic animals
391 (Inskip & Zimmermann, 2009), which would probably occur in these contexts.

392 Therefore, our results raise the question of how to manage jaguar populations in
393 fragmented landscapes. Perhaps jaguar conservation planning should emphasize strategies
394 that increase population size by decreasing human-wildlife conflicts and increasing habitat
395 quality. Decreasing human-wildlife conflict will depend on multiple factors because it has an
396 ecological, social and probable regional context (Zanin et al. unpublished data). Increasing
397 habitat quality is also a complex task because it will involve landscape management - though
398 the field of restoration ecology is rapidly advancing, which will be of assistance in this area.
399 Our research highlights the fact that jaguar conservation is far more complex than the
400 connectivity between two areas, as has been suggested by researchers (Rabinowitz & Zeller,
401 2010; Rodríguez-Soto et al., 2013). Of course, the implementation of dispersion corridors is
402 of fundamental significance for long-term jaguar conservation in some regions, but its
403 applicability should be evaluated carefully and in conjunction with efforts to maintain or grow
404 local jaguar populations.

405

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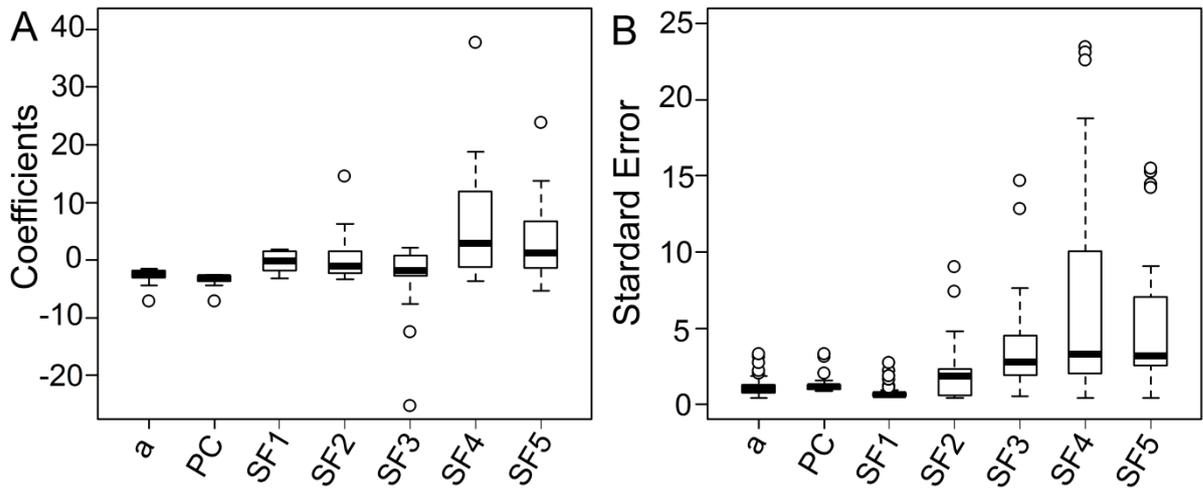
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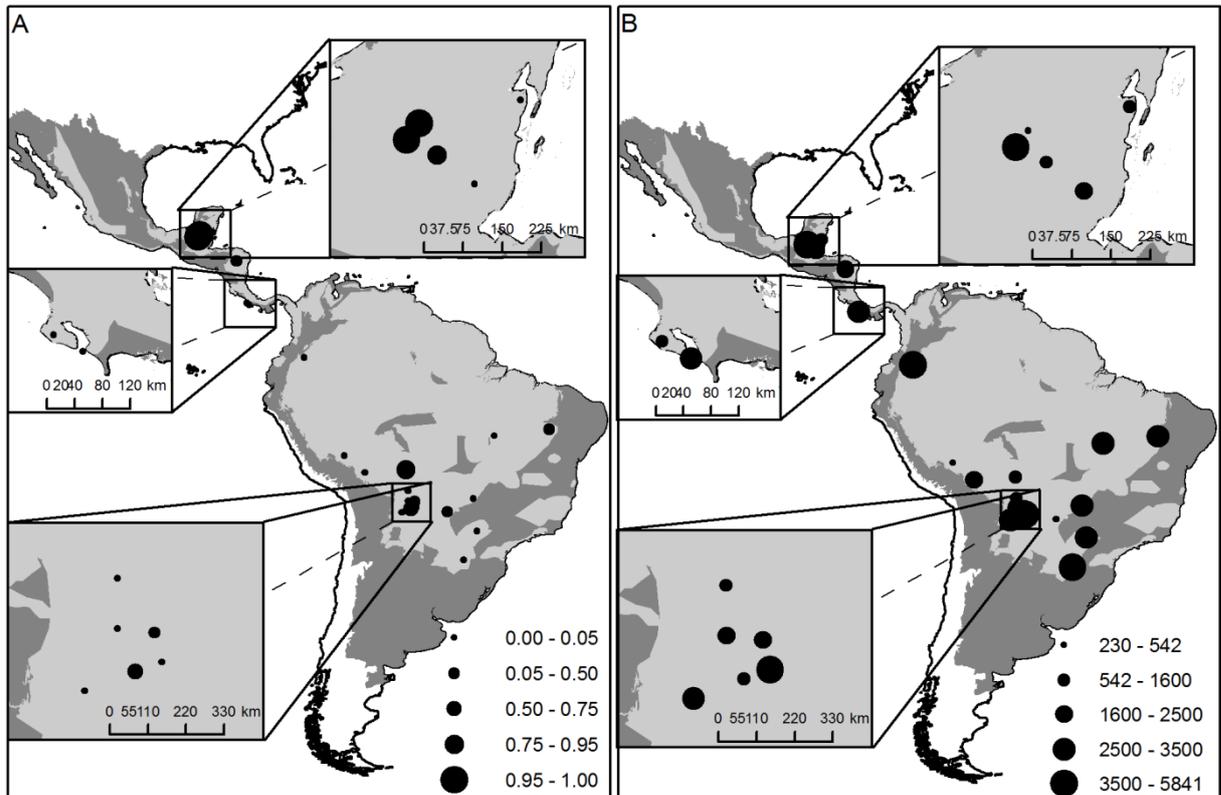
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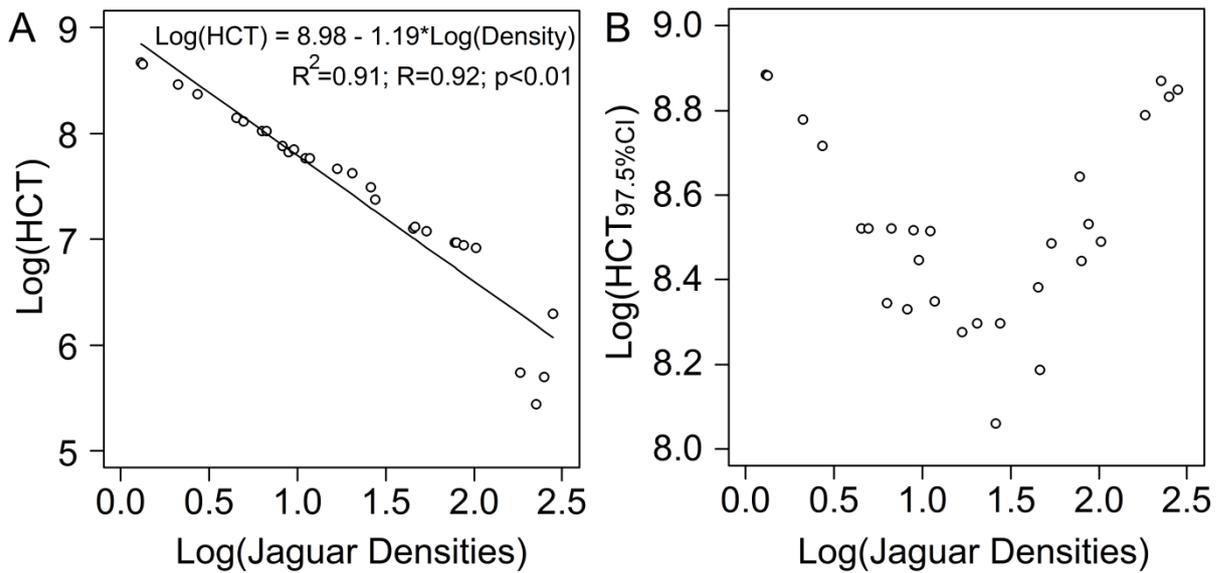
543 Figure 1. Variation in coefficients (A) and standard error (B) of the explanatory variables
 544 employed to describe jaguar persistence probability: a = coefficient of non-linear regression;
 545 PC = first principal component condensing landscape configuration; SF (1-5) = spatial filters
 546 capturing differing spatial structures of selected landscapes.



547

548 Figure 2. Maps of the jaguar populations used in our study according to (A) the area
 549 requirement (in km²) needed to maintain viable populations (also called the habitat loss
 550 critical threshold) and (B) their persistence probabilities in 200 years based on actual
 551 landscape configurations. Dark gray indicates original jaguar distribution range (IUCN, 2013)
 552 and light gray the current distribution (Zeller, 2007).

553



554

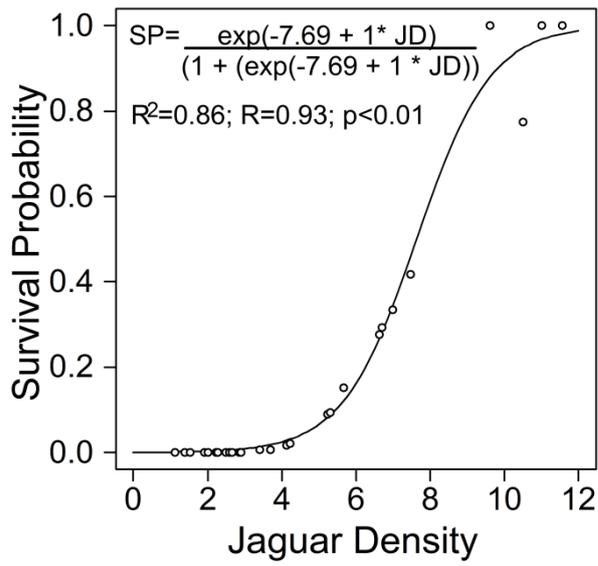
555 Figure 3. Relationship between jaguar density and the habitat loss critical threshold (HCT).

556 (A) Habitat critical threshold estimated to maintain a jaguar population with a high

557 persistence probability. (B) Habitat critical threshold with a 97.5% confidence interval (97.5%

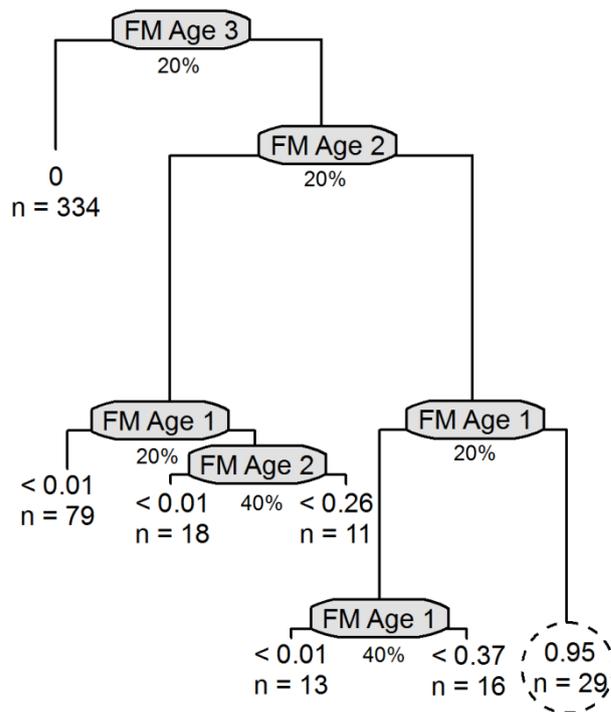
558 CI). The log transformed HCT ranged from 5.3 to 8.9, which is equivalent to a range of 230 to

559 5,841 km².



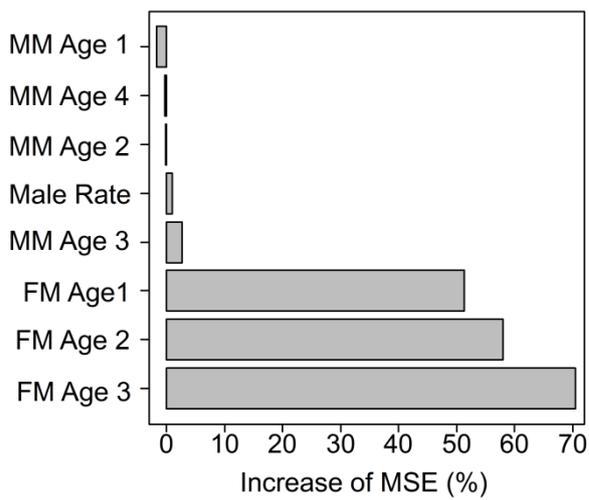
560

561 Figure 4. Persistence probability (SP) of metapopulations relative to jaguar density (JD) in
 562 landscapes composed of two patches, each of 5,000 km².



563

564 Figure 5. Illustration of the regression tree and the relationships between parameters used to
 565 estimate jaguar persistence probability. The significant variables to the regression (gray box)
 566 divided the simulated populations into two groups according a value of the variable
 567 (percentile bellow gray box is the threshold to division). Populations with values lower or
 568 equal than the threshold to division are represented in the left size variable and populations
 569 with higher values are in the right size. The final node indicates the probability values along
 570 with the number of observations (“n”). FM is female mortality. There is only one pathway
 571 (delimited by the circle) that leads to viable populations (high persistence probability).



572

573 Figure 6. Sensitivity of jaguar persistence probability estimates for each variable in the global
 574 sensitivity analysis (MM is male mortality and FM female mortality). Mean standard error
 575 (MSE) was evaluated by random forest.

576 Table 1. Biological and statistical parameters used in the jaguar population viability analysis.

577 EV - environmental variation; SD - standard deviation.

Parameter	Value
Number of interactions	1000
Number of years	200
Extinction	Only 1 sex remains
Inbreeding	Yes (Default)
EV concordance in persistence and reproduction	Yes (Default)
Reproductive system	Polygynous
Age of first offspring for females	3
Age of first offspring for males	4
Maximum age of reproduction	10
Maximum number of progeny per year	4
Sex ratio at birth (% males)	50
Alle parameter, A	0.5
Steepness parameter, B	2
% adult females breeding	$(P0((P0-PK)*((N/K)^2)))*(N/(A+K))$
EV in % breeding	12.5
EV in % breeding	Specific
Adult females producing	
1 young	5%
2 young	40%
3 young	30%
4 young	25%

Parameter	Value
Mortality rates in females	
Age 0-1	34 ± 10
Age 1-2	17 ± 8
Age 2-3 (Subadult)	19 ± 5
Age 3-4 (Adult)	20 ± 5
Mortality rates in males	
Age 0-1	34 ± 10
Age 1-2	17 ± 8
Age 2-3 (Subadult)	35 ± 5
Age 3-4 (Subadult)	30 ± 5
Age 4-5 (Adult)	30 ± 5
Males in breeding pool	90%
Age distribution	Stable
SD carrying capacity	5% of N(0)
Migration rate	20%
Dispersers surviving	90%

579 Table 2. Fragmentation metrics used in this study. Abbreviations used in the fragmentation
 580 metrics formulae: N - patch number (unit); a_{ij} - area of ij patch (m^2); A - total area in the
 581 landscape (m^2); $\max a_{ij}$ - patch with the largest area (m^2); p_{ij} - perimeter of patch ij (unit of
 582 cells); $\min p_{ij}$ - minimum perimeter if patch was maximally aggregated (unit of cells); Z -
 583 total number of cells in the landscape.

Metric	Formula
Proportion of landscape with natural vegetation	$\frac{\sum_{j=1}^N a_{ij}}{A} \cdot 100$
Largest patch index	$\frac{\max(a_{ij})}{A} \cdot 100$
Landscape shape index	$\frac{p_{ij}}{\min p_{ij}}$
Patch number	N
Cohesion	$\left[1 - \frac{\sum_{j=1}^N p_{ij}}{\sum_{j=1}^n p_{ij} \sqrt{a_{ij}}} \right] \cdot \left[1 - \frac{1}{\sqrt{Z}} \right]^{-1} \cdot 100$
Mean size of patch	$\frac{\sum_{j=1}^N a_{ij}}{N}$
Standard deviation of patch area	$\sqrt{\frac{\sum_{j=1}^N \left[a_{ij} - \left(\frac{\sum_{j=1}^N a_{ij}}{N} \right) \right]^2}{N}}$

Table 3. Models with AICc values lower than four describing jaguar persistence probability based on landscape configuration and spatial structure (complete list in Supplementary Material B). PC - first principal component condensing landscape configuration; SF (1-5) - spatial filters capturing the different spatial structures of selected landscapes, DF – degree of freedom, and LL - log-likelihood.

Variables in the model	Δ AICc	AICc Weighted	Residual Standard Error	DF	LL
PC, SF3	0.00	0.24	0.25	25	0.71
PC, SF3, SF5	1.93	0.09	0.25	24	1.24
PC, SF2, SF3	2.17	0.08	0.25	24	1.12
PC	2.53	0.07	0.27	26	-1.93
PC, SF3, SF4	2.80	0.06	0.25	24	0.80
PC, SF1, SF3	2.94	0.05	0.25	24	0.73
PC, SF2, SF5	3.08	0.05	0.26	24	0.66
PC, SF5	3.26	0.05	0.26	25	-0.92