

*This is the peer reviewed version of the following article: Griffiths, B. M., Cooper, W. J., Bowler, M., Gilmore, M. P., & Luther, D. (2021). Dissimilarities in species assemblages among Amazonian mineral licks. *Biotropica*, 00, 1–6. Which has been published in final form at <https://onlinelibrary.wiley.com/doi/10.1111/btp.13012> This article may be used for non-commercial purposes in accordance with Wiley Terms and Conditions for Use of Self-Archived Versions.*

1 **Dissimilarities in species assemblages among Amazonian mineral licks**

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14 Received:\_\_\_\_\_; Revised:\_\_\_\_\_; Accepted:\_\_\_\_\_.

15 **ABSTRACT**

16 Mineral lick elevation, size, and distance to the closest human community are all associated with  
17 mammal and bird species visitations. The most frequently hunted licks have similar species  
18 assemblages. Results indicate high variability in species assemblages at different mineral licks  
19 suggesting different species-specific resource needs at different licks.

20 Keywords: Amazon, bird, camera trap, conservation, geophagy, Loreto, mammal,

21 Mineral licks are natural geologic formations where animals visit and exhibit geophagical  
22 behavior (Klaus et al., 1998; Lee et al., 2010; Panichev et al., 2013). While mineral licks are  
23 widely used by animals around the world (Atwood & Weeks, 2002; Couturier & Barrette, 1988;  
24 Blake et al., 2011; Matsubayashi et al., 2007; Moe, 1993), the motivations behind geophagy are  
25 yet unclear for many species. It is thought that animals visit mineral licks to obtain key  
26 micronutrients missing in their diets or clays that aid in relieving indigestion caused by plant-  
27 based alkaloids (Bravo et al., 2008; Brightsmith et al., 2008; Diamond et al., 1999; Ghanem et  
28 al., 2013; Kreulen, 1985; Mahaney et al., 1997; Matsubayashi et al., 2007). Predators also visit  
29 mineral licks, presumably seeking prey (Griffiths et al., 2020b; Link & Fiore, 2013; Matsuda &  
30 Izawa, 2008). In the Amazon rainforest of South America, several elusive species visit mineral  
31 licks, including the lowland tapir (*Tapirus terrestris*), red brocket deer (*Mazama americana*),  
32 nocturnal curassow (*Nothocrax urumutum*), spider monkeys (*Ateles* sp.), and wild felids (Blake  
33 et al., 2010; Gilmore et al., 2020; Griffiths et al., 2020a; Link et al., 2011; Matsuda & Izawa,  
34 2008; Montenegro, 2004). Overall, mineral licks represent hotspots of diversity, with a  
35 disproportionate number of species visiting discrete locations (Blake et al., 2011) and often being  
36 visited by human hunters (Gilmore et al., 2020). They are also ecologically important for a vast  
37 range of species from a variety of foraging guilds and habitat types in the Amazon (Blake et al.,  
38 2010; Tobler et al., 2009; Tobler, 2008; Voigt et al., 2008).

39 As Blake et al. (2011) pointed out, surveying animals at mineral licks could provide  
40 important insight into the broader regional diversity and conservation of animals. However,  
41 Amazonian mineral licks are often difficult to locate and identify; thus, the few mineral lick  
42 studies that do exist are based on fewer than ten sites (Blake et al., 2010; Blake et al., 2011; Link  
43 et al., 2012) and might not be representative of the greater community of organisms that visit

44 mineral licks. Many species either visit mineral licks infrequently or visit a small proportion of  
45 mineral licks in a region, so they may not be recorded with a sample of only a few mineral licks  
46 (Griffiths, 2020). In this study, we use a relatively large sample size of mineral licks in the same  
47 river basin to assess the medium and large sized animals at mineral licks and investigate the  
48 variation in species assemblage at different licks by addressing the following questions:

49 1. How similar are the species assemblages between different mineral licks?

50 2. What features of the environment are associated with differences in species  
51 assemblages at different mineral licks?

52 Fieldwork was conducted in the northeastern Peruvian Amazon (about 120 km north by  
53 river of Iquitos, Peru) in the titled lands of the Maijuna community of Sucusari and the Maijuna-  
54 Kichwa Regional Conservation area (MKRCA), a 391,039 ha protected area (El Peruano, 2015;  
55 Gilmore et al., 2010) (Figure 1). The Sucusari River is a tributary of the Napo River. The  
56 Sucusari River basin includes both primary upland *terra firme* rainforest and floodplain forest  
57 (Gilmore et al., 2010). The region of the MKRCA is characterized by a mean annual temperature  
58 of 26°C and average precipitation of 3100 mm per year (Marengo, 1998).

59 Motion-activated camera traps (Bushnell Aggressor, Boly Scout Guard) were installed at  
60 52 mineral licks that were identified during participatory mapping exercises with Maijuna  
61 hunters in July 2017 (Gilmore & Young, 2010, 2012; Young & Gilmore, 2013, 2014, 2017) or in  
62 the field with Maijuna hunters in August, 2018. We visited all mineral licks with a Maijuna  
63 hunter in August 2018 and placed camera traps in a series of four rotations, each of which was a  
64 minimum of 60 days. Camera traps placement achieved relatively even coverage of the whole

65 basin during each rotation (Figure S1). Camera traps were all placed at mineral licks located in  
66 *terra firme* forest; placement and methods followed Griffiths et al. (2020a).

67 We identified all medium and large sized mammal and bird species in camera trap  
68 images, removed empty images, and organized data for analyses using CameraBase v1.7 (Tobler,  
69 2015). Birds below 20 cm body size (Mere Roncal et al., 2019) and mammals below 0.5 kg  
70 weight were not included due to inconsistencies in detection from camera trap placement  
71 (Bowler et al., 2017). The number of individuals and species identity in instances where multiple  
72 individuals appeared in the same photograph was also recorded. Mixed species flocks of birds,  
73 primarily parrots (Psittacidae) and pigeons (Columbidae), were also not considered for analysis  
74 since they often could not be identified to a species level. Images were sorted into independent  
75 events, with one hour separating visits by the same species noted as an independent event  
76 (Tobler et al., 2008). All aspects of this study were approved by George Mason University's  
77 Institutional Review Board, project #1288488-1.

78 To assess community similarities between mineral licks, we calculated a series of  
79 pairwise Jaccard's similarity indices ( $n = 1,326$ ). We calculated a generalized dissimilarity  
80 model, which included the number of records of each species, to determine the factors that  
81 influence community similarities between mineral licks, following Ferrier et al. (2007).  
82 Generalized dissimilarity models were constructed using the *gdm* function in the *gdm* package in  
83 R (Fitzpatrick et al., 2020), version 3.6.1 (R Core Team, 2019). Generalized dissimilarity models  
84 are derived from matrix regression and allow comparisons of community similarity between sites  
85 based on geographic distance and continuous and categorical covariates (Ferrier et al., 2007). We  
86 included habitat-specific covariates (elevation, slope, geographic distance between licks, and lick  
87 size), survey-specific covariates (trapping effort), and three different proxies for hunting

88 pressure, distance from the community, access points, and hunting camps (tested one at a time)  
89 (see Griffiths, 2020). All covariates were tested for collinearity before including them in the full  
90 model, with a correlation cutoff of 0.60 for inclusion (Dormann et al., 2013).

91 We constructed a full model and then proceeded with model selection following the  
92 approach described by Ferrier et al. (2007). We used a backward stepwise approach, dropping  
93 one covariate at a time, which resulted in marginal (< 0.1%) or no change in explained deviance,  
94 until an optimal model was obtained where dropping any more covariates resulted in a lower  
95 explained deviance. Then, we set the intercept of the model to 0 since mineral licks in the same  
96 location with the same environmental features would be expected to have the same community  
97 (Allnutt et al., 2008), and used this new model to make predictions of community similarity.

98 Across all 52 mineral licks, we had a total trapping effort of 5,379 camera nights. Once  
99 empty images and small-bodied species were removed, a total of 143,497 images of mammals  
100 and birds remained, describing 5,254 independent visitation events by mammals and 349  
101 independent visitation events by birds. We detected 20 species of medium and large bodied  
102 terrestrial mammals and 10 species of terrestrial birds at mineral licks (Table S1).

103 To assess the similarity among species assemblages at different mineral licks we  
104 summarized Jaccard's similarity indices between mineral lick communities to capture an overall  
105 idea of variation in species visiting mineral licks. The community similarity between mineral  
106 licks was low, with a mean Jaccard's similarity index of 0.332 (SD = 0.174, range 0 - 1.0).  
107 Overall, 87.14% of the comparisons had a similarity index value between 0 and 0.5 (Figure 1),  
108 excluding same-site comparisons. The species recorded at these three sites were the red brocket  
109 deer, paca, Brazilian porcupine, agouti, and tapir.

110           The optimal model of environmental factors associated with species assemblage  
111 similarity at different mineral licks included elevation, slope, lick size, trapping effort, and  
112 distance from community (a proxy for hunting pressure) as important covariates with an  
113 explained deviance of 0.198 (Table S2). Model results showed that distance from community  
114 was the greatest contributor to ecological distance and, therefore, community dissimilarity,  
115 followed by elevation, lick size, and trapping effort (Figure 2, Table S3). Slope had a relatively  
116 small effect on community dissimilarity (Figure 2, Table S3).

117           Similarity results showed high variation between mineral licks. Higher hunting pressure  
118 was associated with higher similarity among assemblages such that it homogenized species  
119 assemblages at mineral licks (Blake et al. 2013), or alternatively, hunters focus on those licks  
120 with the specific animals that they prefer to hunt. The homogenization of species communities  
121 due to hunting has been reported in other locations, where the removal of preferred large bodied  
122 species lowers species diversity of an area (e.g. Endo et al., 2010; Peres, 2000).

123           The natural variation in assemblages between licks is likely due in part to habitat  
124 preferences of species (Tobler et al., 2009). Variation could also be due to small-scale changes in  
125 soil content. For example, in Borneo, mineral licks as close as 16m of each other differed in  
126 composition, which could provide different mineral nutrients to animals that visit licks  
127 (Matsubayashi et al. 2007). However, we were not able to gather explicit data on soil  
128 composition though we encourage future studies to assess the importance of different minerals in  
129 the soil for different species at mineral licks. Species might also need different minerals at  
130 different times of the year, if they exhibit dietary shifts, thus visiting licks more frequently or  
131 different mineral licks depending on seasonal differences. However, since the model had a  
132 relatively low explained deviance of 0.198, habitat features are not the most important factors

133 determining species assemblages at mineral licks. This may indicate that species may travel  
134 across habitats to reach mineral lick sites periodically. For example, lowland tapirs walk over 10  
135 km to visit mineral lick sites, and actively shift their movement to include palm swamps when  
136 the fruit of the aguaje palm (*Mauritia flexuosa*) is in season (Cabrera et al., 2016; González et al.,  
137 2017; Tobler, 2008).

138         The majority of species not detected were not expected to display geophagy such as  
139 armadillos (e.g. *Dasyus kappleri*), and anteaters (e.g. *Myrmecophaga tridactyla*). Several  
140 carnivores, such as jaguars (*Panthera onca*), ocelots (*Leopardus pardalis*), and pumas (*Puma*  
141 *concolour*), were recorded at mineral licks in our study and in other studies (Izawa, 1993; Link &  
142 Fiore, 2013; Matsuda & Izawa, 2008). These species were likely foraging or searching for prey  
143 at mineral licks since they do not exhibit geophagy because of their diet. Only three frugivorous  
144 or folivorous mammals were not detected at the mineral licks: the Allen's olingo (*Bassaricyon*  
145 *alleni*), Spix's night monkey (*Aotus vociferans*), and three-toed sloth (*Bradypus variegatus*).  
146 Several primates which have a heavily frugivorous, but overall omnivorous diet, were not  
147 detected, including the common woolly monkey (*Lagothrix lagotricha*), the monk saki monkey  
148 (*Pithecia monachus*), the white-fronted capuchin (*Cebus albifrons*) and the Spix's night monkey  
149 (Hawkes & Peres, 2014). These species would be expected to exhibit some geophagical  
150 behavior. However, primates have been recorded consuming soil from arboreal termite nests and  
151 other sources rather than descending to feed at mineral licks (Ferrari et al., 2008), which might  
152 explain their absence from the mineral licks. The risk of predation may also contribute to  
153 avoidance of mineral licks by some primates, a phenomenon previously reported for spider  
154 monkeys and howler monkeys (Link et al., 2011).

155           While the study of geophagy is well established for parrots and macaws at rainforest  
156 clearings and edges of riverbanks (Brightsmith et al., 2008; Brightsmith & Muñoz-Najar, 2004;  
157 Lee et al., 2010), the observations of forest interior bird species at mineral licks are less known.  
158 A few avian species that we did not detect but would have expected to record at mineral licks  
159 based on their diet include three tinamou species and the wood quail (*Odontophorus gujanensis*).  
160 Of the three species of tinamou not detected, two of them, the little tinamou (*Crypturellus soui*)  
161 and Bartlett’s tinamou (*Crypturellus bartletti*), tend to prefer thickets and secondary forest  
162 habitats (del Hoyo et al., 2018), which were not in the vicinity of the studied mineral licks. The  
163 absence of the white-throated tinamou (*Tinamus guttatus*) and the wood quail at mineral licks  
164 might be explained by their omnivorous diets, which could provide enough micronutrients that  
165 they don’t need to visit mineral licks, but this hypothesis warrants further investigation.

166           Our results show that there is high natural variability in species assemblages at different  
167 mineral licks, indicating that each of these key resources provide different benefits to different  
168 species. Information gleaned from sampling medium and large sized animals at mineral licks can  
169 provide insight into the health of tropical forest systems, including the impacts of hunting.

170

## 171 **ACKNOWLEDGEMENTS**

172           We would like to acknowledge the Maijuna community of Sucusari for their expertise in  
173 identifying mineral licks and their eagerness to collaborate. We would like to thank OnePlanet,  
174 Inc. for providing financial and in-kind support to this project, as well as the Fulbright  
175 Association for providing a Fulbright U.S. Student Grant to BMG to conduct this research. We  
176 would like to thank the Morpho Institute and Explorama Lodges for providing in-kind support.

177 **AUTHOR CONTRIBUTION STATEMENT**

178 BMG: Conceptualization, data curation, funding acquisition, formal analysis, investigation,  
179 writing – original draft, visualization

180 MB: Funding acquisition, methodology, supervision, writing – review and editing, resources

181 MPG: Funding acquisition, methodology, supervision, writing – review and editing, resources

182 WJC: Formal analysis, methodology, software, writing – original draft

183 DL: Writing – original draft, methodology, data curation

184 **DISCLOSURE STATEMENT**

185 The corresponding author confirms on behalf of all authors that there have been no  
186 involvements that might raise the question of bias in the work reported or in the conclusions,  
187 implications, or opinions stated.

188 **DATA AVAILABILITY STATEMENT**

189 The data that support the findings of this study are openly available in Dryad Data  
190 Repository at <http://doi.org/doi:10.5061/dryad.bcc2fqzb2>.

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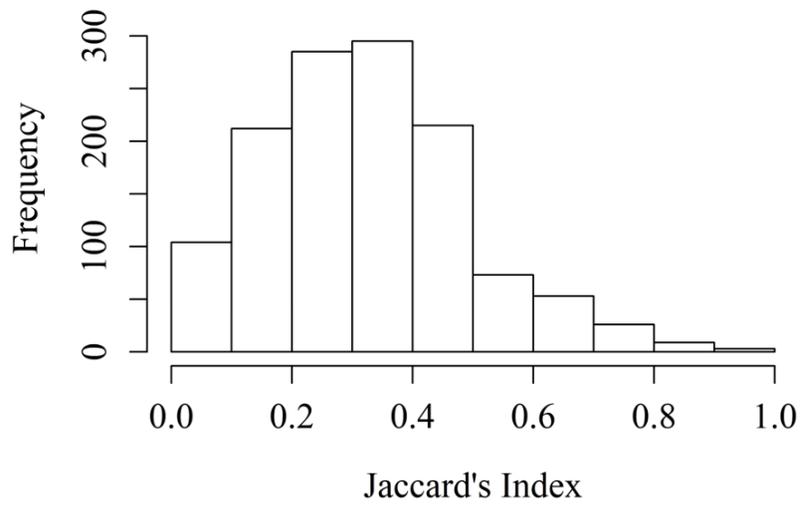
344 **FIGURE LEGENDS**

345 Figure 1. Histogram of Jaccard's indices comparing community similarity of medium- and large-  
346 bodied mammals and birds among 52 mineral licks in the Sucusari River basin in the Peruvian  
347 Amazon.

348 Figure 2. Basis splines calculated from optimal generalized dissimilarity model assessing  
349 dissimilarities of communities of mammals and birds recorded at 52 mineral licks in the Sucusari  
350 River Basin in the northeastern Peruvian Amazon, in order of effect size. Partial ecological  
351 distances on the y-axis represent community dissimilarity and are scaled to show effect size. A  
352 spline slope of zero indicates that the parameter did not have an effect on community  
353 dissimilarity at that level.

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355 **Figures**

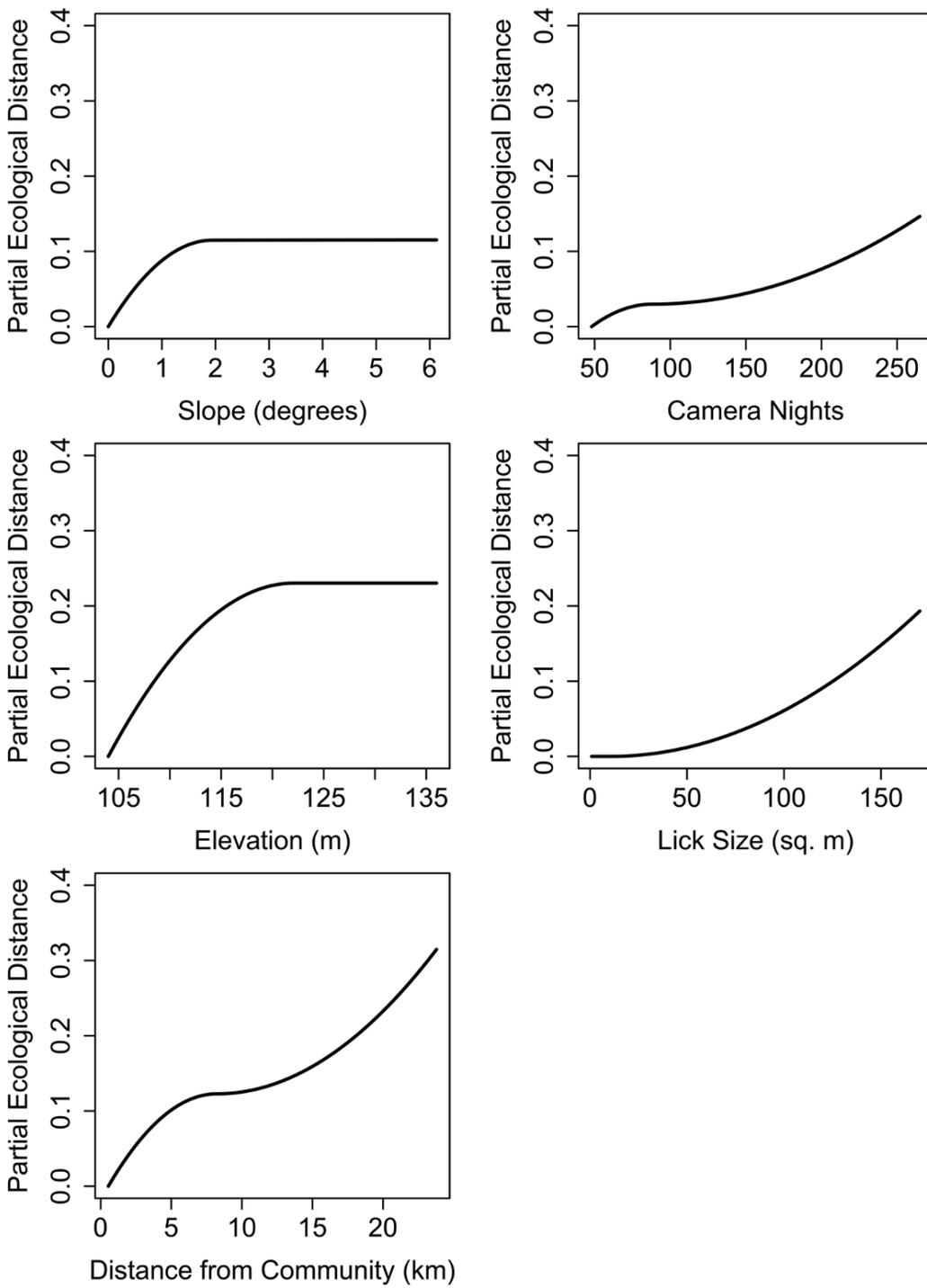


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357 Figure 1.

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361 Figure 2.