Sleeping-tree fidelity of spider monkey shapes community-level seed-rain patterns in continuous and fragmented rain forests

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ABSTRACT

Repeated use of sleeping trees (STs) by frugivores promotes the deposition and aggregation

of copious amounts of seed, thus having key implications for seed dispersal and forest

regeneration. Seed-rain patterns produced by this behaviour likely depend on the frequency

of use of these sites, yet this hypothesis has been poorly tested. We evaluated community-

level seed-rain patterns produced by the spider monkey (*Ateles geoffroyi*) over 13 mo in

latrines located beneath 60 STs in the Lacandona rain forest, Mexico. Because this primate

is increasingly 'forced' to inhabit fragmented landscapes, we tested whether sleeping-tree

fidelity (STF) differed among sites and between continuous and fragmented forests. We

also tested whether seed-rain patterns were associated with STF within each site and forest

type. STF was highly variable among STs (average = 7 mo, range = 1-12 mo), but did not

differ among study sites or forest types. STF was positively associated with seed

abundance, species diversity and species turnover. Nevertheless, STF tended to be

negatively related to seed community evenness. These results are likely due to the most

frequently used STs being in areas with greater food density. Our results demonstrate that

site fidelity shapes community-level seed-rain patterns and thus has key ecological

implications.

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INTRODUCTION

The repeated use of perches, roosting sites, reproductive sites and sleeping sites over time

by frugivorous vertebrates promotes the deposition and aggregation of copious amounts of

seed in these sites (Russo & Augspurger 2004, Wenny 2001). These behaviours have key

implications for seed dispersal and forest regeneration (Jordano & Schupp 2000),

particularly in tropical forests where up to 94% of woody plant species are dispersed by

frugivorous animals (Jordano 1992). The importance of this spatially aggregated pattern of

seed deposition for seed dispersal is largely dependent on site fidelity, that is, on the

frequency of use of these sites over time (Russo & Augspurger 2004, Russo *et al.* 2006);

yet, empirical evidence about this relationship is scarce.

Site fidelity is particularly common in territorial animals (Börger *et al.* 2008), such as

Geoffroy's spider monkey (*Ateles geoffroyi*) (Chapman *et al.* 1995). This primate is a

highly specialized frugivore (González-Zamora *et al.* 2009, Russo *et al.* 2005) that defends

stable home ranges, within which the spider monkey concentrate its activities in areas of

higher quality (i.e. the so-called 'core areas'; Asensio *et al.* 2012a). As multi-central place

foragers (*sensu* Chapman *et al.* 1989), they feed on several plants located near sleeping

trees (STs), and return to the same or different STs after their feeding excursions. An

important fraction of seeds swallowed by these primates are defecated in latrines located

beneath these STs (González-Zamora *et al.* 2014, Russo & Augspurger 2004, Russo *et al.*

2006), particularly beneath in those located within core areas, and hence, variation in

sleeping-tree fidelity (STF) is expected to alter patterns of seed rain within latrines.

Here, we evaluated the frequency of use of 60 STs by *A. geoffroyi* and the seed-rain

patterns produced by this primate during a 13-mo period in two continuous forest sites (CF)

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and three forest fragments (FF) in the fragmented Lacandona rain forest, Mexico. Because

the potential variation between continuous and fragmented forests in STF has not been

previously evaluated, we first tested whether STF (operationally defined as the number of

months each ST is used) differed among the five study sites and between forest types

(continuous and fragmented forests). For each study site and forest type, we assessed the

association between STF and six community-level attributes of seed assemblages

(Tuomisto 2010): abundance of seeds, species diversity of seeds (i.e. species richness,

exponential of Shannon's entropy and inverse Simpson concentration), community

evenness, and seed species turnover (β-diversity) between STs. This information has

critical ecological implications, as *A. geoffroyi* are increasingly forced to inhabit

fragmented landscapes (Ramos-Fernández & Wallace 2008), but we do not know if their

seed-dispersal services may be altered in forest fragments (but see Chaves *et al*. 2011,

González-Zamora *et al*. 2014).

STF of spider monkeys is expected to be higher in forest fragments (González-

Zamora *et al.* 2012), as the home ranges of these primates in fragments are smaller than in

continuous forest sites (Chaves *et al.* 2012). Although it is reasonable to expect that the

abundance and diversity of seeds increase with STF, such associations largely depend on

food availability within the home range. Because the STs most frequently used are expected

to function as key nodes within foraging networks routes that connect core areas (Di Fiore

& Suarez 2007, Suarez *et al.* 2014), we predicted STF to be positively associated with seed

abundance and with all four diversity metrics. Thus, differences between STs in re-use are

expected to result in significant differences in species turnover (i.e. increasing β-diversity)

between STs. Moreover, because the spider monkey shows high selectivity towards the

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consumption of a few genera of plants (Chapman 1988, Milton 1980, Russo *et al.* 2005)

and a large number of species are used opportunistically (González-Zamora *et al.* 2009,

Russo *et al.* 2005), we predicted STF to be negatively associated with community evenness

(i.e. with higher STF the seed rain will be dominated by a fewer species).

METHODS

Study sites

The Lacandona rain forest constitutes the south-western sector of the Mayan forest in

Mexico, and represents a priority area for biodiversity conservation in Mexico and

Mesoamerica (Myers *et al.* 2000). The area is located in the north-eastern portion of the

state of Chiapas, and is delimited by the Guatemalan border on the south and east, and by

the Chiapas highlands on the north and west. Annual precipitation averages 2850 mm, and

average monthly temperatures range between 24°C and 26°C. This region was originally

covered by over 1.4 million ha of rain forest, but deforestation between 1960 and 1990

resulted in the loss of 70% of the original forest cover (Arizpe *et al.* 1993).

Within this region the Montes Azules Biosphere Reserve (MABR) was created in

1978 to protect biodiversity. Adjacent to the southern extreme of MABR, the Marqués de

Comillas Region (MCR) was colonized by humans about 40 y ago and since then MCR has

suffered the rapid loss and fragmentation of the original rain forest (Mora 2008). Currently,

MCR is dominated by different-sized rain forest patches, embedded in a matrix of cattle

pastures, agricultural lands (e.g. corn, oil palm, rubber) and human settlements. The study

was conducted in MCR (eastern side of the Lacantún River; 2039 km^2) and MABR

(western side; 3312 km^2).

Experimental design

Based on a recent study on the density and spatial distribution of sleeping sites, STs and

latrines of the spider monkey (*Ateles geoffroyi*) in the region (González-Zamora *et al.* 2012,

2014), we selected 60 sleeping sites, each composed by one single ST, in two continuous-

forest sites within MABR and three forest fragments in MCR (12 STs per study site). To

increase the independence between the two continuous-forest sites, they were separated by

5 km from each other. The forest fragments FF1, FF2 and FF3 have an area of 1125, 33 and

30 ha, respectively, and were isolated $\geq$ 24 y ago and were immersed in an anthropogenic

matrix of pastures and agricultural lands. The average distance between two fragments was

4.2 km (see further details in Gonzalez-Zamora *et al.* 2012, 2014). We do not have accurate

information on the home range, population size/density and core area size of each primate's

community. Yet a recent study in the same study sites reports that FF1 is occupied by a

community of approximately 40 spider monkeys using a home range of 63 ha, whereas the

communities from FF2 and FF3 have 30 and 39 individuals, respectively, and use the entire

fragment area (Chaves *et al.* 2012). The average home-range size and community size in

the continuous forest of the Lacandona rain forest is 68.4 ha and 40 individuals (Chaves *et

al.* 2012). Unfortunately, we do not have data about the size of core areas in the study sites,

but in Santa Rosa National Park, Costa Rica, Asensio *et al.* (2012b) estimated that spider

monkeys use five core areas of 9.2 ha on average (range = 3.4–19.2 ha) that totalled 46.1 ha

out of the 304 ha of the entire home range.

Seed-rain patterns

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Each selected ST had a single latrine (Gonzalez-Zamora *et al.* 2012, 2014). The STs had a

mean crown projection of approximately 21 ± 21 m^2 (mean $\pm$ SD). This indicates that each

trap covered ca. 3% of the tree crown. Nevertheless, because we located the trap in the

centre of the latrine, which had an average a diameter of 1.5 m (González-Zamora *et al.*

2014), each trap covered approximately 60% of the latrine's area. Traps consisted of a

circular 1.5-m-diameter PVC frame supporting a 0.5-m-deep open-topped nylon mesh bag

suspended 1 m above the ground on three steel posts to prevent the possible predation of

seeds by terrestrial vertebrates. In fact, we did not detect signs of seed predation (i.e. open

husks, teeth marks) in the dispersed seed pool. Although seed traps also captured some

fruits and seeds dispersed by wind or gravity, and would also capture seed dispersed by bird

and bats, we only considered seeds completely immersed within monkey faeces. These

seeds were easily identified in the field based on their typically stained appearance and

characteristic adhesion of faecal matter (González-Zamora *et al.* 2014), thus limiting

greatly the erroneous inclusion of seeds dispersed by wind, gravity, or other animals.

Furthermore, we did not consider seeds < 5 mm in length, which are known to be dispersed

by a wider variety of seed dispersers, including small-to-medium terrestrial mammals, bats

and birds (Janson 1983, Stoner *et al*. 2007), whereas seeds $\geq$ 5 mm in length are frequently

dispersed by primates (Arroyo-Rodríguez *et al.* 2015, Chaves *et al.* 2011, González-

Zamora *et al.* 2014).

During a 13-mo period (1 February 2011-28 February 2012) each trap was emptied

once monthly, and the seeds were collected and afterwards washed for subsequent

identification in the laboratory. All seeds were counted and identified to the species level

based on (1) our own experience with the local flora (from seeds to adults) (Chaves *et al.*

2011, 2012; González-Zamora *et al.* 2012); (2) assistance from a botanical expert familiar

with the flora of the region (G. Ibarra-Manríquez, Universidad Nacional Autónoma de

México, Morelia, Mexico) and a local parataxonomist; and (3) information from seed

catalogues (Ibarra-Manríquez & Cornejo-Tenorio 2010).

Sleeping-tree fidelity

Following Reichard (1998), STF was defined as the number of months each ST was used

during the study period. Given that all traps were checked at the end of each month, the

presence of faeces in the traps was used as an indicator of sleeping-tree use by spider

monkeys during that month. Since all traps were completely emptied each month, we

considered both fresh and old faeces as indicators of sleeping-tree use, thus avoiding the

possibility of overestimating STF. Although our definition of STF does not reflect

accurately the intensity of use of STs (i.e. it would be better to assess STF on a daily or

weekly basis), our results suggest however that our assessment of STF is an appropriate

approximation of the intensity of use, as all community attributes of the seed rain were

significantly related to STF.

Sample completeness

To assess the sample completeness within each ST, we employed the coverage estimator

($\hat{C}_n$) suggested by Chao & Jost (2012), which is a less biased estimator of sample

completeness:

$$\hat{C}_n = 1 - \frac{f_1}{n}\left[\frac{(n-1)f_1}{(n-1)f_1 + 2f_2}\right]$$

where f_1 and f_2 are the number of species represented by one (singletons) and two

(doubletons) individuals in the sample, respectively, and n is the total number of

individuals in the sample. Sample completeness did not differ between sites (Kruskal-

Wallis test, H = 6.7, P = 0.14; mean ± SE: 99% ± 1%, range: 93%-100% per ST). This

indicates that the seed sample was accurate with our sampling effort, and that our results

are not biased by differences in sample completeness among sites (Chao & Jost 2012).

Composition and structure of seed assemblages

Based on our hierarchically nested sampling design (i.e. 60 STs in five sites within two

forest types), we calculated the total abundance and species diversity of seeds for each ST

during the 13-mo period. Patterns of species diversity were analyzed using true diversity

measures (i.e. number equivalents, ^qD). This analytical approach has been recognized as the

most appropriate for diversity comparisons (Chao *et al.* 2012, Jost 2006, 2007; Tuomisto

2010). The formulas are detailed elsewhere (Chao *et al.* 2012, Jost 2006). We considered

true diversities ^0D (species richness), ^1D (exponential of Shannon's entropy) and ^2D

(inverse Simpson concentration). ^0D is not sensitive to species abundances and so gives

disproportionate weight to rare species (Jost 2006, Tuomisto 2010). ^1D weights each

species according to its abundance in the community, and therefore can be interpreted as

the number of 'common' (or typical) species in the community (Chao *et al.* 2012). Finally,

^2D favours very abundant species, and can be interpreted as the number of 'dominant'

species in the community (Chao *et al.* 2012, Jost 2010). These three diversity measures

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were calculated using raw estimators with the 'entropart' package for R (v. 3.1.1) (R Core

Team Development).

We also assessed differences in species dominance among latrines using the evenness

factor proposed by Jost (2010): $EF_{0,2} = {}^2D/{}^0D$. We used this measure because: (1) it is

calculated from true diversity measures; (2) it is independent of the number of species in

the sample; and (3) it is very easy to interpret. It ranges between 1 (when all species are

equally common) and nearly $1/{}^0D$ (when the community is totally dominated by one

species), and can be interpreted as the proportion of dominant species in the community

(Jost 2010).

Statistical analyses

To assess whether STs can be considered independent samples, we used Mantel tests to

correlate the distance between STs with the difference in STF (i.e. differences in the re-use

of different STs). The P-values were calculated using the distribution of the R coefficients

obtained from 10000 permutations. Because the Mantel tests did not detect a significant

spatial autocorrelation of data sets within the continuous forest sites (CF1: r = -0.23, P =

0.05; CF2: r = -0.16, P = 0.17), nor within the forest fragments (FF1: r =0.14, P = 0.24;

FF2: r = 0.02, P = 0.87; FF3: r = 0.10, P = 0.41), we considered the STs as replicates in the

following analyses.

We first tested for differences in STF among sites and between forest types using

analyses of deviance (ANODE) with generalized linear models (GLM). As suggested for

count dependent variables (i.e. number of months), we used a Poisson error and a log link

function, and corrected for data overdispersion (Crawley 2002). We then used analyses of

covariance (ANCOVA) with GLMs to assess the association between each community-

level variable (abundance of seeds, ^0D, ^1D, ^2D, and EF; the dependent variable) and forest

type (categorical factor) and STF (continuous cofactor). The interaction of these two

explanatory variables (forest type × STF) was included in the models to test if the slope of

the association between each response variable and STF differed between forest types. We

also used Mantel tests to evaluate if seed species turnover between STs within each

sampling site was related to the differences between STs in STF. The species turnover

between STs was calculated using multiplicative diversity decomposition of Hill numbers:

$^qD_\beta = {^qD\gamma}/{^qD_\alpha}$ (Jost 2007). These metrics were calculated using the 'entropart' package for

R (<http://CRAN. R-project.org/package=entropart>.) to implement a function to construct

a matrix containing β-diversity values of each pairwise comparison within each sampling

site. Thus, for each ST pair, $^qD\gamma$ was the total (gamma) diversity of the two STs, and $^qD_\alpha$

was the average alpha diversity per ST. This beta can be interpreted as 'effective number of

completely distinct communities' (Jost 2007). In our case, it ranged between 1 (when both

STs showed identical seed rains) and 2 (when the two STs were completely different from

each other).

RESULTS

Sleeping-tree fidelity in continuous and fragmented forests

Overall, STF of spider monkeys was highly variable among sites. It ranged from 3 to 10 mo

in continuous forest sites, and from 1 to 12 mo in forest fragments, but it did not differ

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among sites (GLM; χ^2 = 5.55, df = 4, P = 0.23; Figure 1a) or between forest types (χ^2 =

0.56, df = 1, P = 0.45; Figure 1b).

Association between STF and seed-rain patterns

The generalized linear models showed that STF was positively related to all community

attributes of the seed rain (Table 1; Figure 2). The interaction in the models (forest type ×

STF) was not significant, indicating that this positive association was similar in both

continuous and fragmented forests (Figure 2).

The Mantel tests showed that, in the smallest forest fragments (FF2 and FF3), species

turnover of seeds among STs increased with increasing inter-ST differences in STF (Table

2). This association was also significant in FF1, but only when considering β-diversity of

order 0 and 1 (i.e. $^0D_\beta$ and $^1D_\beta$). Yet, the Mantel tests did not detect a significant correlation

between inter-ST differences in STF and β-diversity for all order q (Table 2).

DISCUSSION

Contrary to our prediction, STF was similar in all study sites and did not differ between

continuous and fragmented forests. This was due to the large variation among STs.

Although STs were used by spider monkeys on average for 7 out of 13 mo, there was a

substantial variation across trees (range = 1-12 mo), which was relatively higher in forest

fragments than in continuous forest sites (Figure 1). Previous studies on the spider monkey

(Chapman *et al.* 1989, Russo & Augspurger 2004, Russo *et al.* 2006) and other primate

species (*Brachyteles arachnoides*: Bueno *et al.* 2013; *Hylobates lar*: Reichard 1998;

Gorilla gorilla: Rogers *et al.* 1998; *Lagothrix lagothricha*: Stevenson 2000) also indicated

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that the use and re-use of STs can be highly variable, with some trees used for long periods, while others only used occasionally (Anderson 1984, 2000; Reichard 1998, Teichroeb *et al.* 2012). In the case of the spider monkey, this pattern results from its temporal and spatial foraging behaviour in different areas with a high concentration of food trees within the home range (Asensio *et al.* 2012b, Ramos-Fernández *et al.* 2013), and then routinely returning at night to the same or different STs located in proximity to these areas with greater food density (i.e. multiple central-place foraging; *sensu* Chapman *et al.* 1989). This behaviour allows the monkey to monitor the resources for future usage (Asensio *et al.* 2012a) and to move back to its STs using route-based mental maps (Di Fiore & Suarez 2007, Ramos-Fernández *et al.* 2004, Suarez *et al.* 2014), thus minimizing travel time (Asensio *et al.* 2012b, Chapman 1989, Teichroeb *et al.* 2012). Yet, during territorial defence (Chapman *et al.* 1995, Wallace 2008), or exploration to monitor feeding sites at a great distance (Di Fiore & Suarez 2007, Ramos-Fernández *et al.* 2004, Valero & Byrne 2007) males of *A. geoffroyi* can use STs for short periods because they usually do not return to the same ST (Ramos-Fernández *et al.* 2004), possibly explaining the low fidelity found for some STs in our study. Therefore, as reported for other primate species (Heymann 1995, Pontes & Soares 2005, Reichard 1998, Sigg & Stolba 1981, Silva Júnior *et al.* 2009, Smith *et al.* 2007), the high variation in STF in the Lacandona rain forest is most likely related to the spatial and temporal changes in the concentration and distribution of food resources and sex differences in the use of space by the spider monkey.

The relatively higher variation in STF in forest fragments than in continuous forest sites can be related to food scarcity in forest fragments (Arroyo-Rodríguez & Mandujano

2006, Chaves *et al.* 2012). In particular, fruit availability is known to be lower in forest fragments than in continuous forest because of the combination of both a lower density of large food trees (dbh > 60 cm), which represent larger fruit patches (Chapman *et al.* 1992), and smaller home-range sizes in fragments (Chaves *et al.* 2012). Thus, the spatial variation in resource availability is expected to be higher in forest fragments than in continuous forest. As consequence, in forest fragments, the STs that are located in areas with higher availability of resources would be used relatively more often than in continuous forest sites, whereas the STs that are located in areas with lower availability of resources would be used relatively less intensively than in continuous forest sites. Consistent with this idea, we found that in forest fragments 15 out of 36 STs were used for 9-12 mo and five were only used for 1-3 mo. In continuous forest, however, all STs were used for between 3 and 10 mo (Figure 1).

The lower variation in STF in continuous than in fragmented forest can explain why seed β-diversity between STs did not increase with increasing inter-tree differences in STF in continuous forest sites. It is well known that the lack of variation in explanatory variables (STF in our case) result in weaker associations between explanatory and response variables (species turnover in our case) (Eigenbrod *et al.* 2011). As discussed above, the lower variation in STF in continuous forest sites may be associated with higher availability of resources in this sites when compared to the smallest fragments, which in turn can contribute to reduce β-diversity between STs within the continuous forest. In contrast, higher spatial variations in the availability of food resources may contribute to increase the

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differences in STF in fragments, and also to significant compositional differentiations in

seed assemblages between sleeping trees (González-Zamora *et al.* 2014).

In agreement with our predictions, STF was positively related to the abundance and

species diversity of seeds in all sites, indicating that the more often a ST is used, the more

seeds from a larger variety of species are deposited under it. Such associations can be

explained by the changes in the frugivorous diet along the year (Chaves *et al.* 2012,

González-Zamora *et al.* 2014) and by the spatial location of the STs in relation to foraging

routes used by spider monkeys (Di Fiore & Suarez 2007, Suarez 2003, Suarez *et al.* 2014),

resulting in an increase in the abundance and species diversity of seeds. In conclusion, our

results suggest that the spatial configuration of seed communities deposited in latrines

depends on the specific location of STs in foraging paths (Di Fiore & Suarez 2007), and by

the spatial and temporal variation in territory quality (Asensio *et al.* 2012a,b).

STF was negatively related to community evenness in all study sites. As expected,

this finding can be related to the fact that the the seeds in the latrines below more frequently

used STs reflect the common feeding pattern of the species, i.e. there is a high selectivity

towards the consumption of a few genera of plants (Chapman 1988, Milton 1980, Russo *et al.* 2005) and the opportunistic use of a large number of other fruit species (Dew 2008,

González-Zamora *et al.* 2009, Link *et al.* 2012, Nunes 1998, Russo *et al.* 2005), thus

reducing the number of common and dominant species, as well as the seed community

evenness.

Conclusions and implications for seed dispersal

Our study demonstrates that STF is a key factor shaping the seed-rain patterns produced by the spider monkey below STs. Therefore, changes in STF (e.g. those associated with logging or habitat fragmentation) could have important implications for seed dispersal and forest regeneration. Of course, this constitutes a very important avenue for future research, as we still do not have data on seed germination, and seedling recruitment and growth in and around spider monkey latrines differing in re-use.

Although we found no differences in STF between continuous and fragmented forests, further studies in highly fragmented landscapes are required to accurately test if STF can be altered in more fragmented landscapes. Deforestation in the study region is moderate (ca. 40% of remaining forest cover), and forest remnants still maintain most of their original vegetation composition and structure (Hernández-Ruedas *et al.* 2014), which may contributed to the apparent lack of differences in STF between forest types.

If STF is higher in fragmented forests, our results indicate that the effectiveness of the spider monkey as a seed disperser (*sensu* Schupp 1993) would change as a result of the increased aggregation of seeds in latrines found in our study. Nevertheless, this will depend on the impact that such increase in seed/seedling aggregation has on seed germination and seedling recruitment. We can anticipate two alternative scenarios. First, because we found that STF is negatively related to community evenness, higher STF would result in a seed rain dominated by a few seed species. Thus, based on the Janzen-Connell model (Connell 1971, Janzen 1970), we would expect higher seed predation (e.g. by rodents, insects, and/or pathogens) toward the most dominant species, which could reduce predation pressure on less abundant species allowing the recruitment of rare species in latrines that are more

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frequently used. Second, an alternative scenario suggests that the low rate of seed arrival in STs less frequently used may allow seeds to avoid the presence of biotic mortality agents, offsetting the lower seed/seedling survival that is expected in such conditions (Bravo 2012, Russo & Augspurger 2004). Since the seed community structure and composition can be decisive for the initial stages of recruitment (Russo & Augspurger 2004, Schupp *et al.* 2010, Wang & Smith 2002), our results call for further studies to assess the persistence of seeds and recruitment of seedlings under different levels of evenness in the seed bank of latrines and to determine which of these two scenarios occurs with increasing STF.

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Table 1. Effect of sleeping-tree fidelity (STF) of *Ateles geoffroyi* on five community-level seed-rain patterns produced by this primate below sleeping trees located in two forest types (continuous forest and forest fragments) in the Lacandona rain forest, Mexico. The effect of STF, forest type and the interaction between the two was tested with Generalized Linear Models.

Response variable/factors	df	χ^2	P
Abundance of seeds			
STF	1	31.3	<0.001
Forest type	1	3.91	0.048
Forest type × STF	1	0.74	0.389
Species richness			
STF	1	40.4	<0.001
Forest type	1	0.01	0.891
Forest type × STF	1	0.36	0.547
Exponential Shannon entropy			
STF	1	19.4	<0.001
Forest type	1	0.27	0.602
Forest type × STF	1	0.002	0.963
Inverse Simpson concentration			
STF	1	11.8	<0.001
Forest type	1	1.42	0.233
Forest type × STF	1	0.44	0.506
Evenness factor			
STF	1	10.6	0.001
Forest type	1	3.33	0.068
Forest type × STF	1	0.002	0.966

Table 2. Correlations between species β-diversity of seeds between sleeping trees and inter-tree differences in sleeping tree fidelity in two continuous forest sites (CF) and three forest fragments (FF) in the Lacandona rain forest, Mexico. The correlation coefficients were calculated with Mantel tests (*P < 0.05;** P < 0.001, after applying a stringent Bonferroni correction to reduce the likelihood of type I statistical errors). $^qD_\beta$ represents the species turnover between sleeping trees, considering three orders q (0, 1 and 2), which determine the sensitivity of each β-diversity component to the relative abundances.

β-diversity component	CF1	CF2	FF1	FF2	FF3
$^0D_\beta$	-0.001	0.182	0.374**	0.542**	0.400**
$^1D_\beta$	0.003	-0.052	0.244*	0.385**	0.453**
$^2D_\beta$	0.083	-0.125	0.175	0.302*	0.523**

Figure legends

Figure 1. Sleeping-tree fidelity of *Ateles geoffroyi* in continuous (CF) and fragmented (FF) forests in the Lacandona region, Mexico. Differences among sites (a) and between forest types (b) are shown.

Figure 2. Effects of sleeping-tree fidelity of *Ateles geoffroyi* on five community-level attributes of seed assemblages in continuous (CF) and fragmented forests (FF) in the Lacandona region, Mexico. a) Abundance of seeds, b) Species richness, c) Exponential Shannon's entropy, d) Inverse Simpson concentration and e) Evenness factor.
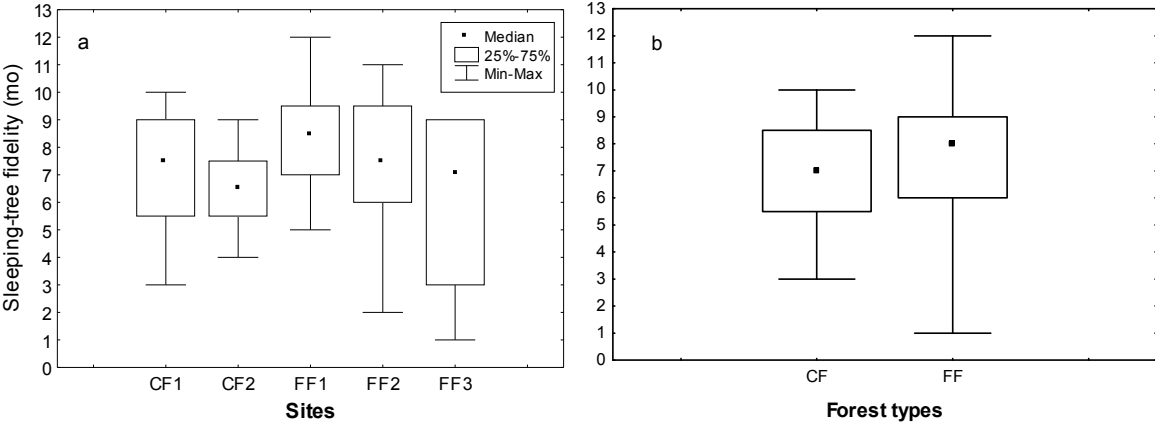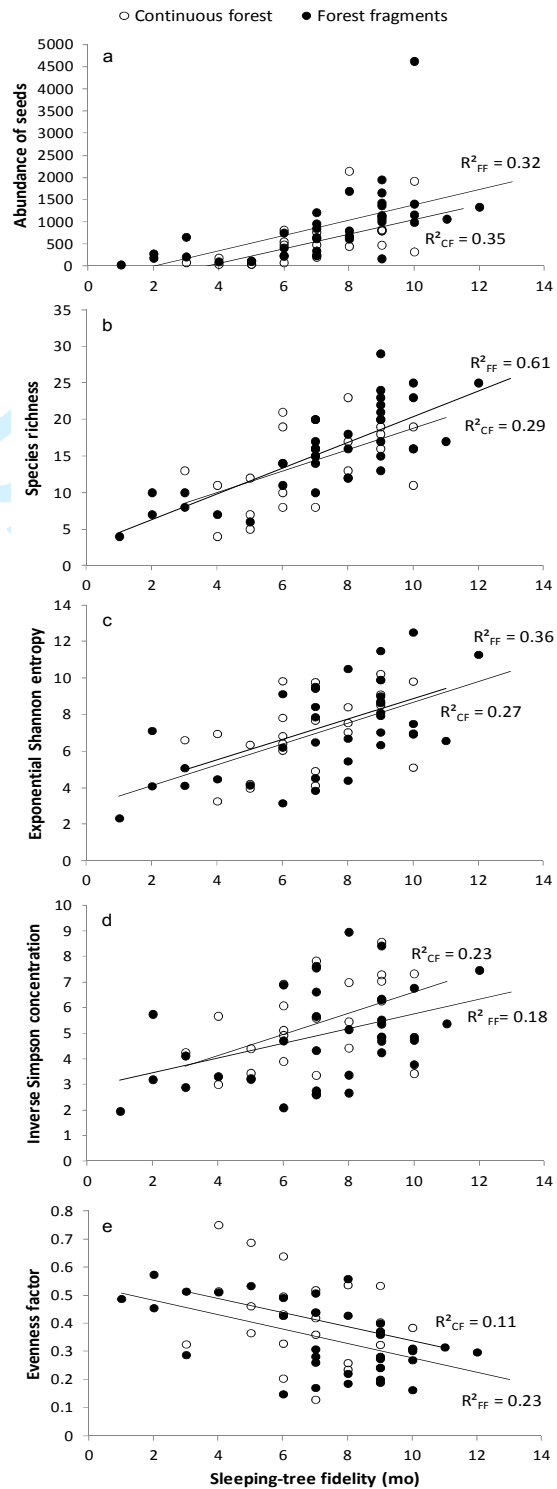
Figure 1

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Figure 2

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