

1 **Convergent character displacement in sympatric tamarin calls (*Saguinus spp.*)**

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40 **Authors' contributions**

41 TVS originally formulated the research topic, collected data, and wrote the original draft. TVS, PACLP,

42 JCD and RMR performed exploratory and current statistical analyses. AAPB, MG, and JCD supervised.

43 TVS and WRS raised funds. AAPB and JCD checked the English. All authors contributed to the writing

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54 **Abstract**

55 Character displacement, or a shift in traits where species co-occur, is one of the most common ecological
56 patterns to result from interactions between closely related species. Usually, character displacement is
57 associated to divergence in traits, though, they might be convergent, especially when used for aggressive
58 interference between species. In the context of animal communication, territorial calls are predicted to
59 converge in order to increase context recognition and decrease the costs of ecological interference
60 competition. However, such signals might also be adapted to characteristics of the shared environment. In
61 this study, we used data from 15 groups of two parapatric tamarins, *Saguinus midas* and *S. bicolor*, to test
62 for similarities in long calls among sympatric and allopatric groups. We hypothesized that calls would
63 converge in sympatric areas, as it would be mutually beneficial if both species recognize territorial
64 contexts, but that convergence would depend on forest type due to acoustic adaptation. As predicted, long
65 calls converged in sympatry, with *S. midas* shifting its calls towards *S. bicolor*'s acoustic pattern.
66 However, this shift only occurred in primary forest. In sympatric areas, *S. midas* produced sounds with
67 narrower bandwidths in primary than in secondary forest, consistent with optimization of sound
68 propagation while both species produced longer calls in primary forests independently of geographic
69 location (i.e. sympatry and allopatry). Our results suggest that both social and environmental pressures are
70 important in shaping tamarin sounds. As their effects can interact, analyses which assume these
71 ecological pressures act independently are likely to miss important patterns.

72

73 **Keywords:** character displacement, acoustic adaptation hypothesis, trait divergence, long call, Amazon
74 *Saguinus midas*, *Saguinus bicolor*.

75

76 **Significance statement**

77 Territorial signals between closely related sympatric species are expected to be convergent to increase
78 context recognition and decrease the costs of interference competition. However, such signals might also
79 be adapted to characteristics of the shared environment, such as forest structure characteristics. We
80 analysed vocalisations from two parapatric tamarins and found that, though their long calls
81 asymmetrically converged in sympatry, only red-handed tamarins shifted towards pied tamarin call type,
82 and this only occurred in primary forest. Our results suggest that both social and environmental pressures

83 are important in shaping primate calls. Because their effects can interact, analyses which assume these
84 pressures act independently are likely to miss important patterns.

85

86 **Introduction**

87 Selection for reducing niche overlap often drives character displacement, i.e. exaggerated differences
88 between species populations in sympatry relative to those in allopatry (Pfennig and Pfennig 2009; Weber
89 and Strauss 2016; Grether et al. 2017; Stuart et al. 2017). Any morphological, ecological, physiological or
90 behavioural trait can follow such a pattern, either through local adaptation or phenotypic plasticity
91 (Brown and Wilson 1956; Grant 1972; Pfennig and Pfennig 2012; Allen et al. 2014; de Moura Bubadué et
92 al. 2016). Traits related to reproductive interference (i.e. sexual interactions between species including
93 courtship and other displays) are more likely to be divergent as pressure for mate recognition and
94 hybridization avoidance is high (West-Eberhard 1983; Okamoto and Grether 2013). Meanwhile, traits
95 related to resource competition and aggressive interference can be convergent or divergent depending on
96 the costs of the interaction between species, the relative abundance of species, and the evolutionary
97 timeframe of interaction between the species (Grether et al. 2017, 2020; Germain et al. 2018). In fact,
98 when analysing multiple traits, some pairs of species can have both convergent and divergent
99 displacement patterns depending on trait function (Miller et al. 2019; Grether 2020). Regardless, evidence
100 for both divergent and convergent character displacement often requires that traits are displaced in areas
101 where species co-occur, independently of other factors (Schluter 2001; Wilkins et al. 2013).

102 Many species have calls that are used as a defensive response to territory intrusions from both
103 conspecifics and heterospecifics (McGregor 1993; Peiman and Robinson 2010; Christensen and Radford
104 2018). Such calls may be considered fitness-related traits, since behavioural interference can affect the
105 rate of population growth (Chesson 2000; Grether et al. 2017, 2020). Therefore, selection can favour
106 convergence of such fitness-related traits in sympatry to minimize competitive asymmetries, when
107 competitors engage in direct conflicts (Germain et al. 2018). Accordingly, many bird species have
108 convergently evolved sounds that facilitate the recognition of the competitive context (Laiolo 2012;
109 Tobias et al. 2014; Kirschel et al. 2019). Also, some pairs of frogs species have convergent territory and
110 release calls, which are traits related to aggressive or “neutral” contexts (Leary 2001; Freitas and Toledo
111 2020; Grether 2020; Grether et al. 2020).

112 Similar environmental characteristics can also promote trait convergence in ecological
113 communities, independently of species interactions (Cardoso and Price 2010). Animal sounds, for
114 instance, are often well-adapted for propagation in the habitats in which the emitting individuals occur
115 (Bradbury and Vehrencamp 1998). The acoustic adaptation hypothesis posits that in woody forests, high-
116 pitched calls of short duration will degrade quickly, whereas calls that are long, low-pitched, and with
117 narrower bandwidths, will propagate more effectively (Morton 1975; Dabelsteen et al. 1993; Holland et
118 al. 1998). This hypothesis has been tested by numerous studies and corroborated by some (Ey and Fischer
119 2009), although little or no effect has been found by others (birds: Bicudo et al. 2016; felids: Peters and
120 Peters 2010; marmots: Daniel and Blumstein 1998; howler monkeys: Holzmann and Areta 2020; and
121 gorillas: Hedwig et al. 2015). Many of the studies that did not find support for the acoustic adaptation
122 hypothesis have suggested that social aspects (mainly intraspecific) are also important in shaping acoustic
123 features, although few have tested both factors together (Tobias et al. 2014b; Kirschel et al. 2019, 2020).

124 The acoustic adaptation hypothesis may be particularly important in understanding the impacts
125 of land use change in human-modified landscapes, as it suggests that habitat modification creates
126 differences in selection pressures for sound propagation optimization. For instance, the significant
127 conversion of tropical forests into secondary forests over the last 50 years (Chazdon 2014; Crist et al.
128 2017) has increased environmental heterogeneity in these landscapes, with remaining forests varying
129 widely in terms of plant species richness, composition, microclimate and above-ground biomass
130 (Guariguata and Ostertag 2001; Montgomery and Chazdon 2001; Rozendaal et al. 2019). Old-growth
131 (primary or pristine) forests, on the other hand, tend to be more complex in terms of canopy stratification,
132 having larger and taller trunks and more closed canopy (Montgomery and Chazdon 2001), all of which
133 could affect sound propagation.

134 Neotropical primates are a useful system for investigating the effects of habitat modification on
135 acoustic adaptation and character displacement given that: 1) primates are generally thought to produce
136 innate calls, and there is little evidence for plasticity in their vocalisations (Egnor and Hauser 2004;
137 Snowdon 2017a); 2) vocal flexibility may be an important aspect in social signal convergence (Laiolo
138 2012); and 3) primates have suffered significant and ongoing modification of their natural tropical forests
139 (Estrada et al. 2018). In Central Amazonia, the red-handed tamarin (*Saguinus midas*) and the pied tamarin
140 (*S. bicolor*) are two closely related primates with parapatric distributions and a narrow sympatric zone
141 (Röhe 2006; Rylands et al. 2016). While *S. midas* occurs over much of the northeastern portion of the

142 Amazon region, *S. bicolor* has one of the smallest ranges of any primate in the world (~7500 km²) (Gordo
143 et al. 2017), being restricted to the interfluvial region between the Amazon, Negro, and Urubu rivers, and
144 much of its range lying within the largest urban area of Amazonia – the city of Manaus (Fig 1; Gordo et
145 al. 2013). *S. bicolor* is currently classified as Critically Endangered by the International Union for the
146 Conservation of Nature (IUCN) (Gordo et al. 2019a) due to fragmentation and habitat loss, as well as
147 possible competition with *S. midas*, and is among the 25 most endangered primate species in the world
148 (Gordo et al. 2019b). Additionally, over the last 30 years, the range of *S. bicolor* has decreased, while that
149 of *S. midas* has not only increased, but it has encroached upon that of *S. bicolor* (Röhe 2006; Gordo et al.
150 2017). Pied and red-handed tamarins are considered potential competitors since both species have very
151 similar body sizes (Hershkovitz 1977), niches (i.e. use of spaces with similar climate, relief, and
152 vegetation types) (Röhe 2006), and they show asymmetrical territorial responses to each other's calls in
153 sympatric areas (Sobroza et al. 2021).

154 Tamarin long calls have an important territorial function (Snowdon 1989, 2017a, b), therefore
155 we hypothesized that acoustic parameters of pied and red-handed tamarin long calls would converge in
156 sympatry after accounting for potential acoustic adaptation to human-driven habitat heterogeneity
157 (primary or secondary forest). Accordingly, the two species should converge in long call acoustic
158 parameters in sympatry as it would be beneficial if both recognize the territorial context, in order to
159 reduce the probability of interference competition. However, we expected frequency convergence to be
160 stronger (or occur only) in primary forests, assuming that populations occurring in older and/or less
161 disturbed forests are more likely to show acoustic adaptation, since frequency features are more likely to
162 be constrained by morphology and genetics (Riede et al. 2005; Kitchen et al. 2019). In contrast, temporal
163 parameters should converge in both forest types, as these traits tend to be more plastic (Janik and Slater
164 1997; Kitchen et al. 2019). We also predicted that, independently of geographic condition (i.e. sympatry
165 and allopatry), both species would produce longer and lower-pitched calls in primary forests compared to
166 secondary forests, as predicted by the acoustic adaptation hypothesis.

167 **Material and methods**

168 *Study site*

169 We carried out the study in the Brazilian Central Amazon, which included allopatric and sympatric areas
170 in the ranges of *S. bicolor* and *S. midas* (Fig. 1). Topography in the region includes an alternation between
171 drainage catchments and plateaus (ca. 60 – 120 m a.s.l.). Native vegetation cover is tropical humid *terra*
172 *firme* forest in both primary and secondary stages of succession, with patches of white sand scrub forest
173 (*campina* and *campinarana*) (Oliveira et al. 2008). Within this region, we chose four sites where the two
174 primates were in allopatry, and four sites in sympatry, for a total of eight sites. We determined the
175 geographic condition (sympatry or allopatry) of groups, based on evidence from previous studies (Ayres
176 et al. 1982; Röhe 2006), data from long-term projects (Pied Tamarin Project and Tropical Ecology,
177 Assessment and Monitoring Network), and co-occurrence modelling (Röhe 2006). Simultaneous
178 observation of both species at the same site, mixed groups, or hybrids (at least those physically evident,
179 e.g. Gordo et al. 2017) were never recorded during this study. All sampled areas contained forests with
180 both primary and secondary growth, but forest cover was continuous in all cases. We categorized the
181 location where the groups were detected as primary or secondary forest based on field observation of
182 structural characteristics of the forest, and the presence of trees commonly found in Amazonian secondary
183 forests such as *Cecropia* spp., *Vismia* spp. and *Bellucia* spp. (Mesquita et al. 2001).

184 *Data collection*

185 Fieldwork was carried out over nine field visits from June 2014 to February 2015 and consisted of
186 recording tamarin long calls following standardized playback trials. A total of 275 calls were recorded in
187 a sampling effort that comprised 690 km walked over 97 days distributed across the eight sites, with
188 around nine consecutive sampling days at each site. Data collection was carried out between 06:30 and
189 16:30, the period when tamarins show the greatest activity (Day and Elwood 1999; Gordo et al. 2017).
190 We used existing trails and roads to survey each area until we found a tamarin group. Once this occurred,
191 we marked the encounter location with a Garmin GPS and characterized the group according to the
192 number of adult individuals. Different sightings at a given site were considered as belonging to the same
193 group when we consistently observed the same number of individuals and the distance between sightings
194 did not exceed 400 m. Although the annual home range size of pied tamarins' group may reach up to 100
195 ha (Gordo et al. 2008), at smaller time scales such as nine days, they rarely exceed 40 ha (Day and
196 Elwood 1999; Monteiro-Neto 2015, TVS and MG pers. obs.). Such small home range sizes are common

197 among callitrichids (Garbino and Martins-Junior 2018), thus supporting the 400 m threshold used here.
198 We considered as independent only those groups separated from each other by at least one km.

199 We recorded tamarin calls for 10 minutes immediately following playback trials (see details at
200 Sobroza et al. 2021). This duration was chosen because the animals were not habituated to the observers
201 and rarely stayed longer than this at the same place. During these trials, once we encountered a tamarin
202 group, we broadcasted long calls from non-neighbouring pied or red-handed tamarins. The sounds used
203 during the playbacks were composed of long calls from both allopatric and sympatric areas, and we
204 presented these to the species in a balanced way across species and geographic condition (i.e. sympatric
205 and allopatric areas). Individual groups were played recordings of long calls from both species (with a
206 minimum interval of one hour) and their responses were recorded. We recorded tamarins with .wav files
207 using a HTDZ HT-81 microphone (Frequency response: 1-16.0 kHz) attached to a Zoom H1 recorder
208 (16-bit, 44 kHz). It was not possible to record data blindly because our study involved focal animals in
209 the field.

210 *Acoustics analysis*

211 We analysed pied and red-handed tamarin long call recordings in Raven 1.4 (Cornell University
212 Laboratory of Ornithology 2010). Long calls are either emitted as a territorial signal during intergroup
213 encounters or as part of intragroup communication and cohesion (Sobroza et al. 2017). Since we recorded
214 the calls after broadcasting playbacks, the behavioural context in which they were engaged was
215 predominantly territorial. We defined a long call as a signal composed of variable number of syllables
216 (not more than 8) with \cap - shaped spectral signature and relatively constant interval between syllables
217 (mean = 0.129 s, SD = 0.045 s). For each call, we analysed nine acoustic parameters (Table 1). We
218 measured temporal parameters from oscillograms and spectral parameters of the first (fundamental)
219 harmonic by analysing power spectra (Sobroza et al. 2017) built with the following configuration: DFT
220 size = 1024 samples, overlap = 80%, window size = 20 ms, window type = *Blackmann*.

221 *Data analysis*

222 The analysed data consisted of acoustic parameters (Table 1) of individual long calls (*S. midas*, N = 151;
223 *S. bicolor*, N = 124) clustered by tamarin group (N = 15) and sampling site (N = 8) (one to three groups
224 per site). Since most acoustic parameters were correlated, data were ordinated using Principal
225 Components Analysis (PCA). We applied the *broken stick* test (Peres-Neto et al. 2005) to separate

226 meaningful information and choose how many PC axes to use in additional analysis. The test identified
227 the first two axes as significantly informative, but we added the third axis, which contained most of the
228 information on the temporal aspects of sound. The first axis captured 31.7 % of the data variability, and
229 the second and third 27.9% and 14.59%, respectively. Therefore, we used PC1, PC2 and PC3 to
230 summarize tamarin sounds and analysed each axis separately as a response variable in Generalized Linear
231 Mixed-effects Models (GLMMs) with Gaussian distribution (Zuur et al. 2009). In all models we tested for
232 the three-way interaction between predictors that were: species (two levels: *S. midas* or *S. bicolor*),
233 geographic condition (two levels: sympatry or allopatry) and forest type (two levels: primary and
234 secondary forests). Group and site identities were used as random factors to account for potential
235 autocorrelation among calls from the same group and groups from the same site. All analyses were
236 performed in R software version 4.0 (R Development Core Team 2020), using packages *nlme*, *vegan* and
237 *vireg* (Dixon 2003; Breheny and Burchett 2017; Pinheiro et al. 2018).

238 **Results**

239 According to the PCA, the red-handed tamarin had a relatively wider acoustic niche, while the pied
240 tamarin appeared to form a nested subgroup within the red-handed tamarin acoustic niche (Fig. 2, Table
241 2, 3). We found that bandwidth mainly contributed to PC1, frequency features to PC2, and duration and
242 entropy features to PC3 (Table 2). We found that allopatric populations of *S.midas* and *S.bicolor* in
243 primary forests were statistically different in their PC1 scores, with sounds of *S. midas* in
244 allopatric/primary forested areas differing markedly from *S. midas* in sympatric/primary forested areas,
245 and from *S. bicolor* in any condition (Table 4, Fig. 3). In sympatric areas, *S. midas* sounds were more
246 similar to those of *S. bicolor* sounds. Thus, *S. midas* displaced towards convergence to *S. bicolor*'s
247 acoustic niche, with higher PC1 scores (i.e. narrower bandwidths), but only in primary forest. In contrast,
248 *S. bicolor* did not show such a pattern (Fig. 3, Table 4). Furthermore, forest type was the only significant
249 predictor of PC2 and PC3 scores (Table 4). PC2 scores were slightly higher in secondary forests than in
250 primary forests (i.e. lower dominant and higher frequencies), while PC3 scores were higher in primary
251 than secondary forests (i.e. longer durations) (Fig. 4).

252 **Discussion**

253 In this study, we tested whether selection would favour acoustic convergence of territorial calls between
254 sympatric tamarin species, assuming this would facilitate context recognition when the risk of conflict is
255 imminent (Laiolo 2012). Our results support this hypothesis, but only for one of the two species (*S.*
256 *midas*) which showed convergent sounds in areas of sympatry. To the best of our knowledge, this is the
257 first record of asymmetric convergent character displacement in primate social signals. Convergence in
258 competitor recognition characters is expected when levels of interspecific aggressions are intermediate
259 (Grether et al. 2020), whereas asymmetry in character displacement can be a result of differential success
260 in resource holding between species (Grether et al. 2020). Indeed, *S. midas* appears to be vocally more
261 territorial than *S. bicolor* during territory intrusion experiments (Sobroza et al. 2021). Nevertheless, the
262 fact that the shift we observed in *S. midas* calls only occurred in primary forests suggests that multiple
263 and interacting selective forces might be shaping tamarin sounds, as observed in birds and rodents
264 (Campbell et al. 2010; Tobias et al. 2014). Secondary forests contain more food resources for tamarins
265 (Gordo 2012) therefore, competition would be reduced and character displacement less likely.

266 Many neotropical primates display long calls, which are sounds with multiple functions
267 (Snowdon et al. 1983; Oliveira and Ades 2004). Both pied and red-handed tamarins make long calls that
268 are used for intra- and intergroup communication to aid in group cohesion, movement coordination, and
269 spacing during territorial contexts (Day and Elwood 1999; Snowdon 2017b; Sobroza et al. 2017). In other
270 primates, long calls may also function in mate defence (Snowdon 1989; Wich and Nunn 2002), but we
271 have no evidence supporting such hypothesis for the pied and red-handed tamarins, and only weak
272 evidence for callitrichids, in general. For instance, if long calls also have a reproductive function, we
273 would expect an asymmetric sex ratio during call emission and responses. In captive colonies of tamarins
274 (*Saguinus oedipus*), results are inconsistent: sometimes males and sometimes females respond more to the
275 opposite sex (McConnell and Snowdon 1986; Scott et al. 2006), while in the field, there are recordings of
276 both males and females of *Saguinus* spp. emitting long calls during group encounters (Garber et al. 1993;
277 Garber 1997). Therefore, while the territorial function of long calls is relatively well accepted and
278 widespread among callitrichids, the hypothesis that it has a possible reproductive function (e.g. mate
279 attraction or mate-guarding) remains poorly supported. When characters have multiple functions,
280 directions of displacement may be less obvious (Grether et al. 2009), though, our results are under what is
281 expected for territorial signals (Drury et al. 2020).

282 As expected, frequency shifts (see PC1 and PC2, Table 2) occurred mainly in primary forests,
283 and were accompanied by shifts in temporal features (PC3, Table 2). Such acoustic changes are only
284 partially following the acoustic adaptation hypothesis, which predicts that in areas with woody vegetation
285 (e.g. primary forest), signals that are longer, lower-pitched and with a narrow bandwidth would be
286 selected (Morton 1975). We found that *S. midas* presented narrower bandwidths in primary forests, in
287 accordance with the acoustic adaptation hypothesis, but mainly in sympatric areas. Sounds with narrower
288 bandwidths propagate better in closed habitats because the intensity is concentrated in specific frequency
289 bands (Morton 1975). One possible explanation for the asymmetry in the displacement is that in areas
290 where a possible competitor is present, *S. midas* emits sounds with narrower bandwidths, and higher
291 amplitude to achieve longer distances, which could also imply an advantage during territorial defence
292 (Ritschard et al. 2012). Even if the effect was not strong, both species produced slightly higher dominant
293 frequencies in primary forests independently of geographic condition. Higher frequencies tend to degrade
294 quickly in closed habitats. So, other strategies that enhance sound propagation may be used by tamarins
295 such as site-selected perching, as occurs in other callitrichids (Sabatini and Ruiz-Miranda 2010). As
296 predicted, both species presented longer calls in primary than in secondary forests, and our findings agree
297 with the idea that frequency features are less plastic than temporal features (Janik and Slater 1997); the
298 strongest effect on frequency features was more evident in primary forests. Amplitude and temporal
299 features are more likely to be modulated in a shorter period through phenotypic plasticity, due to simpler
300 mechanisms of production (Janik and Slater 1997). Plasticity provides an important mechanism that
301 facilitates resource partitioning (Pfennig et al. 2006), but the extent to which the observed acoustic
302 differences reflect plasticity vs. local adaptation is unclear.

303 Whatever mechanism is behind the acoustic variation that we observed, tamarin calls did not
304 differ significantly between species in secondary forests. If long calls also play a role in sex recognition in
305 pied and red-handed tamarins as is suggested for other callitrichids (Weiss et al. 2001; Miller et al. 2004),
306 this may be related to recognition errors that could result in maladaptive mating and hybridization. During
307 the last three decades, the city of Manaus has been growing rapidly, and new roads have been created in
308 areas where the pied and the red-handed tamarins co-occur, thereby increasing the likelihood of
309 hybridization (McFarlane and Pemberton 2019). Hybridization often causes convergence in physical and
310 behavioural aspects of parapatric species (Brockelman and Schilling 1984; Long et al. 1998; Secondi et
311 al. 2003; Kitchen et al. 2019). As the physical appearance of *S. midas* and *S. bicolor* hybrids can be

312 similar to parental species, or a mix of characteristics of parental species (Gordo et al. 2017), it is not
313 possible to rule out the possibility that we recorded individuals that are phenotypically similar to one of
314 the parental species but are hybrids. Many bird species tend to show convergent traits and intense
315 interspecific territoriality when hybridization occurs in sympatric areas (Drury et al. 2020; Cowen et al.
316 2020), which may also be the case for pied and red-handed tamarins. There is no data available on the
317 actual magnitude of gene flow between the red-handed and the pied tamarin hybrids. If the behavioural
318 dominance of *S. midas* (Sobroza et al. 2021) also implies differences of gene flow, this could cause the
319 absence of differentiation between species calls and asymmetrical character displacement (Yikweon
320 2008). Sound signal similarities can be the cause and consequence of hybridization, and the origin or
321 extent to which both processes are occurring in this system remains to be tested.

322 Sobroza et al. (2021) found that red-handed tamarins responded with more territorial calls when
323 listening to pied tamarin calls than to its own species in sympatric areas; while pied tamarins did not
324 respond differently when listening to its species or the congener. Hence, despite the major pattern of
325 convergence in acoustic features recorded here, such sounds must not be functionally interpreted equally
326 by both species. Not only signal production can be susceptible to character displacement, but also its
327 perception (Seddon and Tobias 2010), if pied and red-handed tamarins use different acoustic features as
328 cues for species recognition or are different in terms of tuning capacity (e.g. Curé et al. 2012; Pasch et al.
329 2017), this may also be related to the asymmetries found in responses to the playback. Even closely
330 related species can have asymmetrical cognitive and recognition capacities, and some species are capable
331 of detecting specific signals with minimal variance (Seddon and Tobias 2010; Grether 2011; Pasch et al.
332 2017). It is worth mentioning that in the previous playback experiments Sobroza et al. (2021) did not
333 present congeneric sounds from all possible combinations (i.e. sympatric\primary forest;
334 sympatric\secondary forest; allopatric\primary forest, and allopatric\ secondary areas), which may be a
335 non-biological explanation related to their findings of asymmetrical responses.

336 Generally, character displacement and competitor recognition are phenomena involving many
337 signal components, sensory modalities and genes (Ortiz-Barrientos et al. 2004; Grether 2011; Pureswaran
338 et al. 2016). Therefore, even if acoustic signals are convergent and can be influenced by hybridization,
339 species discrimination can still be possible if this function is retained in at least one signal. Many animals
340 are flexible enough to quickly shift communication modalities when the signal transmission is impaired
341 (*sensu* Partan 2017). Secondary forests usually have a more open canopy, fewer obstacles such as large

342 trunks and lower relative humidity, features that might favour visual and chemical long-distance
343 communication (Müller-Schwarze 2006; Sicsú et al. 2013). Thus, we cannot underestimate the
344 recognition capacity of pied and red-handed tamarins in sympatric areas based only on our acoustic
345 results.

346 It is instructive to consider the extent to which other factors not linked to forest structure could
347 affect our results. For instance, some gregarious species have sounds that are group-specific (Crockford et
348 al. 2004; Zaccaroni et al. 2012; Mumm and Knörnschild 2017). If tamarins also have sounds that act as
349 group identifiers and the density of tamarins in secondary forest is higher, then acoustic diversity related
350 to group identity may be increased. Indeed, red-handed tamarins are known to occur at higher densities in
351 secondary forests than in primary forests (Lenz et al. 2014). Our statistical analysis included the identity
352 of the groups as a random factor – therefore our results are unlikely to be related to group identity.
353 Primary and secondary forests will also have a distinct composition of vocally-active species other than
354 tamarins (e.g. birds, anurans and insects), such as, creating a local soundscape that might also drive
355 acoustic divergence and sound diversification (Naugler and Ratcliffe 1994; Snowdon and de la Torre
356 2002; Gasc et al. 2013; Bicudo et al. 2016). Finally, secondary forests themselves can be highly variable
357 in terms of acoustically-relevant structural properties (Wiley and Richards 1978; Montgomery and
358 Chazdon 2001), though, it does not explain the observed displacement among sympatric and allopatric
359 areas. Accounting for all these potential effects is logistically challenging, but our findings provide a
360 template upon which more detailed hypotheses can be elaborated.

361 In summary, *S. midas* seems to have a wider acoustic niche and greater vocal flexibility than *S.*
362 *bicolor*, responding both to the presence of the congener and forest type. In allopatric areas and primary
363 forest, both species have a unique sound structure. Yet, this structure is consistent with the acoustic
364 adaptation hypothesis, suggesting it optimizes sound propagation in these habitats. In contrast, in
365 sympatric areas, the major pattern of variation in the acoustic features converge, consistent with selection
366 for enhanced context recognition and, thus, reduce interference competition. Our results suggest that both
367 social and physical constraints interact asymmetrically to shape the sound produced by parapatric
368 tamarins. Thus, analyses that account for these pressures independently are likely to miss important
369 patterns in ecological systems of co-occurring species.

370

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377 *Conflicts of interest*

378 The authors declare that they have no conflict of interest.

379

380 *Ethical approval*

381 All applicable international, national, and/or institutional guidelines for the use of animals were followed.

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385

386 *Data availability*

387 Data are available as supplementary material.

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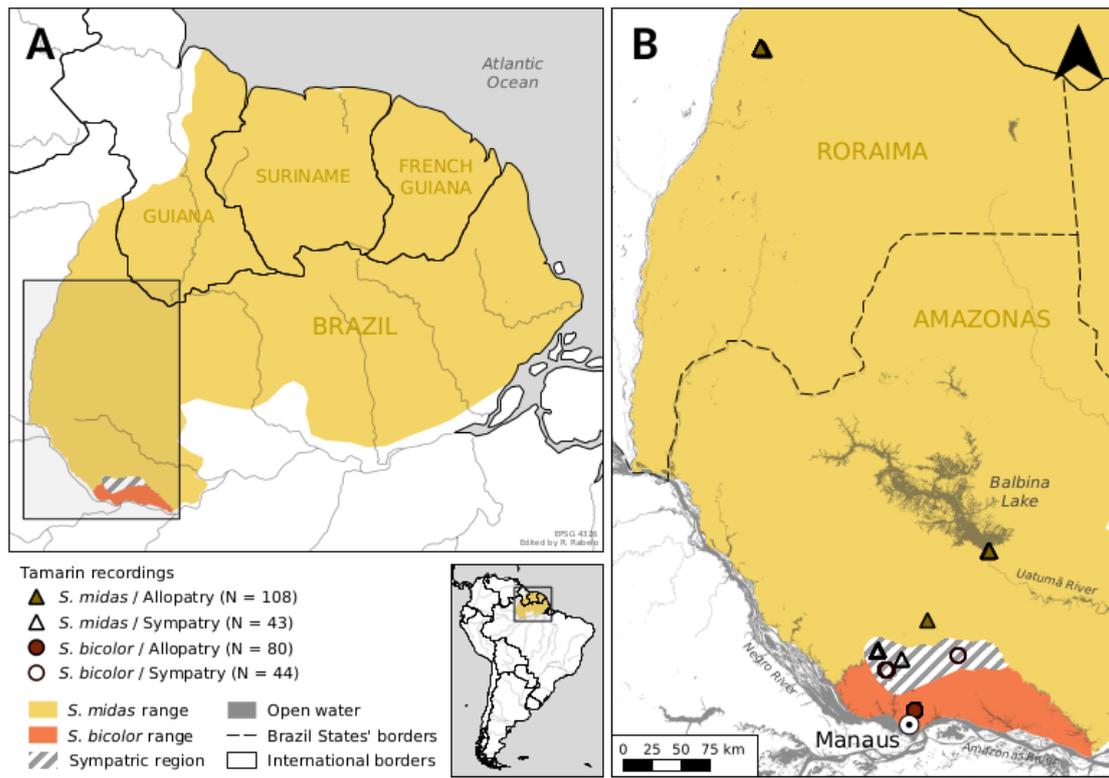
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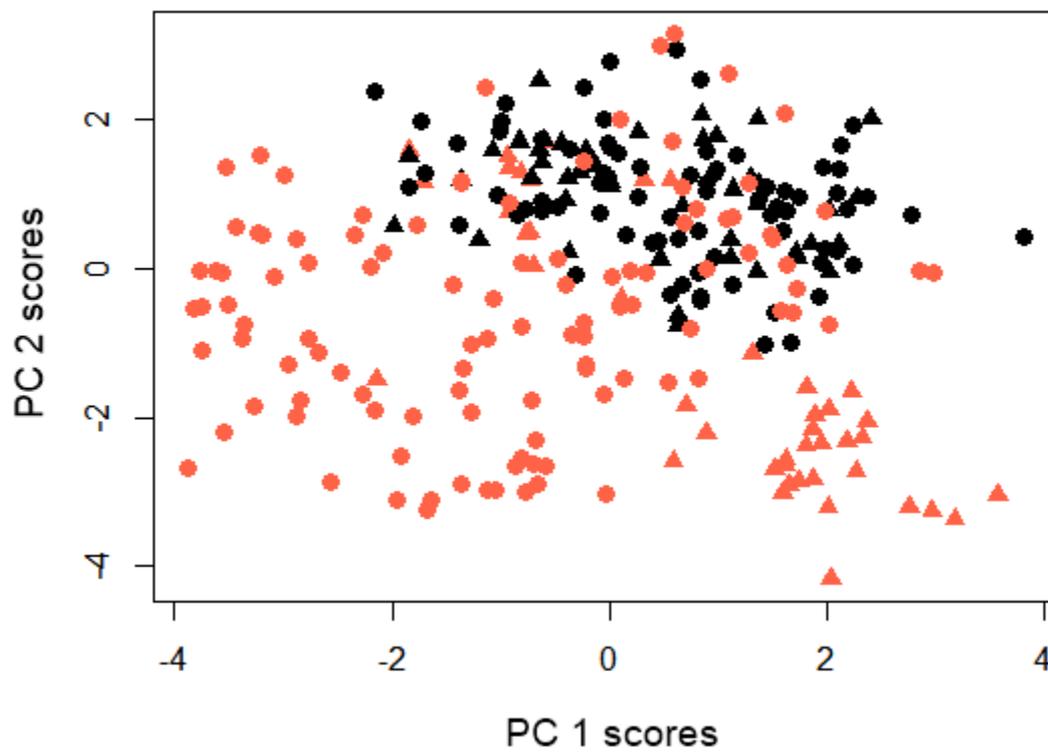


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678 **Fig. 1** Species distribution ranges and location of sampling sites. A) Map of *Saguinus midas* and *S.*

679 *bicolor* ranges and putative sympatric area (based on Röhe 2006). B) Sampling sites of *S. bicolor* and *S.*

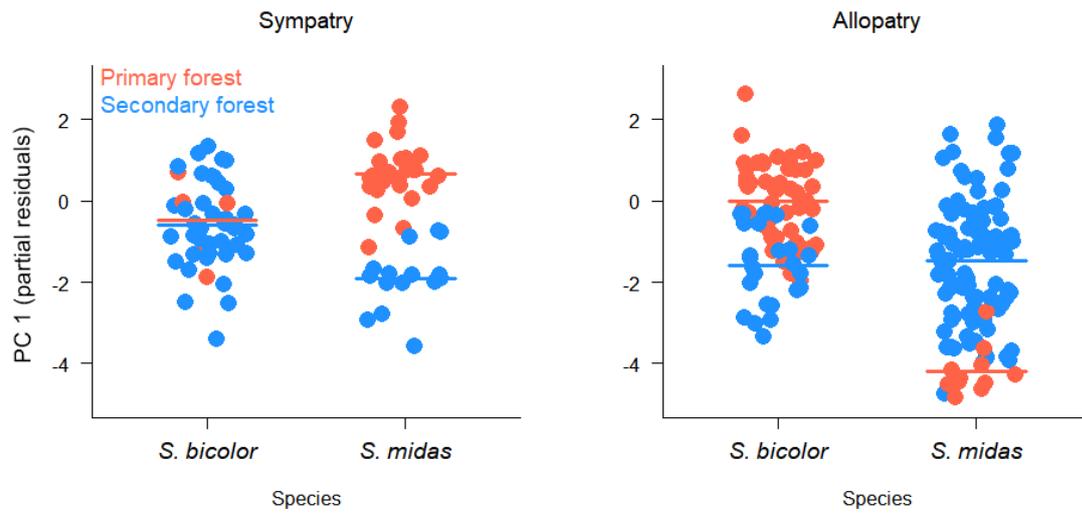
680 *midas* in areas of sympatry and allopatry.



681

682 **Fig. 2** Acoustic niche of pied and red-handed tamarins. The first two axes of a Principal Component
 683 Analysis (PCA) were used to represent long calls based on nine acoustic parameters. Each point in the
 684 graph represents a long call of pied tamarins (black symbols) (n=124) and red-handed tamarins (red
 685 symbols) (n=151) in sympatry (triangles) and allopatry (circles).

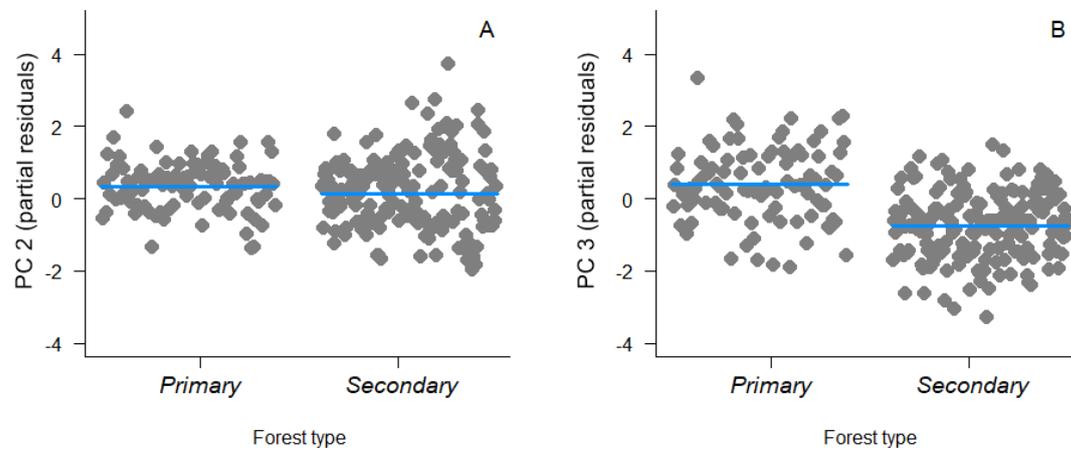
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689 **Fig. 3** Differences of acoustic features of pied and red-handed tamarins relative to interactive effects of
 690 habitat type (red=primary forest and blue=secondary forest), and geographic condition (allopatry and
 691 sympatry), based on the Generalized Linear Mixed Model (GLMM). Each point represents the PC1 score
 692 of a long call (n=275); lines represent predicted means for each group of observations. Plots use partial
 693 residuals of the response variable and thus show the effect of a given interaction while controlling for the
 694 effects of remaining predictors.

695



697

698 **Fig. 4** Differences of acoustic features of pied and red-handed tamarins relative to effects of habitat type
 699 (red=primary forest and blue=secondary forest) based on the Generalized Linear Mixed Model (GLMM).
 700 Each point represents A) PC 2 and B) PC 3 scores of long calls (n=275); lines represent predicted means
 701 for each group of observations. Plots use partial residuals of the response variable and thus show the
 702 effect of a given variable while controlling for the effects of remaining predictors