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ORIGINAL ARTICLE

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

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Abstract

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

Significance statement

Territorial signals between closely related sympatric species are expected to be convergent to increase context recognition and decrease the costs of interference competition. However, such signals might also be adapted to characteristics of the shared environment, such as forest structure characteristics. We analysed vocalisations from two parapatric tamarins and found that, though their long calls asymmetrically converged in sympatry, only red-handed tamarins shifted towards pied tamarin call type, and this only occurred in primary forest. Our results suggest that both social and environmental pressures are important in shaping primate calls. Because their effects can interact, analyses which assume that these pressures act independently, are likely to miss important patterns.

Keywords Character displacement · Acoustic adaptation hypothesis · Trait divergence · Long call · Amazon *Saguinus midas* · *Saguinus bicolor*

Introduction

Selection for reducing niche overlap often drives character displacement, i.e. exaggerated differences between species populations in sympatry relative to those in allopatry (Pfennig and Pfennig 2009; Weber and Strauss 2016; Grether et al. 2017; Stuart et al. 2017). Any morphological, ecological, physiological or behavioural trait can follow such a pattern, either through local adaptation or phenotypic plasticity (Brown and Wilson 1956; Grant 1972; Pfennig and Pfennig 2012; Allen et al. 2014; de Moura Bubadué et al. 2016). Traits related to reproductive interference (i.e. sexual interactions between species including courtship and other displays) are more likely to be divergent as pressure for mate recognition and hibridization avoidance is high

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(West-Eberhard 1983; Okamoto and Grether 2013). Meanwhile, traits related to resource competition and aggressive interference can be convergent or divergent depending on the costs of the interaction between species, their relative abundance, and the evolutionary timeframe of interaction between the species (Grether et al. 2017, 2020; Germain et al. 2018). In fact, when analysing multiple traits, some pairs of species can have both convergent and divergent displacement patterns depending on trait function (Miller et al. 2019; Grether 2020). Regardless, evidence for both divergent and convergent character displacement often requires that traits are displaced in areas where species co-occur, independently of other factors (Schluter 2001; Wilkins et al. 2013).

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

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

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

Neotropical primates are a useful system for investigating the effects of habitat modification on acoustic adaptation and character displacement given that (1) primates are generally thought to produce innate calls, and there is little evidence for plasticity in their vocalisations (Egnor and Hauser 2004; Snowdon 2017a); (2) vocal flexibility may be an important aspect in social signal convergence (Laiolo 2012) and (3) primates have suffered significant and ongoing modification of their natural tropical forests (Estrada et al. 2018). In Central Amazonia, the red-handed tamarin (*Saguinus midas*) and the pied tamarin (*S. bicolor*) are two closely related primates with parapatric distributions and a narrow sympatric zone (Röhe 2006; Rylands et al. 2016). While *S. midas* occurs over much of the northeastern portion of the Amazon region, *S. bicolor* has one of the smallest ranges of any primate in the world (~ 7500 km^2) (Gordo et al. 2017), being restricted to the interfluvial region between the Amazon, Negro, and Urubu rivers, and much of its range lying within the largest urban area of Amazonia — the city of Manaus (Fig. 1; Gordo et al. 2013). *S. bicolor* is currently classified as Critically Endangered by the International Union for the Conservation of Nature (IUCN) (Gordo et al. 2019a) due to fragmentation and habitat loss, as well as possible competition with *S. midas*, and is among the 25 most endangered primate species in the world (Gordo et al. 2019b). Additionally, over the last 30 years, the range of *S. bicolor* has decreased, while that of *S. midas* has not only increased, but it has encroached upon that of *S. bicolor* (Röhe 2006; Gordo et al. 2017). Pied and red-handed tamarins are considered potential competitors since both species have very similar body sizes (Hershkovitz 1977), niches (i.e. use of spaces with similar climate, relief, and vegetation types) (Röhe 2006), and they show asymmetrical territorial responses to each other's calls in sympatric areas (Sobroza et al. 2021).

Tamarin long calls have an important territorial function (Snowdon 1989, 2017a, b), therefore, we hypothesized that acoustic parameters of pied and red-handed tamarin long calls would converge in sympatry after accounting for potential acoustic adaptation to

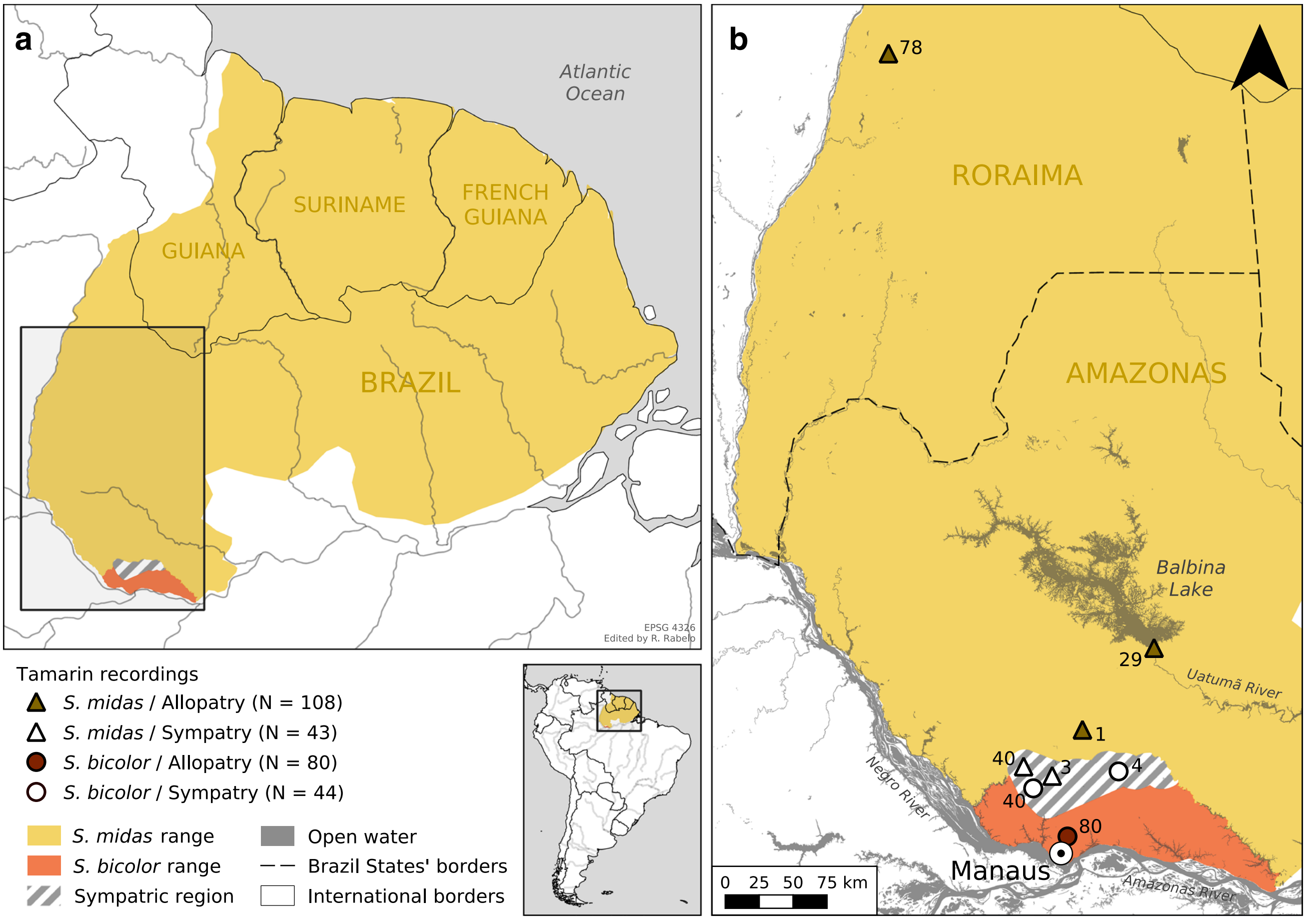

Fig. 1 Species distribution ranges and location of sampling sites. (**a**) Map of *Saguinus midas* and *S. bicolor* ranges and putative sympatric area (based on Röhe 2006). (**b**) Sampling sites of *S. bicolor* and *S. midas* in areas of sympatry and allopatry

human-driven habitat heterogeneity (primary or secondary forest). Accordingly, the two species should converge in long call acoustic parameters in sympatry as it would be beneficial if both recognize the territorial context, in order to reduce the probability of interference competition. However, we expected frequency convergence to be stronger (or occur only) in primary forests, assuming that populations occurring in older and/or less disturbed forests are more likely to show acoustic adaptation, since frequency features are more prone to be constrained by morphology and genetics (Riede et al. 2005; Kitchen et al. 2019). In contrast, temporal parameters should converge in both forest types, as these traits tend to be more plastic (Janik and Slater 1997; Kitchen et al. 2019). We also predicted that, independently of geographic condition (i.e. sympatry and allopatry), both species would produce longer and lower-pitched calls in primary forests compared to secondary forests, as predicted by the acoustic adaptation hypothesis.

Material and methods

Study site

We carried out the study in the Brazilian Central Amazon, which included allopatric and sympatric areas in the ranges of *S. bicolor* and *S. midas* (Fig. 1). Topography in the region includes an alternation between drainage catchments and plateaus (ca. 60–120 m a.s.l.). Native vegetation cover is tropical humid *terra firme* forest in both primary and secondary stages of succession, with patches of white sand scrub forest (*campina* and *campinarana*) (Oliveira et al. 2008). Within this region, we chose four sites where the two primates were in allopatry, and four sites in sympatry, for a total of eight sites. We determined the geographic condition (sympatry or allopatry) of groups, based on evidence from previous studies (Ayres et al. 1982; Röhe 2006), data from long-term projects (Pied Tamarin Project and Tropical Ecology, Assessment and Monitoring

Network), and co-occurrence modelling (Röhe 2006). Simultaneous observations of both species at the same site, mixed groups, or hybrids (at least those physically evident, e.g. Gordo et al. 2017) were never recorded during this study. All sampled areas contained forests with both primary and secondary growth, but forest cover was continuous in all cases. We categorized the location where the groups were detected as primary or secondary forest based on field observation of structural characteristics of the forest, and the presence of trees commonly found in Amazonian secondary forests such as *Cecropia* spp., *Vismia* spp. and *Bellucia* spp. (Mesquita et al. 2001).

Data collection

Fieldwork was carried out over nine field visits from June 2014 to February 2015 and consisted of recording tamarin long calls following standardized playback trials. A total of 275 calls were recorded in a sampling effort that comprised 690 km walked over 97 days distributed across the eight sites, with around nine consecutive sampling days at each site. Data collection was carried out between 06:30 and 16:30, the period when tamarins show the greatest activity (Day and Elwood 1999; Gordo et al. 2017). We used existing trails and roads to survey each area until we found a tamarin group. Once this occurred, we marked the encounter location with a Garmin GPS and characterized the group according to the number of adult individuals. Different sightings at a given site were considered as belonging to the same group when we consistently observed the same number of individuals and the distance between sightings did not exceed 400 m. Although the annual home range size of pied tamarins' group may reach up to 100 ha (Gordo et al. 2008), at smaller time scales such as 9 days, they rarely exceed 40 ha (Day and Elwood 1999; Monteiro-Neto 2015 TVS and MG pers. obs.). Such small home range sizes are common among callitrichids (Garbino and Martins-Junior 2018), thus supporting the 400 m threshold used here. We considered as independent only those groups separated from each other by at least 1 km.

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

Acoustics analysis

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

Table 1 Definitions of acoustic parameters measured in pied and red-handed tamarin long calls

Parameter	Definition
Low frequency (kHz)	Lowest frequency from the call
High frequency (kHz)	Highest frequency from the call
Dominant frequency (kHz)	Frequency with the highest energy
Bandwidth (kHz)	Difference between low frequency and low frequency of the long call
Bandwidth of the first syllable (kHz)	Difference between lower and upper frequency of the first syllable of the long call
Bandwidth of the last syllable (kHz)	Difference between lower and upper frequency of the last syllable of the long call
Average entropy (u)	Average of the entropy values in each spectrogram time slice of the vocalization
Delta time (s)	Time elapsed between initiation and ending of the vocalization
Number of syllables	Number of elements of one call

samples, overlap = 80%, window size = 20 ms, window type = *Blackmann*.

Data analysis

The analysed data consisted of acoustic parameters (Table 1) of individual long calls (*S. midas*, $N = 151$; *S. bicolor*, $N = 124$) clustered by tamarin group ($N = 15$) and sampling site ($N = 8$) (one to three groups per site). Since most acoustic parameters were correlated, data were ordinated using Principal Components Analysis (PCA). We applied the *broken stick* test (Peres-Neto et al. 2005) to separate meaningful information and choose how many PC axes to use in additional analysis. The test identified the first two axes as significantly informative, but we added the third axis, which contained most of the information on the temporal aspects of sound. The first axis captured 31.7% of the data variability, and the second and third 27.9 and 14.59%, respectively. Therefore, we used PC1, PC2 and PC3 to summarize tamarin sounds and analysed each axis separately as a response variable in Generalized Linear Mixed-effects Models (GLMMs) with Gaussian distribution (Zuur et al. 2009). In all models, we tested for the three-way interaction between predictors that were species (two levels: *S. midas* or *S. bicolor*), geographic condition (two levels: sympatry or allopatry) and forest type (two levels: primary and secondary forests). Group and site identities were used as random factors to account for potential autocorrelation among calls from the same group and groups from the same site. All analyses were performed in R software version 4.0 (R Development Core Team 2020), using packages *nlme*, *vegan* and *vireg* (Dixon 2003; Breheny and Burchett 2017; Pinheiro et al. 2018).

Results

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

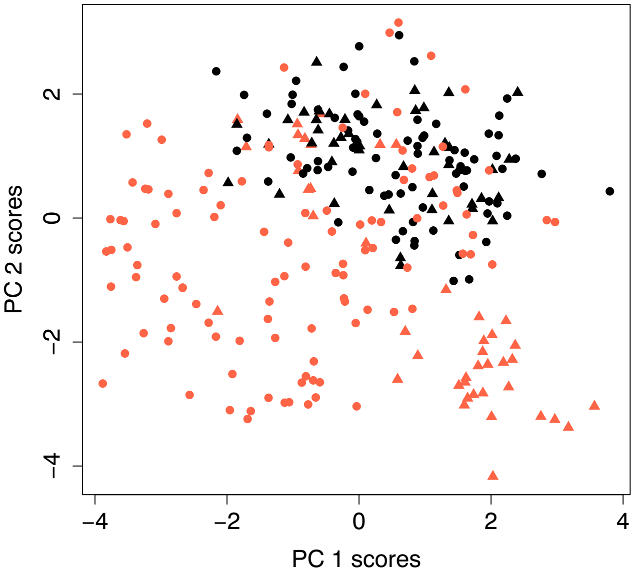

Fig. 2 Acoustic niche of pied and red-handed tamarins. The first two axes of a Principal Component Analysis (PCA) were used to represent long calls based on nine acoustic parameters. Each point in the graph represents a long call of pied tamarins (black symbols) ($n = 124$) and red-handed tamarins (red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

Table 2 Loadings and percent of variance explained by Principal Components extracted from *Saguinus bicolor* and *S. midas* long calls. Highest loadings ($r > 0.5$) are in bold

Acoustic feature	PC1	PC2	PC3
Low frequency (kHz)	0.39	−0.36	0.32
High frequency (kHz)	−0.22	**−0.54**	0.20
Dominant frequency (kHz)	0.10	**−0.51**	0.37
Bandwidth (kHz)	**−0.52**	−0.18	−0.11
Bandwidth of the first syllable (kHz)	−0.19	−0.18	−0.39
Bandwidth of the last syllable (kHz)	**−0.52**	−0.15	−0.11
Average entropy (u)	−0.01	0.14	0.34
Delta time (s)	−0.27	0.25	**0.51**
Number of syllables	−0.35	0.33	0.37
% Variance explained	31.73	27.25	14.59

Table 3 Summary measurements of the acoustic structure of the vocal signals emitted by pied and red-handed tamarins (*S. bicolor* and *S. midas*) in areas of sympatry and allopatry ($\overset{\lambda''''}{x}$ = mean; SD = standard deviation). Sounds were recorded in the municipalities of Manaus and Rio Preto da Eva, Amazonas State, and Caracaraí, Roraima State, Brazil

	Saguinus midas (allopatry)		*Saguinus midas* (sympatry)		*Saguinus bicolor* (allopatry)		*Saguinus bicolor* (sympatry)	
Parameter	$\overset{\lambda''''}{x}$	SD	$\overset{\lambda''''}{x}$	SD	$\overset{\lambda''''}{x}$	SD	$\overset{\lambda''''}{x}$	SD
Low frequency (kHz)	6477.43	702.76	7848.77	1578.37	6818.52	985.98	6515.38	855.95
High frequency (kHz)	9885.61	1065.71	10,112.91	816.52	8848.68	559.69	8688.01	575.33
Dominant frequency (kHz)	8942.23	1200.79	9567.96	963.44	8531.25	583.14	8314.09	635.73
Bandwidth 90% (kHz)	2499.48	1018.33	1725.10	666.25	1497.04	489.11	1578.83	558.31
Bandwidth of the first syllable (kHz)	1388.72	700.87	1366.60	506.28	948.55	800.41	1213.80	558.86
Bandwidth of the last syllable (kHz)	3124.73	1258.63	2146.49	869.06	1945.24	944.97	2057.07	811.97
Average entropy (u)	2.65	0.59	2.31	0.59	3.44	1.37	2.56	0.62
Delta time (s)	2.28	0.76	2.26	0.97	2.46	0.77	3.05	0.76
Number of syllables	4.41	1.44	3.23	1.17	4.14	1.16	4.35	0.86

Discussion

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

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

Table 4 Summary of GLMMs results on the effect of geographic condition (sympatry or allopatry) and forest type (primary or secondary) on pied and red-handed tamarins (*S. bicolor* and *S. midas*) calls. Acoustic features were summarized in PC1, PC2 and PC3 ordinations (response variable). Sounds were recorded in the municipalities of Manaus, Rio Preto da Eva and Caracaraí, Amazonas State, Brazil, from 2014 to 2015 ($N=275$). *Results statistically significant ($P<0.05$)

Response variable	Parameter	Estimate	SE	*T*	*P*
PC1	Species	−4.19	0.87	−4.80	0.0086*
	Geographic condition	−0.47	0.91	−0.51	0.6332
	Forest type	−1.60	0.27	−5.82	<0.0001*
	Species* Geographic condition	5.32	1.30	4.06	0.0153*
	Geographic condition*Forest type	1.46	0.63	2.29	0.0224*
	Species* Forest type	4.32	0.67	6.42	<0.0001*
	Species* Geographic condition* Forest type	−6.75	1.27	−5.29	0.0018*
PC2	Species	−0.82	0.99	−0.82	0.4542
	Geographic condition	−1.04	1.01	−1.03	0.3600
	Forest type	0.65	0.22	2.84	0.0047*
	Species* Geographic condition	−1.77	1.51	−1.17	0.3064
	Geographic condition* Forest type	0.39	0.53	0.73	0.4631
	Species* Forest type	−0.84	0.61	−1.38	0.1676
	Species* Geographic condition* Forest type	2.56	1.40	1.82	0.1174
PC3	Species	−0.55	0.95	−0.58	0.59
	Geographic condition	−0.04	1.03	−0.04	0.96
	Forest type	−1.54	0.23	−6.68	<0.0001*
	Species* Geographic condition	−0.63	1.34	−0.47	0.66
	Geographic condition* Forest type	0.67	0.52	1.27	0.20
	Species* Forest type	0.41	0.46	0.88	0.37
	Species* Geographic condition* Forest type	0.58	0.76	0.76	0.47

multiple functions, directions of displacement may be less obvious (Grether et al. 2009), though, our results are under what is expected for territorial signals (Drury et al. 2020).

As expected, frequency shifts (see PC1 and PC2, Table 2) occurred mainly in primary forests, and were accompanied by shifts in temporal features (PC3, Table 2). Such acoustic changes are only partially following the acoustic adaptation hypothesis, which predicts that in areas with woody vegetation (e.g. primary forest), signals that are longer, lower-pitched and with a narrow bandwidth would be selected (Morton 1975). We found that *S. midas* presented narrower bandwidths in primary forests, in accordance with the acoustic adaptation hypothesis, but mainly in sympatric areas. Sounds with narrower bandwidths propagate better in closed habitats because the intensity is concentrated in specific frequency bands (Morton 1975). One possible explanation for the asymmetry in the displacement is that in areas where a possible competitor is present, *S. midas* emits sounds with narrower bandwidths, and higher amplitude to achieve longer distances, which could also imply an advantage during territorial defence (Ritschard et al. 2012). Even if the effect was not strong, both species produced slightly

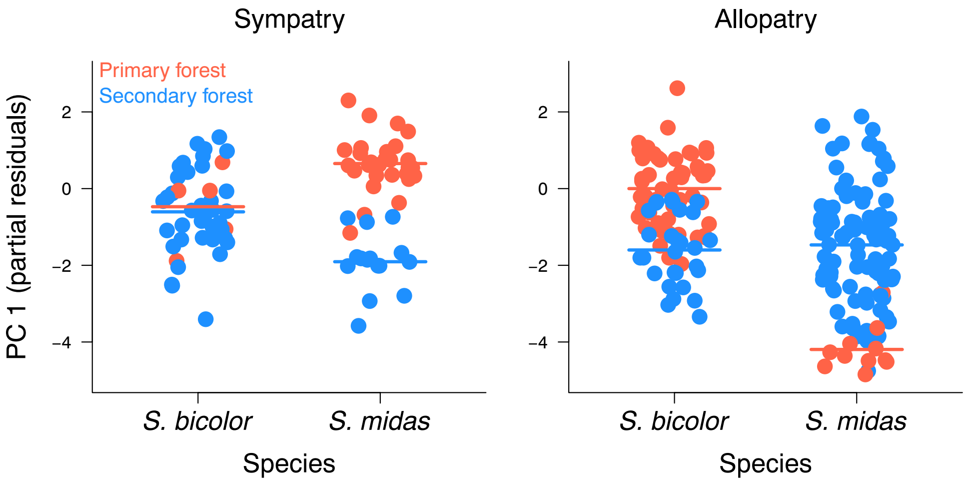

Fig. 3 Differences of acoustic features of pied and red-handed tamarins relative to interactive effects of habitat type (red = primary forest and blue = secondary forest), and geographic condition (allopatry and sympatry), based on the Generalized Linear Mixed Model (GLMM). Each point represents the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

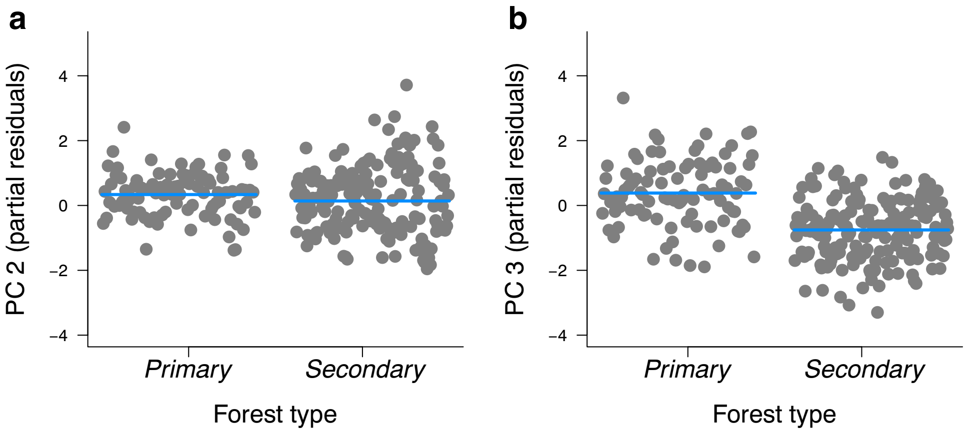

Fig. 4 Differences of acoustic features of pied and red-handed tamarins relative to effects of habitat type (red = primary forest and blue = secondary forest) based on the Generalized Linear Mixed Model (GLMM). Each point represents (**a**) PC 2 and (**b**) PC 3 scores of long calls ($n = 275$); lines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

higher dominant frequencies in primary forests independently of geographic condition. Higher frequencies tend to degrade quickly in closed habitats. So, other strategies that enhance sound propagation may be used by tamarins such as site-selected perching, as occurs in other callithrichids (Sabatini and Ruiz-Miranda 2010). As predicted, both species presented longer calls in primary than in secondary forests, and our findings agree with the idea that frequency features are less plastic than temporal features (Janik and Slater 1997); the strongest effect on frequency features was more evident in primary forests. Amplitude and temporal features are more likely to be modulated in a shorter period through phenotypic plasticity, due to simpler mechanisms of production (Janik and Slater 1997). Plasticity provides an important mechanism that facilitates resource partitioning (Pfennig et al. 2006), but the extent to which the observed acoustic differences reflect plasticity vs. local adaptation is unclear.

Whatever mechanism is behind the acoustic variation that we observed, tamarin calls did not differ significantly between species in secondary forests. If long calls also play a role in sex recognition in pied and red-handed tamarins as is suggested for other callitrichids (Weiss et al. 2001; Miller et al. 2004), this may be related to recognition errors that could result in maladaptive mating and hybridization. During the last three decades, the city of Manaus has been growing rapidly, and new roads have been created in areas where the pied and the red-handed tamarins co-occur, thereby increasing the likelihood of hybridization (McFarlane and Pemberton 2019). Hybridization often causes convergence in physical and behavioural aspects of parapatric species (Brockelman and Schilling 1984; Long et al. 1998; Secondi et al. 2003; Kitchen et al. 2019). As the physical appearance of *S. midas* and *S. bicolor* hybrids can be similar to parental species, or a mix of characteristics of parental species (Gordo et al. 2017), it is not possible to rule out the possibility that we recorded individuals that are phenotypically similar to one of the parental species but are hybrids. Many bird species tend to show convergent traits and intense interspecific territoriality when hybridization occurs in sympatric areas (Drury et al. 2020; Cowen et al. 2020), which may also be the case for pied and red-handed tamarins. There is no data available on the actual magnitude of gene flow between the red-handed and the pied tamarin hybrids. If the behavioural dominance of *S. midas* (Sobroza et al. 2021) also implies differences of gene flow, this could cause the absence of differentiation between species calls and asymmetrical character displacement (Yikweon 2008). Sound signal similarities can be the cause and consequence of hybridization, and the origin or extent to which both processes are occurring in this system remains to be tested.

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

Generally, character displacement and competitor recognition are phenomena involving many signal components, sensory modalities and genes (Ortiz-Barrientos et al. 2004; Grether 2011; Pureswaran et al. 2016). Therefore, even if acoustic signals are convergent and can be influenced by hybridization, species discrimination can still be possible if this function is retained in at least one signal. Many animals are flexible enough to quickly shift communication modalities when the signal transmission is impaired (sensu Partan 2017). Secondary forests usually have a more open canopy, fewer obstacles such as large trunks and lower relative humidity, features that might favour visual and chemical long-distance communication (Müller-Schwarze 2006; Sicsú et al. 2013). Thus, we cannot underestimate the recognition capacity of pied and red-handed tamarins in sympatric areas based only on our acoustic results.

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

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

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Author contribution TVS originally formulated the research topic, collected data, and wrote the original draft. TVS, PACLP, JCD and RMR performed exploratory and current statistical analyses. AAPB, MG, and JCD supervised. TVS and WRS raised funds. AAPB and JCD checked the English. All authors contributed to the writing and reviewing.

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Data availability Data are available as supplementary material.

Declarations

Ethics approval and consent to participate All applicable international, national, and/or institutional guidelines for the use of animals were followed. The study was non-invasive and complied with Brazilian law (permit for Viruá National Park access 47755–1; and for *S. midas* and *S. bicolor* research 10286 – 3 issued by SISBIO/Brazilian Ministry of Environment).

Conflicts of interest The authors declare no competing interests.

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