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The role of fragmentation and landscape changes in the ecological release of common nest predators in the Neotropics

Loss of large mammalian carnivores may allow smaller mesopredators to become abundant and threaten other community members. There is considerable debate about mesopredator release and the role that other potential factors such as landscape variables and human alterations to land cover lead to increased mesopredator abundance. We used camera traps to detect four mesopredators (tayra, *Eira barbara*; white-nosed coati, *Nasua narica*; northern raccoon, *Procyon lotor*; and common opossum, *Didelphis opossum*) in a biological corridor in Costa Rica to estimate habitat covariates that influenced the species' detection and occurrence. We selected these mesopredators because as semi-arboreal species they might be common nest predators, posing a serious threat to resident and migratory songbirds. Pineapple production had a pronounced positive effect on the detectability of tayras, while forest cover had a negative effect on the detection of coatis. This suggests that abundance might be elevated due to the availability of agricultural food resources and foraging activities are concentrated in forest fragments and pineapple edge habitats. Raccoon and opossum models exhibited little influence on detection from habitat covariates. Occurrence models did not suggest any significant factors influencing site use by nest predators, revealing that all four species are habitat generalists adapted to co-existing in human altered landscapes. Furthermore, fragmentation and land cover changes may predispose nesting birds, herpetofauna, and small mammals to heightened predation risk by mesopredators in the Neotropics.

1 **The role of fragmentation and landscape changes in the ecological release of common nest**
2 **predators in the Neotropics**
3

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17 **Keywords:** camera traps, carnivores, coati, fragmentation, mesopredator release, Neotropics,

18 nest predators, pineapple production, raccoon, tayra

19 **1. INTRODUCTION**

20 Large carnivores receive substantial attention from the scientific community due to their
21 charismatic status and their importance as keystone species in maintaining community structure
22 (Morrison et al., 2007). Due to the loss of large carnivores from many systems, medium-sized
23 carnivores and carnivorous marsupials (collectively known as mesopredators) have recently
24 gained more attention (Roemer et al., 2009) because of their potential threat to migratory song
25 birds (Crooks and Soulé, 1999; Donovan et al., 1997; Elmhagen and Rushton, 2007; Garrott et
26 al., 1993). The most commonly cited hypothesis for the increased abundance of mesopredators is
27 the Mesopredator Release Hypothesis (MRH –Crooks and Soulé, 1999), but there is much debate
28 that remains over the process of mesopredator release (Cove et al., 2012a; Gerht and Clark,
29 2003; Elmhagen and Rushton, 2007). The MRH has support within some families, most notably
30 the Canidae, where larger canids drive the population dynamics and habitat associations of
31 smaller canids (Donadio and Buskirk, 2006; Gehrt and Clark, 2003). However, interspecific
32 killing and interference competition are less common among different families (Donadio and
33 Buskirk, 2006).

34 The top predators in Central America are jaguars (*Panthera onca*), pumas (*Puma concolor*),
35 and, coyotes (*Canis latrans* – Cove et al., 2012b; Wainwright, 2007). All three predators partake
36 in interspecific killing and may affect the distribution and habitat associations of smaller
37 mesopredators (Donadio and Buskirk, 2006; Palomares and Caro, 1999). The large cats are often
38 hunted due to cattle depredation and are rare. Coyotes are recent invaders and, because they
39 prefer disturbed open habitat, are seemingly rare in many intact forested areas. Mesopredators
40 are common in Central America which may result from the rarity of the top predators, thus,
41 supporting the MRH and a “top down” view of their release. Another plausible explanation is

42 that mesopredators are better adapted to coexisting with humans in disturbed habitats and, as
43 omnivores, are able to supplement their diets with agricultural resources via a “bottom up”
44 release (Elmhagen and Rushton, 2007; Garrott et al., 1993; Roemer et al., 2009).

45 Several studies in the United States attempted to model relative abundance of mesopredators
46 as functions of landscape and local habitat variables and predict predation risk for forest-nesting
47 birds (Crooks and Soulé, 1999; Dijack and Thompson, 2000; Donovan et al., 1997). These
48 studies determined that mesopredator abundance, activities, and hence nest predation increased
49 in fragmented areas and within forest edge habitats, particularly surrounding agricultural lands.
50 However, no similar studies have examined mesopredator occurrence in Central America.

51 This study integrated data collected from camera traps and the occupancy modeling
52 framework developed by MacKenzie et al. (2005, 2006) in order to examine habitat associations
53 of four common mesopredators from three different families in a fragmented biological corridor
54 in Costa Rica. We selected tayra (*Eira barbara*), white-nosed coati (*Nasua narica*), northern
55 raccoon (*Procyon lotor*), and common opossum (*Didelphis opossum*) as the species of interest
56 because they are common, adapted to human presence, and are important nest predators due to
57 their semi-arboreal nature.

58 **2. METHODS**

59 *Study site*

60 The San Juan – La Selva Biological Corridor is the northernmost portion of the
61 Mesoamerican Biological Corridor in Costa Rica linking the Indio-Maíz Biological Reserve of
62 southeastern Nicaragua to the Braulio Carrillo National Park of central Costa Rica. Although
63 deforestation still occurs within the corridor, government incentives (Forestry Law no. 7575)
64 have encouraged reforestation and tree plantations (Morse et al., 2009). Most of the land within

65 the corridor is privately owned with some reserves and lodges established to mitigate small scale
66 agriculture, yet large scale pineapple plantations and cattle operations continue to expand in the
67 corridor and surrounding landscape (Fagen et al., 2013). We selected 16 survey sites to be
68 representative of the land cover in the corridor; selection was loosely based on accessibility and
69 forest size. All forest sites were located on eco-lodge forest reserves, tree plantations, cattle
70 ranches and agricultural plantations. In an effort to ensure independence among forest sites, we
71 selected sites a minimum of 2 km apart.

72 *Camera Trapping*

73 We surveyed fourteen forest sites over two field seasons (July-August 2009 and June-August
74 2010), while two additional sites were surveyed from October-November 2009. Information was
75 lost from one of these sites and was excluded from further analysis. To avoid the pitfalls of using
76 a single camera as a defined “site” representative of an entire forest (Efford and Dawson, 2012),
77 we decided to aggregate several traps in arrays at each site. Arrays consisted of a central camera
78 station and three additional camera stations surrounding the central station spaced at >250 m
79 apart, for a total of four cameras in the 2009 surveys. Cameras were arranged in an array of six
80 spaced >250 m apart in the 2010 surveys. Previous research suggested that although this resulted
81 in variable trapnights among sites, there were no strong differences in detection as result of the
82 varying numbers of cameras (Cove et al., 2013). Each camera station consisted of a remotely
83 triggered infrared camera (Scout Guard SG550, HCO Outdoor Products, Norcross, GA, USA) or
84 a remotely triggered flash camera (Stealth Cam Sniper Pro Camera 57983, Stealth Cam, LLC,
85 Grand Prairie, TX, USA) secured to a sturdy tree 0.25-0.5 m off the ground. The camera was
86 directed at an opposing tree, 3-4 m away, baited with a secured can of sardines 1-1.5 m off the
87 ground. Although other camera trap studies set cameras along human trails and roads (Tobler et

88 al., 2008), we avoided areas of high human use due to threat of theft focusing on animal game
89 trails. Trail cameras were left at each site for 24-38 days and checked weekly for rebaiting and
90 battery changes.

91 All of our research was in accordance with the guidelines established by The American
92 Society of Mammalogists (Gannon et al., 2007). The camera trapping protocol was approved by
93 the University of Central Missouri Institutional Animal Care and Use Committee (IACUC --
94 Permit No. 10-3202).

95 *Habitat Variables and Analysis*

96 Using ArcGIS 10.0 (ESRI, 380 New York Street, Redlands, CA 92373, USA), we overlaid
97 camera trap locations onto a digitized land use-land cover map. We created a 1-km radius buffer
98 at each site using a central point among the cameras to measure landscape covariates. Habitat
99 covariate selection was based on known ecology of the mesopredators and factors that might
100 affect their detection and occurrence (Gompper, 1995; Lotze and Anderson, 1979; McManus,
101 1974; Presley, 2000; Wainwright, 2007).

102 We measured the distance to the nearest village, creating an index of human presence and/or
103 disturbance. Forest cover is the percentage of buffer covered by primary and secondary forest
104 and tree plantations. Because pineapple plantations are prevalent in the region, we used a
105 binomial covariate to indicate this land use within each site buffer. The proposed Maquenque
106 National Park is also within the northern extent of the corridor and we used a similar binomial
107 covariate to denote sites as within or outside the proposed park boundaries. The final covariate
108 was the total number of patches within each site buffer, which is an index of habitat
109 heterogeneity and habitat fragmentation. We standardized all continuous covariates to z scores
110 for analysis, but performed no other transformations (Long et al., 2011).

111 We combined all mesopredator photos from both field seasons to organize and manage
112 binary detection histories (1= detected, 0= not detected). We partitioned detection histories into
113 five day blocks for a maximum total of seven repeat surveys per species per site. We used the
114 detection histories and habitat covariates within a single-season occupancy model in program
115 PRESENCE 2.4 (Hines, 2009). Although the data were collected over two field seasons, we did
116 not resample any sites. This analysis refers to Ψ as “site use” as opposed to “occurrence,” so
117 grouping of the field seasons does not violate any of the assumptions of the modeling process
118 (MacKenzie et al., 2005).

119 Given our data, we developed six relatively simple *a priori* models for each species (Table
120 1), including a global model, to estimate the influence of habitat covariates on detection
121 probabilities in the individual mesopredator detection models. Although detection probability is
122 often considered a nuisance parameter, there is an apparent relationship between detection
123 probability and local abundance because as local abundance increases the probability of
124 detecting a species will increase making it a parameter of interest in our study (O’Connell and
125 Bailey, 2011). We did not use a seasonal covariate because all surveys were conducted during
126 the rainy season. We then used the covariates that contained high model support and had strong
127 effects on detection as a constant covariate set in the subsequent occurrence models (Long et al.,
128 2011). For the occurrence models, we used seven *a priori* models (Table 2).

129 We determined the best approximating models based on the Akaike Information Criterion
130 corrected for small sample size (AIC_c) and Akaike weights (ω_i). To evaluate model fit, we
131 performed 10,000 simulated parametric bootstraps for the global model (all covariates) to
132 determine if there was evidence of overdispersion (Burnham and Anderson, 2002). We

133 considered all models contained within the 90% CI ($\sum\omega_i>0.90$) to have substantial support as the
134 top-ranking models (Burnham and Anderson, 2002).

135 3. RESULTS

136 From 2,286 camera trapnights, we obtained 23 independent photographs of tayras (10.06
137 photos/1000 trapnights), 33 photos of coati (14.44/1000 trapnights), 7 photos of raccoons
138 (3.06/1000 trapnights), and 23 photos of opossums (10.06/1000 trapnights). At least one nest
139 predator species was detected at every site, but only one site had detections of all four species.
140 There was no evidence of overdispersion and we evaluated all models by their AIC_c and their
141 Akaike weights.

142 Detection covariates affected each species differently (Table 3). Pineapple production had
143 high model support ($\sum\omega_i=0.75$) and a strong positive influence on detection probability for tayras
144 and was used as the constant detection covariate in subsequent occurrence models. Forest cover
145 had high model support ($\sum\omega_i=0.67$) and a negative influence on detection probabilities for coatis
146 and was used as the constant detection covariate in coati occurrence models. Raccoon and
147 opossum models contained minimal support for habitat covariates influencing detection and we
148 used a constant detection probability in the eventual occurrence models.

149 From the occurrence models, no covariates that we examined explained significant changes
150 in mesopredator occurrence at the study sites (Table 4). The top-ranking models for tayra and
151 raccoon suggested a negative influence of forest cover on both species' occurrence, but were
152 highly variable. The constant occurrence model was top-ranking for both coati and opossum.

153 4. DISCUSSION

154 No large cats were photographed during the surveys and only a single coyote was
155 photographed at one site (Cove et al., 2013). Local interviews and cattle depredation were

156 evidence that large cats occur in the corridor; however, the sparse records suggest rarity and
157 precluded the use of these presence/absence data as model covariates. Therefore, we were unable
158 to assess the impact and influence of these top predators on the four mesopredator species
159 through trophic interactions, but the observed detection rates are higher than other Neotropical
160 studies with intact top predator communities (Tobler et al., 2008).

161 Landscape changes did affect detection parameters for the tayra and coati. Because camera
162 traps operate 24-hr per day, heightened detection corresponds with increased local abundance or
163 increased localized activity of mesopredators as influenced by landscape covariates. Pineapple
164 production had a strong positive influence on the detection probability of the tayra. This is most
165 likely an effect of the additional food resources from pineapple production leading to higher
166 local tayra abundance or concentrated foraging activities in pineapple-forest edge habitats. This
167 may also be a consequence of concentrated foraging activities within smaller forest patches that
168 occur in close proximity to pineapple plantations (Cove et al., 2013). The fruits not only provide
169 direct food resources to tayras but other food resources may be indirectly provided from
170 pineapple pests including small rodents, insects, and nesting birds (Presley, 2000). Pineapple
171 production also had a positive influence on coati detection, but the effect was less pronounced.
172 This suggests that coati abundance is also influenced by agricultural food resources provided
173 from pineapple production. The effect was opposite for raccoons and opossums suggesting that
174 pineapple production has a negative but weak influence on their detection. This may be an
175 artifact of limited raccoon detections or avoidance of areas of high use by tayras and coatis.

176 Forest cover had a negative effect on detection probability of coatis. This suggests that coatis,
177 which occur in large groups, concentrate their foraging activities in small forest patches, making
178 them more easily detectable. This relationship was similar for the detection of tayras and

179 raccoons in the study area. The consequence of concentrated foraging activities in small forest
180 patches and forest edges is also responsible for exposing nesting song birds to increased
181 predation risk (Cove et al., 2012c; Dijack and Thompson, 2000; Donovan et al., 1997). None of
182 the habitat covariates examined in this analysis were significant predictors of mesopredator
183 occurrence. The coefficients for habitat effects generally agreed with *a priori* expectations that
184 increased forest cover would have a negative but variable influence on occurrence. This suggests
185 that the broad range of habitats used by these mesopredators could have drastic consequences for
186 nesting song birds, small mammals, and herpetofauna if fragmentation and forest loss continues.

187 Although low detections of large predators made it difficult to provide direct support for the
188 MRH, the rarity of these species most likely plays a role in the distribution and habitat use by
189 mesopredators. More importantly, the compounding factors of increasing human presence,
190 decreasing forest cover, and increasing pineapple production play an important role in
191 mesopredator release and potentially heightened local abundance. Further sampling of
192 mesopredator communities, as well as large predator-specific surveys and avian point count
193 surveys, will elucidate trophic interactions and the risk of predation to migratory and resident
194 song birds.

195

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Table 1. Descriptions and expected direction of *a priori* detection (p) models for mesopredators from camera trap surveys in the San Juan - La Selva Biological Corridor, Costa Rica, 2009-2010.

Hypothesis	Model	Model Structure	Expected Result
No habitat covariates affect detection	$p(.)$	β_0	–
Mesopredator abundance and foraging increase in close proximity to villages so as distance to village increases detection decreases	$p(\text{dist})$	$\beta_0 + \beta_1(\text{dist})$	$\beta_1 < 0$
Habitat heterogeneity and fragmentation increase forest edge and lead to higher foraging and detection	$p(\text{tnp})$	$\beta_0 + \beta_1(\text{tnp})$	$\beta_1 > 0$
Pineapple production provides food resources and increases abundance and detection	$p(\text{pina})$	$\beta_0 + \beta_1(\text{pina})$	$\beta_1 > 0$
Increasing forest cover will have a negative effect on detection because activities will be less concentrated	$p(\text{for})$	$\beta_0 + \beta_1(\text{for})$	$\beta_1 < 0$
Distance to village, habitat heterogeneity, pineapple production, and forest cover all affect detection	$p(\text{global})$	$\beta_0 + \beta_1(\text{dist}) + \beta_2(\text{tnp}) + \beta_3(\text{pina}) + \beta_4(\text{for})$	$\beta_1 < 0, \beta_2 > 0, \beta_3 > 0, \beta_4 < 0$

Table 2. Descriptions and expected direction of *a priori* occurrence (Ψ) models for mesopredators from camera trap surveys in the San Juan - La Selva Biological Corridor, Costa Rica, 2009-2010.

Hypothesis	Model	Model Structure	Expected Result
No habitat effects on occurrence	$\Psi(.)$	β_0	–
Negative effect on occurrence within Maquenque National Park	$\Psi(\text{Maq})$	$\beta_0 + \beta_1(\text{Maq})$	$\beta_1 < 0$
Negative effect on occurrence as distance to village increases	$\Psi(\text{dist})$	$\beta_0 + \beta_1(\text{dist})$	$\beta_1 < 0$
Positive effect on occurrence as habitat heterogeneity increases	$\Psi(\text{tnp})$	$\beta_0 + \beta_1(\text{tnp})$	$\beta_1 > 0$
Positive effect on occurrence as forest cover increases	$\Psi(\text{for})$	$\beta_0 + \beta_1(\text{for})$	$\beta_1 > 0$
Positive effect on occurrence with pineapple production present	$\Psi(\text{pina})$	$\beta_0 + \beta_1(\text{pina})$	$\beta_1 > 0$
Maquenque National Park, distance to village, habitat heterogeneity, forest cover, and pineapple production all affect occurrence	$\Psi(\text{global})$	$\beta_0 + \beta_1(\text{Maq}) + \beta_2(\text{dist}) + \beta_3(\text{tnp}) + \beta_4(\text{for}) + \beta_5(\text{pina})$	$\beta_1 < 0, \beta_2 < 0, \beta_3 > 0, \beta_4 > 0, \beta_5 > 0$

Table 3. Selected top models and untransformed coefficients of habitat variable effects on detection probability (\hat{p}) for mesopredators from camera trap surveys in the San Juan - La Selva Biological Corridor, Costa Rica, 2009-2010.

Species	Untransformed coefficients of covariates (SE)								
	Model	Δ_i	ω_i	K	Intercept	Pineapple	Total number of patches	Distance	Forest
Tayra									
<i>p</i> (pina)	0.00	0.611	3	-2.695 (0.662)	2.211 (0.743)	-	-	-	-
<i>p</i> (global)	2.97	0.138	6	-3.646 (0.837)	2.626 (0.918)	1.016 (0.423)	0.659 (0.338)	-0.303 (0.502)	-
<i>p</i> (tnp)	3.38	0.113	3	-1.311 (0.465)	-	0.701 (0.368)	-	-	-
<i>p</i> (.)	3.89	0.087	2	-0.807 (0.355)	-	-	-	-	-
Coati									
<i>p</i> (for)	0.00	0.667	3	-0.214 (0.291)	-	-	-	-	-0.784 (0.330)
<i>p</i> (.)	2.93	0.154	2	-0.329 (0.279)	-	-	-	-	-
<i>p</i> (pina)	4.26	0.079	3	-0.705 (0.409)	0.763 (0.567)	-	-	-	-
<i>p</i> (dist)	4.65	0.065	3	-0.313 (0.279)	-	-	-0.322 (0.271)	-	-
Raccoon									
<i>p</i> (.)	0.00	0.383	2	-1.157 (0.599)	-	-	-	-	-
<i>p</i> (tnp)	1.15	0.216	3	-1.793 (0.805)	-	0.691 (0.471)	-	-	-
<i>p</i> (dist)	2.15	0.131	3	-1.035 (0.570)	-	-	0.819 (0.747)	-	-
<i>p</i> (pina)	2.46	0.112	3	-0.444 (0.915)	-1.007 (1.144)	-	-	-	-
<i>p</i> (for)	2.55	0.107	3	-2.494 (1.176)	-	-	-	-	-0.780 (0.637)
Opossum									
<i>p</i> (.)	0.00	0.545	2	-0.621 (0.323)	-	-	-	-	-
<i>p</i> (pina)	3.08	0.117	3	-0.543 (0.402)	-0.207 (0.660)	-	-	-	-
<i>p</i> (for)	3.12	0.115	3	-0.612 (0.324)	-	-	-	-	0.080 (0.339)
<i>p</i> (tnp)	3.17	0.112	3	-0.628 (0.335)	-	-0.025 (0.291)	-	-	-
<i>p</i> (dist)	3.17	0.112	3	-0.621 (0.323)	-	-	0.039 (0.417)	-	-

Models presented make up the 95% confidence set, where Δ_i is AIC_c difference, ω_i is the Akaike weight, and K is the number of model parameters. Model covariates were used as a constant detection set for occurrence models for species that did not exhibit the *p*(.) as the top ranking model (tayra and coati).

Covariates: pina is the binomial term to identify large-scale pineapple production within the site buffer; tnp is the total number of patches within the buffer; dist is the linear distance (km) to the nearest village; for is the total percent of forest cover (primary, secondary, and tree plantations) within the site buffer.

Table 4. Selected top models and untransformed coefficients of habitat variable effects on occurrence models (Ψ) for mesopredators from camera trap surveys in the San Juan - La Selva Biological Corridor, Costa Rica, 2009-2010.

Species Model	Δ_i	ω_i	K	Untransformed coefficients of covariates (SE)					
				Intercept	Forest	Maquenque	Total number of patches	Pineapples	Distance
Tayra									
$\Psi(\text{for})$	0.00	0.432	4	1.568 (2.074)	-2.874 (2.709)	-	-	-	-
$\Psi(\text{Maq})$	1.96	0.162	4	1.820 (1.333)	-	-2.875 (1.849)	-	-	-
$\Psi(\text{tnp})$	2.14	0.148	4	1.485 (1.365)	-	-	1.507 (1.478)	-	-
$\Psi(\text{pina})$	2.83	0.105	4	-0.464 (1.393)	-	-	-	2.313 (1.955)	-
$\Psi(\text{dist})$	3.35	0.081	4	1.905 (1.651)	-	-	-	-	0.393 (1.144)
Coati									
$\Psi(.)$	0.00	0.487	3	0.532 (0.569)	-	-	-	-	-
$\Psi(\text{for})$	2.63	0.131	4	0.679 (0.676)	-0.678 (0.673)	-	-	-	-
$\Psi(\text{Maq})$	2.77	0.122	4	0.055 (0.727)	-	1.247 (1.307)	-	-	-
$\Psi(\text{tnp})$	2.95	0.111	4	0.528 (0.579)	-	-	0.593 (0.667)	-	-
$\Psi(\text{dist})$	3.74	0.075	4	0.544 (0.577)	-	-	-	-	0.162 (0.576)

Models presented make up the 90% confidence set, where Δ_i is AIC_c difference, ω_i is the Akaike weight, and K is the number of model parameters. Coefficients are in logit space and relate to standardized covariates.

Covariates: for is the total percent of forest cover (primary, secondary, and tree plantations) within the site buffer; Maq is the binomial term for sites within the proposed Maquenque National Park; tnp is the total number of patches within the buffer; pina is the binomial term to identify large-scale pineapple production within the site buffer; dist is the linear distance (km) to the nearest village.

Table 4 continued.

Species	Untransformed coefficients of covariates (SE)									
	Model	Δ_i	ω_i	K	Intercept	Forest	Maquenque	Total number of patches	Pineapples	Distance
Raccoon										
$\Psi(\text{for})$	0.00	0.623	3	-1.940 (1.218)	-2.052 (1.203)	–	–	–	–	–
$\Psi(\cdot)$	2.52	0.177	2	-1.129 (0.729)	–	–	–	–	–	–
$\Psi(\text{pina})$	4.64	0.061	3	-1.845 (1.115)	–	–	–	1.444 (1.458)	–	–
$\Psi(\text{tnp})$	4.69	0.060	3	-1.270 (0.789)	–	–	0.699 (0.718)	–	–	–
Opossum										
$\Psi(\cdot)$	0.00	0.456	2	0.276 (0.569)	–	–	–	–	–	–
$\Psi(\text{tnp})$	2.11	0.159	3	0.287 (0.594)	–	–	-0.600 (0.604)	–	–	–
$\Psi(\text{for})$	3.07	0.098	3	0.278 (0.573)	-0.198 (0.600)	–	–	–	–	–
$\Psi(\text{Maq})$	3.08	0.098	3	0.118 (0.757)	–	0.349 (1.133)	–	–	–	–
$\Psi(\text{pina})$	3.13	0.096	3	0.381 (0.743)	–	–	–	-0.258 (1.138)	–	–

Models presented make up the 90% confidence set, where Δ_i is AIC_c difference, ω_i is the Akaike weight, and K is the number of model parameters. Coefficients are in logit space and relate to standardized covariates.

Covariates: for is the total percent of forest cover (primary, secondary, and tree plantations) within the site buffer; Maq is the binomial term for sites within the proposed Maquenque National Park; tnp is the total number of patches within the buffer; pina is the binomial term to identify large-scale pineapple production within the site buffer; dist is the linear distance (km) to the nearest village.

