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FROM THE COVER

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Biodiversity and vector-borne diseases: Host dilution and vector amplification occur simultaneously for Amazonian leishmaniases

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Abstract

Changes in biodiversity may impact infectious disease transmission through multiple mechanisms. We explored the impact of biodiversity changes on the transmission of Amazonian leishmaniases, a group of wild zoonoses transmitted by phlebotomine sand flies (Psychodidae), which represent an important health burden in a region where biodiversity is both rich and threatened. Using molecular analyses of sand fly pools and blood-fed dipterans, we characterized the disease system in forest sites in French Guiana undergoing different levels of human-induced disturbance. We show that the prevalence of *Leishmania* parasites in sand flies correlates positively with the relative abundance of mammal species known as *Leishmania* reservoirs. In addition, *Leishmania* reservoirs tend to dominate in less diverse mammal communities, in accordance with the dilution effect hypothesis. This results in a negative relationship between *Leishmania* prevalence and mammal diversity. On the other hand, higher mammal diversity is associated with higher sand fly density, possibly because more diverse mammal communities harbor higher biomass and more abundant feeding resources for sand flies, although more research is needed to identify the factors

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that shape sand fly communities. As a consequence of these antagonistic effects, decreased mammal diversity comes with an increase of parasite prevalence in sand flies, but has no detectable impact on the density of infected sand flies. These results represent additional evidence that biodiversity changes may simultaneously dilute and amplify vector-borne disease transmission through different mechanisms that need to be better understood before drawing generalities on the biodiversity-disease relationship.

KEYWORDS
amplification effect, Culicidae, dilution effect, iDNA, metabarcoding, phlebotomine sand fly, zoonotic disease

1 | INTRODUCTION

The current biodiversity crisis alters ecosystem functioning and human well-being through a variety of processes that are still debated (Cardinale et al., 2012; Oliver et al., 2015). In this context, the impact of biodiversity loss on infectious disease transmission and spread has become an important research topic during the last two decades. Particular attention has been given to the potential regulation of pathogens in ecosystems by the presence of species that are inefficient for their transmission, a mechanism referred to as the "dilution effect" (Keesing et al., 2010; Ostfeld & Keesing, 2012). Theoretical investigations as well as laboratory and field experiments have allowed defining the conditions under which a dilution effect is expected to occur (Dobson, 2004; Johnson et al., 2008, 2009; Mihaljevic et al., 2014; Norman et al., 1999; Ostfeld & LoGiudice, 2003; Roche et al., 2012; Rudolf & Antonovics, 2005; Suzán et al., 2009; Van Buskirk & Ostfeld, 1995), and empirical studies have suggested its existence in numerous disease systems (Clay et al., 2009a, 2009b; Derne et al., 2011; Ezenwa et al., 2006; Gilbert et al., 2001; Gottdenker et al., 2012; LoGiudice et al., 2003; Ostfeld & Keesing, 2000; Telfer et al., 2005; Weinstein et al., 2017). Considering a local community of hosts composed of species that differ in their competence for a given pathogen (i.e., their ability to get infected and transmit), a dilution effect may occur if the presence of the least competent hosts reduces contact rates between the most competent hosts and the pathogen or decreases the density of competent hosts. Additionally, if the less competent hosts are also those that tend to be extirpated from species-depleted communities, biodiversity loss should result in enhanced transmission. The idea that the dilution effect may produce a beneficial impact of biodiversity conservation on public health in most disease systems, has triggered important interest as well as strong criticism (Civitello et al., 2015; Halsey, 2019; Keesing et al., 2010; Lafferty & Wood, 2013; Levi et al., 2016; Randolph & Dobson, 2012; Salkeld et al., 2013; Wood et al., 2014). Advances in disease ecology have allowed a more detailed understanding of biodiversity-disease relationships, and the field has progressed beyond initial debates about the generality of the dilution effect. Studies have highlighted the importance of accounting for different factors such as the geographical scale, the nature and extent of biodiversity changes, the transmission mode, and the taxa involved in the disease system under consideration (Cohen et al., 2016; Faust et al., 2017; García-Peña et al., 2016; Gibb et al., 2018; Halliday & Rohr, 2019; Halliday et al., 2020; Johnson et al., 2015, 2019; Keesing & Ostfeld, 2021; Morand et al., 2014; Rohr et al., 2020; Weinstein et al., 2017; Wood & Lafferty, 2013; Young et al., 2017). It has been shown that changes in biodiversity can either amplify or dilute pathogen transmission, through multiple mechanisms which can sometimes occur within the same system (Clay et al., 2009a; 2009b; Faust et al., 2017; Huang et al., 2015; Luis et al., 2018; Miller & Huppert, 2013; Ogden & Tsao, 2009; Roche & Guégan, 2011; Rohr et al., 2015; Swei et al., 2011; Wood et al., 2020). In the case of vector-borne diseases, it has been stressed that the ecology and feeding habits of arthropod vectors must also be considered (Carlson et al., 2009; Hamer et al., 2011; Laporta et al., 2013; Loss et al., 2009; McGregor et al., 2018; Miller & Huppert, 2013; Ogden & Tsao, 2009; Park et al., 2016; Randolph & Dobson, 2012; Roche & Guégan, 2011; Roche et al., 2013; Swei et al., 2011; Titcomb et al., 2017; Vinson & Park, 2019).

Overall, there is a need for more field studies on various systems to further disentangle the mechanisms underlying biodiversity-disease relationships and to inform epidemiological predictions. However, conducting such studies can be highly challenging, since it requires generating data on wild vertebrate and arthropod fauna as well as on circulating pathogens in numerous study sites and, often, in difficult environmental contexts (e.g., tropical regions). Here, we used recently developed molecular tools to explore the effects of mammal diversity on the transmission of Amazonian leishmaniases. Leishmaniases are a group of human vector-borne diseases endemic to different tropical and subtropical regions, caused by parasites of the genus *Leishmania* (Kinetoplastida: Trypanosomatidae) and transmitted by hematophagous phlebotomine sand flies (Psychodidae) (reviewed in Bañuls et al., 2007). In Amazonian ecosystems, several zoonotic *Leishmania* species typically coexist, with distinct sylvatic transmission cycles involving different sand fly vector species and wild mammal reservoir hosts (Lainson & Shaw, 2010; Rotureau, 2006). Amazonian leishmaniases represent a significant public health

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burden in a biodiversity-rich region threatened by human activities (Chavy et al., 2019; Pan American Health Organization, 2019; Rangel et al., 2014). However, the mechanisms through which biodiversity may impact the transmission of these wild zoonoses remain largely unexplored.

2 | MATERIALS AND METHODS

2.1 | Sampling

Sampling was performed between 2015 and 2017 in 19 different forest sites in French Guiana (Figure 1, Table 1, Supporting Information data S1). Sites were separated by at least ~5-km distance and chosen to represent sylvatic environments with variable levels of human-induced disturbance, ranging from remote and protected areas to forest patches in the vicinity of urbanized zones. When several sites were sampled within a same area (i.e., Saint-Georges, Belizon, Kaw or Counami), those were specifically chosen to represent contrasting situations with respect to hunting pressure (e.g., closer to or further from the nearest city or accessible road, inside or outside of a protected area). Human-induced disturbance was measured using the average Human FootPrint index (HFP; de Thoisy et al., 2010; updated in 2012; Table 1, Supporting Information data S1). In each site, sand flies were collected using US Centres for Disease Control and Prevention (CDC) miniature light traps set up across a c. 1 ha plot. Traps were separated by c. 50-m distance from each other and left for up to six consecutive nights. Each morning, the contents of each trap was collected. Sand fly females were sorted using a stereo microscope and kept in pools (corresponding to each trap-night) in microcentrifuge tubes with 95% ethanol for later molecular analyses. A maximum of 50 individuals was included in a pool, and several pools were made when more than 50 specimens were caught in a given trap (with a maximum of four pools per trap, i.e., 200 individuals). The total number of sand flies caught in each trap was systematically recorded, unless the contents of the trap was importantly damaged or partially lost (mainly due to rainy conditions or manipulation during collection). Visibly blood-fed dipterans, including sand flies, mosquitoes (Culicidae), and biting midges (Ceratopogonidae), were kept individually in microcentrifuge tubes with 95% ethanol for molecular analyses. Additional blood-fed dipterans resting during the day along tree trunks were collected using a Prokopack aspirator (John W. Hock Co.) and conserved in the same way.

2.2 | Laboratory

We analysed sand fly pools to identify their species composition using a previously developed DNA metabarcoding protocol (Kocher, Gantier, et al., 2017). *Leishmania* DNA detection and identification was performed on the same pools using high-throughput sequencing of kDNA minicircle amplicons (Kocher et al., 2018). For each blood-fed specimen, the dipteran species and blood meal source were identified individually as previously described (Kocher, de Thoisy, Catzeflis, Valière, et al., 2017). Sand fly pools were homogenized using a Qiagen TissueLyser 2 (Qiagen), and DNA was extracted with the Qiagen DNeasy Blood and Tissue kit. For individual blood-fed specimens, a modified Chelex (Bio-Rad) protocol was used for DNA extraction (Casquet et al., 2012). The Ins16S_1 (F: TRRGACGAGAAGACCCTATA; R: TCTTAATCCAACATCGAGGTC; [Clarke et al., 2014]), 12S-V5 (F: TAGAACAGGCTCCTCTAG; R: TTAGATACCCCACTATGC; [Riaz et al., 2011]) and leishmini (F: 5′-GGKAGGGGCGTTCTGC-3′; R: 5′-STATWTTACACCAACCCC-3′; Kocher et al., 2018) PCR primers were used to amplify short fragments of dipteran, vertebrate and *Leishmania* DNA, respectively. Tags of eight base pairs with at least five differences between them were added at the 5′ end of each primer to enable multiplexing of PCR products for subsequent sequencing (Binladen et al., 2007). A Latin square design was used for PCR multiplexing to allow for the detection and filtering of mistagged sequencing read (Esling et al., 2015). For sand fly metabarcoding, two PCR replicates were performed. PCR products were pooled according to the multiplexing design and used for sequencing library preparation and high-throughput sequencing on Illumina Hiseq or Miseq platforms at the GeT-PlaGe core facilities of Genotoul (Toulouse, France).

2.3 | Bioinformatic analyses

Bioinformatic analyses were performed using the OBITools 1.2.9 package (Boyer et al., 2016) and R 4.0.3 (R Core Team, 2020). Paired-end reads were merged with illuminapairedend and demultiplexed based on PCR primer tags using ngsfilter. Reads were dereplicated using obiuniq and sequences supported by <10 reads in a given sample were discarded using obigrep. Taxonomic assignments were performed using ecotag, with customized reference DNA sequence data sets for each studied taxonomic group. For dipteran identifications, we used previously published reference data sets for neotropical sand flies (Kocher, Gantier, et al., 2017) and mosquitoes (Talaga et al., 2017), to which we added mosquito reference sequences corresponding to the targeted 16S region, which we extracted from NCBI GenBank using ecoPCR. For vertebrate identifications, we used a previously published reference data set for Amazonian mammals (Kocher, Thoisy, Catzeflis, Huguin, et al., 2017), completed with vertebrate reference sequences corresponding to the targeted 12S region extracted from GenBank. For *Leishmania* identifications, we used a previously published data set of kDNA minicircle reference sequences (Kocher et al., 2018). ecotag employs a lower common ancestor algorithm that allows to perform taxonomic assignments based on the percentage of identity with multiple matches in a reference data set. In other words, a sequence matching similarly to several members of a given taxon will be assigned to the corresponding taxon. For dipteran and vertebrate identifications, we considered taxonomic assignments at the genus level at best if the percentage of identity with the closest match was lower than 97%, in order to avoid biases due to reference data set incompleteness (i.e.,

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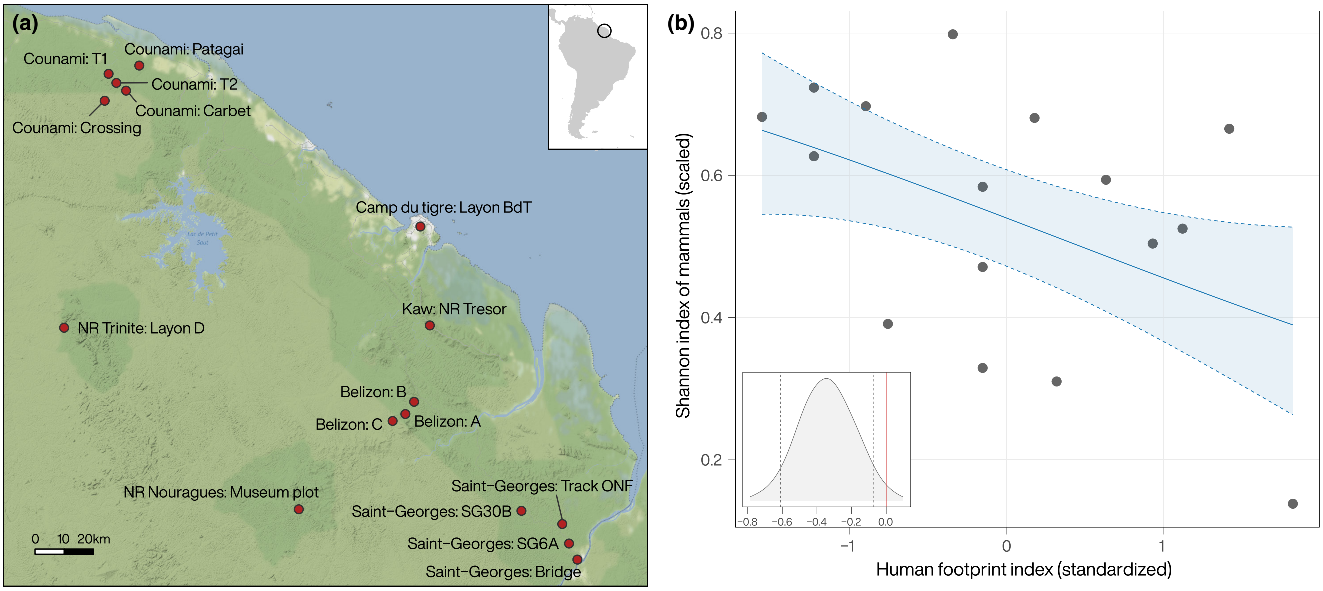

FIGURE 1 (a) Location of study sites (French Guiana). (b) Regression of the Shannon index of mammals on human-induced disturbance. Shannon indices of mammals were estimated through dipteran blood meals in each site. The level of human-induced disturbance was measured using the human footprint index (de Thoisy et al., 2010). The mean prediction curve is depicted with 90% CI. In the inlet figure, the posterior density of the regression's slope coefficient is represented (dotted lines are positioned at 5 and 95% quantiles; the red line is positioned at $x = 0$)

artefactual species-level identifications in cases where only one species was represented in the data set for a given genus). We then performed de novo sequence clustering using sumaclust 1.0.31 (Mercier et al., 2013) with a 97% threshold. We defined molecular taxonomic units (MOTU) based on ecotag results in case of species-level identifications, and based on de novo clustering otherwise, in order to identify putative species within upper-level taxa. Vertebrate identifications were adjusted when only a subset of the matched species was known to be present in French Guiana. Because no reference sequence was available for local biting midge species, we defined MOTUs within the Ceratopogonidae family based on de novo clustering only.

For each sequencing library, we used the number of sequencing reads found with non-used primer tag combinations to perform MOTU-based filtering of mistagged reads, as suggested previously (Esling et al., 2015). Additionally, MOTUs supported by less than 100 reads in a given sample were filtered out. For sand fly metabarcoding, we further filtered MOTUs that (i) were not identified as Phlebotominae, (ii) were not recovered in two PCR replicates, and (iii) were supported by least 2% of the sequencing reads in a given sample (a maximum of 50 sand flies were included in each analysed pool). For individual blood-fed specimens, the most supported dipteran and vertebrate MOTUs were retained (i.e., we did not consider the possibility of multiple blood meal sources, as a conservative measure). In a few cases, the resulting dipteran identification did not match the expected dipteran group (sand fly, mosquito, or biting midge) and was therefore discarded. For blood meal identifications, results were discarded if the majority sequence was identified as human or other potential laboratory contaminants which were not expected in our study sites, as well as sequences assigned to above-order taxonomic levels which probably represented molecular or sequencing artifacts. For *Leishmania* detection, only species-level identifications were considered, and the majority *Leishmania* species was retained in each positive sample.

2.4 | Estimating mammal diversity from individual dipteran blood meals

iDNA has recently emerged as a promising tool to perform vertebrate inventories at lower cost and effort (Calvignac-Spencer et al., 2013; Kocher, de Thoisy, Catzeflis, Valière, et al., 2017; Schnell et al., 2015). Here, we used a probabilistic approach to generate estimates of host community composition and diversity from our iDNA data (i.e., blood meal identifications of individual dipteran specimens) while accounting for invertebrate host preferences. The model is represented by a Bayesian network in Figure S1. We assume that the probability p_{sih} that a blood-fed invertebrate of species i has fed on a host of species h in site s depends on r_{sh}, the relative abundance of h in s, and on α_{sh}, the relative preference of i for h. We further assume that the relative probability of insect i feeding on host h_j rather than on host h_k in site s is given by:

$$\frac{p_{sih_j}}{p_{sih_k}} = \frac{r_{sh_j}\alpha_{ih_j}}{r_{sh_k}\alpha_{ih_k}} \tag{1}$$

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TABLE 1 Details of the study sites, including sampling size and estimates of the different variables used to describe the ecological system

Site	Nb. sand flies	Number of blood-fed dipterans (successfully identified)	Human Footprint Index	Mammal diversity (Shannon index)[a]	Proportion of *Leishmania* reservoirs[a]	Sand fly density (number of individuals per trap)[a]	Sand fly diversity (Shannon index)[a]	*Leishmania* prevalence rate (%)[a]
Belizon: A	1028	17 (13)	36.0	2.22 (1.53, 2.83)	0.42 (0.19, 0.67)	44.35 (42.27, 46.45)	2.18 (2.16, 2.16)	1.05 (0.8, 1.33)
Belizon: B	1176	67 (38)	30.1	1.68 (1.16, 2.18)	0.66 (0.38, 0.89)	55.75 (53.31, 58.25)	2.07 (2.04, 2.04)	1.64 (1.37, 1.92)
Belizon: C	1298	22 (10)	17.0	1.95 (1.23, 2.66)	0.71 (0.43, 0.95)	58.69 (56.17, 61.26)	1.72 (1.71, 1.71)	1.71 (1.46, 1.98)
Camp du tigre: Layon BdT	450	43 (30)	40.9	0.46 (0.13, 0.95)	0.98 (0.91, 1)	11.87 (10.97, 12.79)	2.38 (2.35, 2.35)	3.13 (2.18, 4.22)
Counami: Carbet	349	60 (40)	21.0	2.27 (1.69, 2.79)	0.65 (0.43, 0.87)	15.18 (14.11, 16.3)	1.45 (1.4, 1.4)	1.4 (1.09, 1.77)
Counami: Crossing	719	35 (32)	17.0	1.1 (0.49, 1.85)	0.87 (0.58, 1)	38.17 (36.06, 40.33)	1.48 (1.46, 1.46)	2.2 (1.7, 2.78)
Counami: Patagai	572	13 (6)	17.0	1.57 (0.69, 2.45)	0.49 (0.13, 0.87)	19.43 (18.16, 20.7)	1.69 (1.67, 1.67)	1.08 (0.83, 1.35)
Counami: T1	376	13 (8)	9.7	1.3 (0.36, 2.2)	0.3 (0.04, 0.68)	12.6 (11.58, 13.65)	2.52 (2.47, 2.47)	0.89 (0.54, 1.31)
Counami: T2	817	97 (74)	4.0	2.09 (1.52, 2.61)	0.69 (0.49, 0.87)	30.7 (29.06, 32.39)	1.9 (1.88, 1.88)	1.64 (1.38, 1.93)
Kaw: NR Tresor	2964	50 (31)	8.0	2.32 (1.75, 2.83)	0.61 (0.41, 0.82)	109.27 (106.04, 112.56)	1.68 (1.68, 1.68)	1.46 (1.15, 1.79)
NR Nouragues: Museum plot	2676	196 (146)	4.0	2.41 (2.08, 2.7)	0.18 (0.09, 0.29)	142.16 (138.52, 145.78)	1.93 (1.93, 1.93)	0.68 (0.47, 0.93)
NR Trinite: Layon D	795	14 (9)	0.0	2.27 (1.59, 2.87)	0.48 (0.27, 0.72)	26.56 (25.05, 28.13)	1.56 (1.55, 1.55)	1.04 (0.81, 1.3)
Saint-Georges: Bridge	1647	100 (70)	32.4	1.75 (1.4, 2.11)	0.53 (0.31, 0.76)	54.83 (52.06, 57.66)	0.94 (0.93, 0.93)	1.06 (0.76, 1.4)
Saint-Georges: SG30B	182	38 (36)	22.7	1.03 (0.37, 1.75)	0.89 (0.66, 1)	15.25 (13.49, 17.05)	2.39 (2.32, 2.32)	2.67 (1.93, 3.52)
Saint-Georges: SG6A	1606	38 (27)	26.5	1.98 (1.42, 2.52)	0.67 (0.48, 0.84)	89.1 (85.42, 92.83)	1.2 (1.19, 1.19)	1.49 (1.13, 1.9)
Saint-Georges: Track ONF	749	35 (21)	14.7	2.66 (2.19, 2.99)	0.35 (0.19, 0.52)	42.64 (40.22, 45.05)	1.4 (1.39, 1.39)	0.8 (0.59, 1.03)

[a] Mean estimate (90% HPD).

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From (equation 1) it follows that the probability p'_{sih} that an invertebrate of species i has fed on host h in site s, given that it has fed on one of the H host species identified in our data set, is:

$$p'_{sih} = \frac{r_{sh}\alpha_{ih}}{\sum_{k=1}^{H} r_{sk}\alpha_{ik}} \tag{2}$$

Denote $\{N\}_{si} = \{n_{si1,\ldots,}n_{siH}\}$ the data vector of the number of occurrences of invertebrate i having fed on each of the H host species in site s. The probability of this data is given by the multinomial distribution with parameters $\{p'\}_{si} = \{p'_{si1}, \cdots, p'_{siH}\}$ and $Y_{si} = \sum_{k=1}^{H} n_{sik}$:

$$P(\{N\}_{si} | \{p'\}_{si}, Y_{si}) = \text{Multinomial}(\{N\}_{si} | \{p'\}_{si}, Y_{si}) \tag{3}$$

Given S sites and I invertebrate species across all sites, we denote $\{N\} = \{\{N\}_{si}\}$ the whole data set, $\{p'\} = \{\{p'\}_{si}\}$ the set of probability vectors and $\{Y\} = \{Y_{si}\}$ the set of sample sizes, with $i = 1,2,\ldots I$ and $s = 1,2,\ldots,S$. The likelihood of the full data set is then given by:

$$P(\{N\} | \{p'\}, \{Y\}) = \prod_{s=1}^{S} \prod_{i=1}^{I} \text{Multinomial}(\{N\}_{si} | \{p'\}_{si}, Y_{si}) \tag{4}$$

The model was implemented in a Bayesian framework in Stan (Carpenter et al., 2017) through its R interface rstan, in order to sample the posterior probability density of the parameters using Monte Carlo Markov chain (MCMC; see Supporting Information and Figure S2 for details about the choice of priors and simulation results, as well as the *Stan* code). Joint samples of mammal's relative abundances in each site were used to derive the Shannon index of diversity ($-\sum_h r_{sh}\log(r_{sh})$) and the overall proportion of species known as *Leishmania* reservoirs. Closely related dipteran species appeared to feed on similar ranges of hosts (e.g., sand flies of the *Nyssomyia* genus feeding mostly on arboreal mammals, sand flies of the *Psychodopygus* genus feeding mostly on armadillos, mosquitoes of the *Culex* genus feeding on a wide range of vertebrates or observed ceratopogonids feeding mostly on amphibians; Table 2; Figure S3). Therefore, we estimated feeding preferences at the genus level (or at the family level in the case of ceratopogonids), in order to increase statistical power. Additionally, we assumed that dipterans had identical preferences for vertebrates of the same order which exhibit similar morphological and ecological features (with the exception of rodents which were separated into terrestrial and arboreal rodents; Figure S3). Sites in which less than five dipteran blood meals could be identified were not retained for the analysis. The posterior distribution of the parameters was sampled using MCMC with 3 chains of 40,000 iterations, including 4000 iterations for warmup. Convergence and mixing were assessed using trace plots and ESS values, which were >200 for all parameters (Figures S4 and S5). The prior distribution of the parameters was obtained by running the same MCMC sampling scheme as for the posterior, with the likelihood fixed to a constant. The comparison of posterior and prior densities allowed us to assess to what extent the posterior was driven by the data (Figures S4 and S5). The mean posterior estimates of parameters were computed and used as variables for the generalized linear models (GLM) described in the next section (we initially attempted to jointly estimate mammal relative abundances and GLM's parameter but this led to MCMC mixing issues).

2.5 | Effect of mammal diversity on Leishmania transmission

In addition to the measures of vertebrate communities obtained from individual blood meal identifications, sand fly counts in traps and molecular analyses of sand fly pools were used to estimate the abundance and diversity of sand flies as well as the *Leishmania* prevalence rate in sand flies. All of these variables were used in a series of Bayesian GLMs to explore the impact of mammal diversity changes on the disease system (Figure 1, Supporting Information data S2). We assessed the relationship between human-induced disturbance and mammal diversity using a regression of the Shannon index of mammals on the HFP. We assessed whether changes of mammal diversity led to predictable changes of the mammal community competence for *Leishmania* parasites using a regression of the relative abundance of *Leishmania* reservoirs on the Shannon index of mammals. Furthermore, we assessed the effect of changes of mammal diversity on sand fly density and diversity by regressing the number of sand flies collected in each trap and the Shannon index of sand flies (estimated from metabarcoding results with the R package iNext [Hsieh et al., 2016]) on the Shannon index of mammals. We then assessed the effect of mammal community competence, sand fly density and sand fly diversity on *Leishmania* transmission using a regression of *Leishmania* prevalence rates in sand flies on the relative abundance of *Leishmania* reservoirs, the expected number of sand flies collected per trap and the Shannon index of sand flies (used as predictor variables in the same regression). We checked for spatial autocorrelation of the different variables with the Moran's *I* autocorrelation index as implemented in the R package ape (Paradis et al., 2004), using the inverse of pairwise geographical distances between sites as the weight matrix. For all regressions, predictor variables were standardized, and weakly informative normal priors were used for regression coefficients. Prior distributions of slope coefficients were centred around 0, while that of regression intercepts were centered around the mid-range value of the corresponding dependent variable. The posterior distributions of slope coefficients were used to assess the significance of inferred relationships. We evaluated the cumulative effect of mammal diversity changes on *Leishmania* transmission by generating posterior predictions of the *Leishmania* prevalence rate and of the expected number of infected sand flies per trap for different values of the Shannon index of mammals. We visualized sampled mean prediction curves against the Shannon index of mammals (across the range of values observed in our study), and used the distribution of their average slope to measure the predicted effects.

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TABLE 2 List of vertebrates identified in blood meals of each dipteran species or molecular taxonomic units (MOTU)

Species/MOTU	Nb.	Vertebrates identified
Ceratopogonidae MOTU 1	3	*Rhinella* cf. *margaritifera* (67%); Hyloidea MOTU 1 (33%)
Ceratopogonidae MOTU 2	2	*Osteocephalus* MOTU 1 (50%); *R.* cf. *margaritifera* (50%)
Ceratopogonidae MOTU 3	1	*Choloepus didactylus* (100%)
Ceratopogonidae MOTU 4	1	*Osteocephalus* MOTU 1 (100%)
Ceratopogonidae MOTU 5	2	*Osteocephalus* MOTU 1 (100%)
Aedini MOTU 1	1	*Adenomera andreae* (100%)
Culex imitator	1	Squamata MOTU 1 (100%)
Culex MOTU 1	58	*Proechimys cuvieri* (36%); *Thamnophilus nigrocinereus* (28%); *Cuniculus paca* (7%); *Dasyprocta leporina* (3%); *Didelphis marsupialis* (3%); *Mazama nemorivaga* (3%); *Proechimys guyannensis* (3%); *Thamnophilus* MOTU 1 (3%); *Bradypus tridactylus* (2%); *Chelonoidis denticulatus* (2%); *Dasypus novemcinctus* (2%); *Echimys chrysurus* (2%); *Metachirus nudicaudatus* (2%); *Oecomys rutilus* (2%); *Tapirus terrestris* (2%)
Culex MOTU 2	14	Squamata MOTU 1 (14%); *T. nigrocinereus* (14%); Accipitrinae MOTU 1 (7%); *Anolis fuscoauratus* (7%); *Bothrops atrox* (7%); *D. leporina* (7%); *D. novemcinctus* (7%); *Gonatodes humeralis* (7%); *Hypsiboas* MOTU 1 (7%); *Philander opossum* (7%); *Polychrus marmoratus* (7%); *Thamnophilus* MOTU 1 (7%)
Culex MOTU 3	2	*D. marsupialis* (50%); *T. nigrocinereus* (50%)
Culex sp.stJ	1	*Thamnophilus* MOTU 2 (100%)
Culex sp.stK	1	*D. leporina* (100%)
Culex sp.stL	1	*Osteocephalus* MOTU 1 (100%)
Culicinae MOTU 1	3	*P. cuvieri* (67%); *Thamnophilus* MOTU 1 (33%)
Limatus flavisetosus	1	*Tinamus major* (100%)
Ochlerotatus serratus	5	*D. leporina* (40%); *Thamnophilus* MOTU 1 (40%); *M. nemorivaga* (20%)
Psorophora ferox	1	*Myoprocta acouchy* (100%)
Sabethini MOTU 1	4	*D. leporina* (25%); *D. novemcinctus* (25%); *G. humeralis* (25%); *P. opossum* (25%)
Bichromomyia flaviscutellata	5	*D. leporina* (40%); *P. guyannensis* (40%); *P. cuvieri* (20%)
Evandromyia brachyphalla	1	*P. cuvieri* (100%)
Ev. infraspinosa	4	*D. novemcinctus* (50%); *C. didactylus* (25%); *M. acouchy* (25%)
Ev. monstruosa	1	*D. leporina* (100%)
Ev. sericea	5	*Lachesis muta* (60%); *M. acouchy* (40%)
Ev. walkeri	1	*Isothrix sinnamariensis* (100%)
Pintomyia serrana	5	*Alouatta seniculus macconnelli* (60%); *C. didactylus* (20%); *Pithecia pithecia* (20%)
Micropygomyia rorotaensis	1	Squamata MOTU 1 (100%)
Nyssomyia sylvicola	2	*D. leporina* (100%)
Ny. umbratilis	138	*C. didactylus* (49%); *Coendou melanurus* (15%); *A. macconnelli* (14%); *Ateles paniscus* (9%); *D. novemcinctus* (4%); *Coendou prehensilis* (3%); *Tamandua tetradactyla* (2%); *Cebus olivaceus* (1%); *Nasua nasua* (1%); *P. pithecia* (1%); *Psophia crepitans* (1%)
Ny. yuilli pajoti	18	*A. macconnelli* (17%); *C. didactylus* (17%); *A. paniscus* (11%); *C. melanurus* (11%); *D. novemcinctus* (11%); *P. crepitans* (11%); *T. tetradactyla* (11%); *C. prehensilis* (6%); *T. terrestris* (6%)
Pi. pacae	1	*M. nemorivaga* (100%)
Pressatia choti	7	*D. leporina* (86%); *G. humeralis* (14%)
Psychodopygus amazonensis	32	*D. novemcinctus* (44%); *D. leporina* (16%); *T. terrestris* (16%); *Dasypus kappleri* (12%); *D. marsupialis* (6%); *Mazama americana* (3%); *Tayassu pecari* (3%)
Ps. ayrozai	79	*D. novemcinctus* (84%); *D. kappleri* (15%); *Thamnophilus* MOTU 1 (1%)
Ps. claustrei	11	*C. paca* (36%); *M. acouchy* (36%); *D. leporina* (18%); *M. nemorivaga* (9%)
Ps. hirsutus	34	*D. novemcinctus* (59%); *M. americana* (15%); *T. terrestris* (15%); *D. kappleri* (12%)
Ps. MOTU 1	8	*D. novemcinctus* (50%); *D. leporina* (12%); *D. kappleri* (12%); *M. acouchy* (12%); *T. terrestris* (12%)
Ps. MOTU 10	1	*D. novemcinctus* (100%)

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TABLE 2 (Continued)

Species/MOTU	Nb.	Vertebrates identified
Ps. MOTU 2	5	*D. novemcinctus* (40%); *T. terrestris* (40%); *Pecari tajacu* (20%)
Ps. MOTU 3	5	*D. novemcinctus* (60%); *D. kappleri* (40%)
Ps. MOTU 5	3	*D. novemcinctus* (100%)
Ps. panamensis	3	*D. leporina* (100%)
Ps. s. maripaensis	120	*D. novemcinctus* (67%); *M. americana* (11%); *D. kappleri* (10%); *T. terrestris* (5%); *M. nemorivaga* (3%); *C. paca* (2%); *A. paniscus* (1%); *P. guyannensis* (1%); *Thamnophilus* MOTU 1 (1%)
Sciopemyia sordellii	2	*Chiasmocleis shudikarensis* (50%); Hyloidea MOTU 2 (50%)
Trichophoromyia ininii	1	*C. paca* (100%)
Trichopygomyia trichopyga	6	*D. novemcinctus* (50%); *C. paca* (33%); *D. kappleri* (17%)
Viannamyia tuberculata	1	*C. melanurus* (100%)

3 | RESULTS

3.1 | Sampling and molecular analyses

In total, we collected 18,508 sand fly females, which were gathered in 666 pools used for sand fly metabarcoding and *Leishmania* detection (Table 1, Supporting Information data S1). After DNA extraction and amplification, high-throughput sequencing and bioinformatic filtering, 600 (90.1%) sand fly pools could be characterized with metabarcoding, and *Leishmania* DNA was detected in 175 (26.3%) of them. We further collected 855 blood-fed dipterans, including 715 sand flies, 123 mosquitoes and 17 biting midges that were analysed individually (Table S1). Dipteran identification was successful in 91.7% of the individuals (although not necessarily at the species level), and their blood meal content was identified in 75.9% of the cases. Both dipteran and blood meal identifications were successful for 602 (70.4%) individuals. Three sites in which less than five blood-fed dipterans could be identified were not retained for statistical analyses (Figure 1, Table 1).

3.2 | Sand fly, vertebrate and Leishmania identifications

In total, we identified 63 sand fly MOTUs in sand fly pools (Table S1, Supporting Information data S1), which is fairly consistent with the known sand fly species richness of French Guiana (about 80 species recorded so far). A total of 34 of these were identified at the species level, including seven known or suspected *Leishmania* vector species in the region: *Bichromomyia flaviscutellata*, *Nyssomyia umbratilis*, *Psychodopygus ayrozai*, *Ps. panamensis*, *Ps. squamiventris maripaensis*, *Trichophoromyia ubiquitalis*, *Viannamyia furcata* (Rotureau, 2006). The most abundant species were *Ps. squamiventris maripaensis*, *Th. ininii*, *Trichopygomyia trichopyga* and *Th. ubiquitalis* (25.2%, 18.3%, 18.0% and 10.9% of the estimated number of individuals, respectively). Five *Leishmania* species were detected in sand fly pools: *L. lainsoni*, *L. amazonensis*, *L. naiffi*, *L. braziliensis*, *L. guyanensis*; the most frequent being *L. lainsoni* and *L. naiffi* (48.6% and 43.4% of the positive samples, respectively). Blood-fed specimens belonged to 51 dipteran MOTUs, and blood meal analyses revealed a total of 52 vertebrate MOTUs (Table 2, Figure S3, Supporting Information data S1), including 28 mammals, among which 11 were recognized *Leishmania* reservoir hosts in the region: *Didelphis marsupialis*, *Philander opossum*, *Metachirus nudicaudatus*, *Choloepus didactylus*, *Dasypus novemcinctus*, *Tamandua tetradactyla*, *Coendou melanurus*, *C. prehensilis*, *Dasyprocta leporina*, *Proechymis cuvieri* and *P. guyannensis* (Rotureau, 2006). Our results revealed contrasting host preferences across sand fly species, and were consistent with existing knowledge (e.g., *Nyssomyia* spp. feeding mostly on sloth and other arboreal mammals [Christensen et al., 1982], *B. flaviscutellata* feeding mostly on terrestrial rodents [Lainson & Shaw, 1968], and *Psychodopygus* spp. feeding mostly on armadillos [Le Pont, 1990]; Table 2; Figure S3).

3.3 | Statistical analyses

We estimated mammal diversity (Shannon index) and the relative abundance of *Leishmania* reservoirs in each site based on dipteran blood meal identifications using a probabilistic approach (Figures S1 and S2). We then used these estimates in a series of Bayesian regressions to investigate the effect of mammal diversity on the transmission of *Leishmania* parasites. MCMC trace plots and ESS values indicated convergence and correct sampling of the posterior distribution for all parameters (Figures S4–S5). Mean estimates of the Shannon index of mammals across our study sites ranged from 0.46 to 2.7 (Table 1), and these correlated negatively with the human footprint index (HFP; (de Thoisy et al., 2010); mean effect: −0.34, 90% CI: −0.61, −0.07; Figure 1b). Spatial autocorrelation was not detected for the HFP (expected/observed Moran's I: −0.067/0.056; p-value: .3), nor for the Shannon index of mammals (expected/observed Moran's I: −0.067/−0.13; p-value: .6). The Shannon index of mammals correlated negatively with the relative abundance of *Leishmania* reservoirs (−0.68, 90% CI: −0.99, −0.38; Figure 2a), positively with sand fly density (0.4, 90% CI: 0.13, 0.67; Figure 2b), and

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negatively (but weakly) with the Shannon index of sand flies (−0.19, 90% CI: −0.38,0; Figure S4A). Furthermore, we estimated that the prevalence rate of *Leishmania* in sand flies correlated positively with the relative abundance of *Leishmania* reservoirs (0.43, 90% CI: 0.27, 0.59; Figure 2c), but did not correlate with sand fly density or diversity (0.03, 90% CI: −0.12, 0.17 and 0.08, 90% CI: −0.07, 0.23, respectively; Figures S7B,C). Finally, posterior predictions indicated that the Shannon index of mammals correlated negatively with the *Leishmania* prevalence rate in sand flies but did not correlate with the density of infected sand flies (Figure 2d,e).

4 | DISCUSSION

With this work, we show that wild vector-borne disease systems can be efficiently studied using DNA metabarcoding of arthropod vectors, which allows measuring arthropod, vertebrate and parasite communities altogether. Dipteran blood meal analyses allowed to identify a large variety of vertebrates across our study sites, confirming the potential of invertebrate-derived DNA (iDNA) approaches for biodiversity monitoring (Calvignac-Spencer et al., 2013; Kocher, de Thoisy, Catzeflis, Valière, et al., 2017; Schnell et al., 2015). Based on blood meal identifications, we estimated the Shannon index of mammals, which correlated negatively with the human footprint index (Figure 1b), as expected (de Thoisy et al., 2010). This suggests that the variation of mammal diversity across our study sites was, at least partly, linked to human-induced disturbance. We then explored the effect of mammal diversity on *Leishmania* disease systems and transmission. In particular, we assessed the occurrence of a dilution effect potentially leading to reduced transmission with higher mammal diversity. In the case of vector-borne diseases, a dilution effect can be expected only if arthropod vectors feed on various host species, including some that are poorly competent for pathogen transmission. This is the case for Amazonian leishmaniases, since sand fly vector species from which blood meals could be analysed were observed to have fed on different hosts, including some that are not known as *Leishmania* reservoirs (Table 2, Figure S3). For example, while most *Ny. umbratilis* individuals had fed on two-toed sloths (main vector and reservoir of *L. guyanensis*, respectively), and most *Psychodopygus* spp. had fed on nine-banded armadillos (main vector and reservoirs of *L. naiffi*), a significant proportion of them had fed, respectively, on different primates and large terrestrial mammals which are not known to act as *Leishmania* reservoirs. Therefore, *Leishmania* parasites may indeed end up in "diluting" hosts which could contribute to reduced transmission of these disease agents. This was further supported by the observation of a positive correlation between the relative abundance of *Leishmania* reservoir hosts and *Leishmania* prevalence rate in sand flies (Figure 2c).

Another important assumption of the dilution effect hypothesis is that species contributing the most to pathogen transmission dominate in disturbed and less diverse communities. Ecological and evolutionary hypotheses have suggested the existence of such a positive relationship between host competence for pathogens and resilience to disturbance, leading to a general increase of the overall community competence with biodiversity loss (Johnson et al., 2015; Keesing et al., 2010; Ostfeld & Keesing, 2012). Species that are resilient to changing environments are frequently characterized by fast life history strategies, including low investment in adaptive immunity and high reproductive rate, yielding an important influx of susceptible individuals in the population. In addition, pathogens may adapt predominantly to resilient host species, because these hosts are generally widespread, mobile and abundant, therefore constituting the most frequently encountered resource. Empirical evidence has supported these ideas (García-Peña et al., 2016; Han et al., 2015; Johnson et al., 2012, 2013, 2019), although it seems that the situation may vary depending on the taxa under consideration (Gibb et al., 2018; Young et al., 2013). Here, we show that mammal species known as *Leishmania* reservoirs indeed dominate less diverse mammal communities, with a 233.6% (90% CI: 293.0%, 190.8%) increase of their relative abundance along the range of estimated mammal's Shannon index (Figure 2a). In sum, these results suggest a predictable effect of local mammal diversity changes on the overall host community competence for *Leishmania* parasites, contributing to an increase of vectorial transmission with decreasing mammal diversity, in accordance with the dilution effect hypothesis.

However, arthropod vector ecology should also be accounted for when investigating the impact of biodiversity changes on a vector-borne disease. In particular, higher vector density should be associated with more frequent host-pathogen contacts and increase transmission (Smith et al., 2012). Additionally, when several arthropod species can act as vectors for a given pathogen, higher arthropod diversity can result in higher pathogen transmission through an overall increase of vector abundance, or due to functional complementarity between vector species (Park et al., 2016; Roche et al., 2013). Given that vertebrates constitute trophic resources for blood-feeding arthropods, it can be expected that arthropod communities are partially driven by the abundance and composition of local vertebrate fauna. This might, however, depend on the ecology of the considered arthropod species. For instance, highly mobile mosquitoes might be little affected by changes in host density, which is a classical assumption in epidemiological models (Dobson, 2004), while ticks may be more sensitive to the presence of suitable hosts in their immediate environment (Ogden & Tsao, 2009; Randolph & Dobson, 2012; Swei et al., 2011; Titcomb et al., 2017). Little is known in this regard for sand flies, which, despite being flying insects, have relatively small flight ranges (Casanova et al., 2005; Morrison et al., 1993). Here, we observed a positive relationship between mammal diversity and sand fly density (Figure 2b), which suggests that sand flies may indeed be affected by changes in local mammal communities. Such a relationship could be mediated by a correlation between mammal diversity and overall mammal biomass, resulting in greater availability of blood meal resources for sand flies in more diverse ecosystems. However, our data does not provide information regarding the absolute abundance of mammals, and it is difficult draw conclusions about the causality of such a relationship since some environmental factors could affect both mammal and

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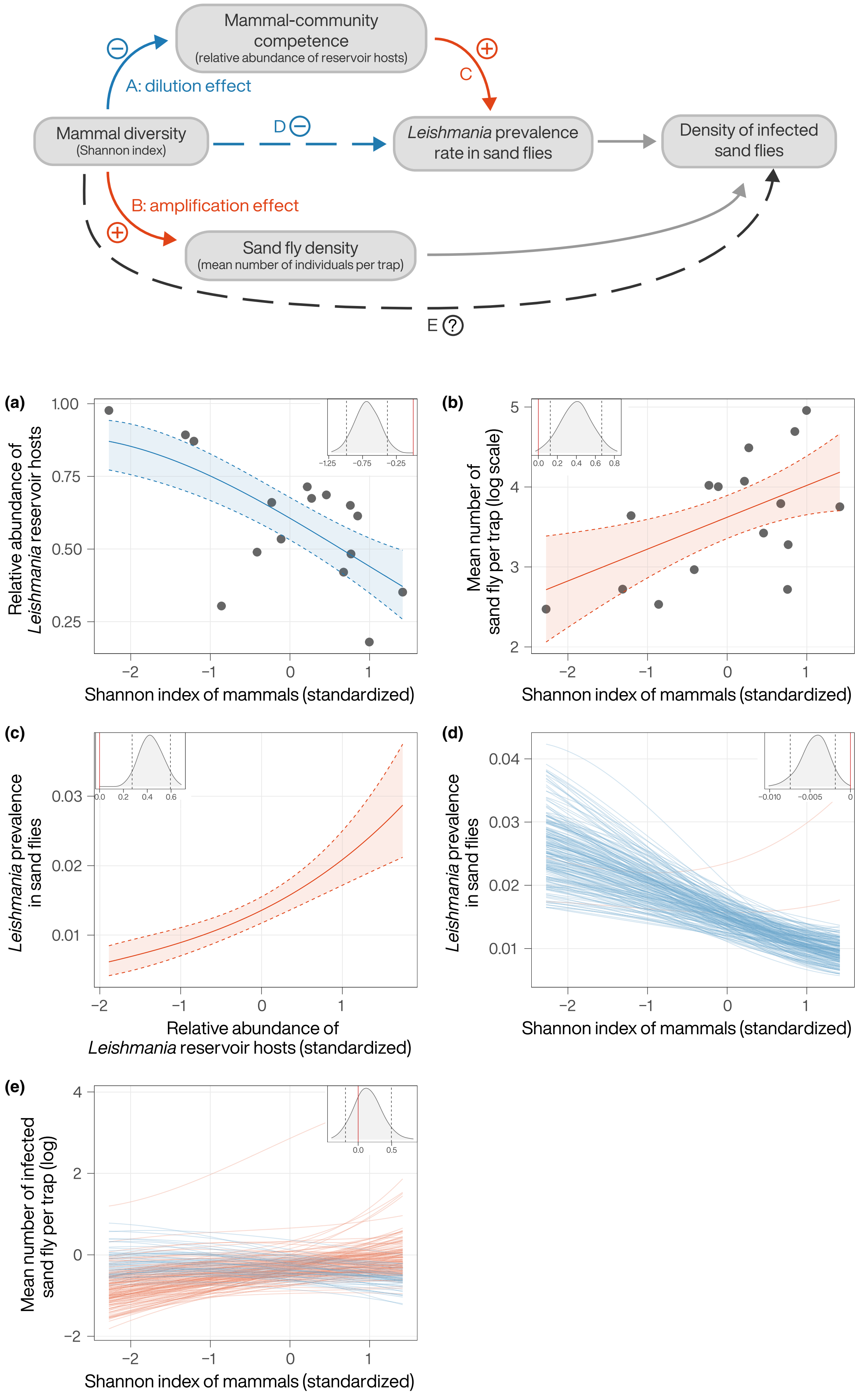

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FIGURE 2 Effect of mammal diversity changes on *Leishmania* transmission, assessed by a series of Bayesian regressions and posterior simulations. The most significant relationships are summarized in the top-panel diagram (but see Figure S7 for the complete model). Direct and indirect relationships are represented with solid and dashed arrows, respectively. Positive, negative, and nonsignificant effects are represented by red, blue and black arrows, respectively. Light grey arrows represent deterministic relationships. For each studied relationship, regression plots are presented and referenced with the corresponding letter in the lower panels. (a–c) Regression curves are depicted with 90% CI, and the posterior density of regression's slopes are represented in inlet plots (dotted lines are positioned at 5 and 95% quantiles; the red line is positioned at $x = 0$). (d, e) The indirect (cumulative) effect of mammal diversity on *Leishmania* transmission was assessed by using posterior samples of model parameters to predict the *Leishmania* prevalence rate and the expected number of infected sand flies per trap. Sampled mean prediction curves are plotted (a subset of 200 curves, in order to facilitate visualization). Curves indicating an overall increase or decrease across the range of predictor values are depicted in red and blue, respectively. Inner plots represent the posterior density of the average slope of mean prediction curves

arthropod species communities. On the other hand, our results point to a negative correlation between mammal and sand fly diversity (although weakly significant; effect 90% CI: −0.38%, 0.00%; Figure S7A), which suggest that different factors might shape mammal and sand fly communities. This further highlights the need for more research to understand the factors shaping sand fly assemblages in sylvatic systems and their potential consequences for *Leishmania* transmission.

Our results did not reveal an effect of sand fly density or diversity on the prevalence rate of *Leishmania* parasites in sand flies (Figures S7B,C). Thus, the proportion of *Leishmania* reservoir hosts in mammal communities appeared as the main driver of *Leishmania* transmission, resulting in a negative effect of mammal diversity on *Leishmania* prevalence rate, through host dilution (Figure 2d). However, the prevalence of a pathogen in vectors is not necessarily a relevant measure of disease transmission, and the density of infected vectors should rather be considered for this matter. For a given prevalence rate, higher vector density should be associated with a higher density of infected vectors. Therefore, the positive relationship observed between mammal diversity and sand fly density across our study sites might act on leishmaniasis transmission in opposition to the dilution effect, which it may attenuate, cancel, or even reverse. This shows that the alteration of mammal diversity is associated with changes in the ecosystem that independently impact *Leishmania* transmission in contrasting ways. Posterior predictions of the density of infected sand flies indicate a weak overall impact of mammal diversity changes on *Leishmania* transmission (Figure 2e). Therefore, it seems that the observed dilution and amplification effects compensate for each other in the system studied here. However, one or the other could predominate in other contexts depending on characteristics of the considered system and environmental conditions that need to be further determined. This constitutes additional evidence that biodiversity changes may impact vector-borne pathogen transmission through concurrent mechanisms, and further stresses the importance of better accounting for arthropod vector ecology in biodiversity-disease research.

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AUTHOR CONTRIBUTIONS

Jérôme Murienne, Arthur Kocher, Benoit de Thoisy, Anne-Laure Bañuls and Jean-François Guégan designed the study. Arthur Kocher, Jérôme Murienne, Jean-Charles Gantier, Agathe Chavy, Benoit de Thoisy, Anne-Laure Bañuls, Marine Ginouves, Ghislaine Prévot, Romain Girod, Isabelle Dusfour and Pierre-Michel Forget conducted the fieldwork. Arthur Kocher and SM performed the laboratory work. Arthur Kocher and Josselin Cornuault analysed the data. Arthur Kocher wrote the initial version of the manuscript, which was edited by Jérôme Murienne, Josselin Cornuault, Benoit de Thoisy and Jean-François Guégan, and all authors contributed to its improvement.

DATA AVAILABILITY STATEMENT

Sample metadata: Data and code used for statistical analyses are available as Supporting Information.

Genetic data: Sequencing data has been deposited at the Dryad database (https://doi.org/10.5061/dryad.44j0zpcfp).

Benefits generated: Benefits from this research accrue from the sharing of our data and results on public databases as described above.

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