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Research Article

Biological correlates of extinction and persistence of primates in small forest fragments: a global analysis

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Abstract

Habitat loss and fragmentation are two of the main threats facing wildlife. The species at risk in small fragments are not a random subset of the original community. Understanding the biology behind the distinction between species at risk and more persistent species should help inform conservation efforts. We attempted to identify risky traits in a well-known taxon, the primates, by asking which traits distinguished taxa that differed in the size of the smallest fragment in which they were recorded. We assumed that taxa that could persist in smaller fragments were at less risk of extinction than those that needed larger fragments. The traits investigated are indicative of amount of habitat needed, reproductive rate, and specialization. We obtained from the literature information on the presence-absence of 68 primate species of 36 genera in forest fragments of less than 100 km^2. Association between size of smallest fragment and biology was tested with regressions, Spearman correlations, two-sample *t* tests, and non-parametric Wilcoxon tests. We found no significant relationships between area of smallest fragment in which species or genera persisted and any of the biological parameters. We suggest that the most likely explanation for this unexpected finding is that the smallest fragments in which primates are currently studied are usually so small that all primate species in them are doomed in the long-term and therefore, no biological traits distinguish taxa at risk. The finding implies that conservation research and efforts should be directed at assessing the efficacy of forest fragments and small biological preserves in conserving primate species.

Key words: biogeography, conservation, fragmentation, primates.

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Introduction

Habitat loss and fragmentation are associated with fewer resources, greater isolation, and more intense and far-reaching edge effects [1], and both are considered major threats to wildlife. In brief, smaller areas often contain fewer taxa than do larger areas [2]. Conservationists have known for a long time that the species at risk in small fragments are often not a random subset of the original community [3, 4]. Understanding of the biology of extinction, of why some species are more at risk than are others under the same environmental change, should help refine conservation efforts, [5-7]. Nevertheless, knowledge of the biology of susceptibility is far from complete.

Our aim here is to contribute to the understanding of the biology of extinction by elucidating the risky traits in an unusually well-known taxon of tropical forest mammals, primates. Primates are no different from other taxa in that they often suffer from loss and fragmentation of their habitat [8-10]. The traits that enhance extinction risk can change with the nature of the threat [11-13]. We here analyze in more detail than hitherto, and over a broader geographical range, the traits that distinguish primate taxa susceptible to fragmentation from those that are less susceptible.

We do so by comparing taxa that differ in the size of the smallest forest fragment in which they have been recorded as present. Our assumption was that taxa that are present and thereby assumed as persisting (in this study) in smaller fragments are less susceptible to extinction than are taxa that need larger fragments in which to persist.

Whether fragmentation is a threat varies not just with the size of the fragment, but of course with many other factors, such as isolation by both distance and the nature of the matrix, the amount of viable habitat within a fragment, and the nature of human-caused disturbance [14, 15]. Nevertheless, we correlate biological traits that distinguish extinct from persistent taxa only with size of fragment. Our justification is two-fold. First, the area of a fragment will often correlate with many of the other factors, such that, for example, small fragments are situated in more adverse matrices [16]. Second, the fact that the species-area relationship is usually so obvious, despite all the potential confounds, indicates that correlating only area with probability of extinction and thence biological traits of risk should be usefully informative.

From previous analyses of the biology of extinction of primates, we predicted that primates with greater body weights, greater group masses, larger group sizes, lower population densities, larger annual home ranges, slower rates of reproduction, more specialized diets and habitats, lower maximum altitudes and latitudes, and smaller geographic ranges will be more likely to suffer extinction, and therefore will be found only in larger fragments [3, 4, 8, 17-20].

Methods

Data and sources

To test whether there are biological traits that predispose primates in forest fragments to extinction, we compared the biological traits of 65 primate species from 36 genera that are found in forest fragments ranging from less than 1 km^2 to our defined upper limit for a fragment of 100 km^2 (Table 1). Taxa in this study include primates from Asia (5 genera, 12 species), Africa (9 genera, 15 species), Madagascar (9 genera, 9 species), and the Americas (13 genera, 32 species).

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Definitions of what size of area constitutes a fragment are of necessity more or less arbitrary. An analysis of minimum area requirements for long-term persistence of Asian primates indicated that only the small-bodied loris (Nycticebus) and a widespread weed species of macaque (Macaca) persist on islands of less than 100 km^2 [21]. We therefore chose≤ 100 km^2 as the definition of a fragment. Data from which we calculated minimum size of fragments are from sources listed in the online appendix of Harcourt and Doherty [9].

We obtained from the literature the data on the biological traits for each species, 15 traits in total. In brief, we predicted, based on many peoples' past work on a variety of mammalian taxa, that taxa which (a) require a lot of resources, (b) breed slowly, or (c) are specialized, are less likely to persist in the face of fragmentation of their habitat. In other words, the minimum fragment size in which they were recorded would be larger than the minimum fragment of less-susceptible taxa. Traits indicative of the amount of resources needed were: body mass (kg), group mass (kg), adult group size (# of adults), population density (# individuals per km^2), and annual home range (km^2). Traits indicative of reproductive rate were: age at first reproduction (years), birth interval (years), r_{max} (intrinsic rate of natural increase), and maximum lifespan (years). Traits indicative of the degree of specialization were: frugivory (as a percentage of total diet), number of different items in diet, number of different habitats used, maximum altitude (m), maximum latitude (degrees), and geographic range (km^2). Preference was given to biological data from long-term studies in the wild, but some data were from captivity.

Analysis

The aim was to test if any of the 15 biological traits predicted the size of the smallest fragment in which a species or genus was reported to exist. The traits are not independent of one another. For instance, body size is correlated with many of them, including annual home range, adult group mass, and all the reproductive variables. The reproductive variables all correlate closely with one another as do geographic range and maximum latitude. Nevertheless, we initially analyzed the traits separately, because correlations and disjunctions in the traits associated with extinction are in themselves informative [18, 19].

Only the Americas had a median sample size per trait of greater than 20, and therefore large enough in our estimation to be analyzed separately. Consequently, we combined results from all continents in a global analysis, and conducted a separate analysis only on the Americas.

We performed four forms of statistical tests, with JMP 6.0 [22]. The analysis of regression (of size of smallest fragment on trait) was the most sensitive test used, but its requirement for normality of error on the Y-axis was not always met by our dataset. Therefore, we also conducted non-parametric Spearman correlation tests.

In order to increase the chances of detecting a difference in biology of vulnerable and less vulnerable taxa we also compared taxa in only the lowest and highest quartiles of minimum fragment size. Again, and for the same reasons as stated already, we used both a parametric two-sample test, the *t* test, and a non-parametric one, the Wilcoxon test (equivalent to the Mann-Whitney *U* test).

We performed these tests at both the level of species and the level of genera. Some object to using genera as data. Justification for doing so is given in detail elsewhere [23, 24].

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To test the results for species independently of any phylogenetic constraints, we used the Comparative Analysis by Independent Contrasts (CAIC) software [25], version 2.6.9. We performed the test using 10 of the original 15 biological variables. We omitted the reproductive variables because they all correlate so closely with body mass; and we omitted group size, because we considered group mass to be a better indicator of resource requirements. Using the biological trait as the predictor variable, we then ran analyses of regression on these contrasts.

A lot of splitting has occurred in primate taxonomy in the last two decades [26]. It is almost entirely a result of raising sub-species to the level of species. Because data are unavailable for so many of these former sub-species, we largely ignore the new taxonomy. Instead, the phylogeny used in CAIC is based on Purvis' [27, 28], with alterations made to account for the split of the Asian colobines into *Trachypithecus* and *Presbytis* [29, see also 30], and the separation of *Lophocebus* from *Cercocebus* [31]. Branch lengths (i.e., times from evolutionary splits and therefore times available to change), are as in Purvis [27]. The added colobine splits were timed at the relative midpoints of the branches following the *Semnopithecus* branch (*Presbytis entellus* in Purvis' [27] phylogenetic tree). *Lophocebus* was placed as a branch of *Papio* [31]. Finally, without humans in the sample, it seemed sensible to retain the old family of Pongidae, rather than split it into the Ponginae and Paninae.

With so many tests performed on so many variables, some significant results could be expected by chance. We did not count as significant any probability value of > 0.05 after Bonferroni-correction, i.e., after multiplying dividing the P value by the number of tests. In science, it is bad practice to allow an outlying minority of the data to influence the statistical result. Hence the existence of outlier detector facilities in statistical programs. We used JMP's Mahalanobis outlier detection facility to eliminate outliers from analysis. All reported probability values are two-tailed.

Results

With a sample of 65 species globally for which we had information on the minimum size of forest fragment occupied, we found, without phylogenetic correction, only one significant biological correlate of extinction risk among the 15 biological traits tested: species with fewer categories of habitat occupied were found less in the smallest fragments (Table 1A). For South America, only the number of dietary categories significantly predicted size of the smallest fragment occupied. One of 15 variables significant is close to what one might expect by chance, and indeed Bonferroni correction produced a non-significant result.

At the level of genus, we found no significant relationships between the smallest fragment area in which genera persisted and any of the 15 biological parameters in 36 genera (Table 1B).

Accounting for phylogeny with CAIC, and after removal of outliers, only the number of dietary items was significantly related to minimum fragment size (Table 2). This variable, though, was not significant in the direction we had predicted: species with fewer dietary categories existed in smaller fragments. Again, Bonferroni correction made the result non-significant.

With no reliable significant association detected between size of smallest-fragment occupied and any one biological trait, we did not deem it useful or sensible to conduct multi-variate analyses to search for any minimum model of traits to explain contrasts between taxa in the size of the smallest fragment that they were recorded to occupy. Such analyses would find a minimum model (they always do), but we do not consider that it would be meaningful.

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Discussion

Across many taxa, several variables, such as home range size, body size, population size, reproductive rate, and specialization, have fairly consistently emerged as important biological indicators of extinction risk in a variety of sorts of analysis, and despite a considerable number of ignored confounding variables. Nevertheless, in this analysis of the biology of extinction of primates in small forest fragments, we found no obvious biological trait of risk. In other words, no obvious trait distinguished taxa liable to extinction in small fragments of habitat from those able to persist. Certainly we have not tested all possible traits, nor have we used all possible statistical means to discern potential traits of risk. However, the more traits and the more tests, the more likely is a spurious finding without correction for number of traits and tests. With correction, the influence of the trait would have to be so large that any effect would, we suggest, have already been detected via its correlation with the already tested traits.

One possibility for the finding of no association between biology and risk of extinction as measured here is that, in this analysis, confounding factors were so influential that the traits of risk were hidden. Obvious ones are the variable quality of the original data (a potential problem with all comparative analyses), other influences (such as isolation of fragments), ignorance of variation of habitat quality within fragments, the surrounding habitat amount [32], and of course, the influence of the nature of the matrix between fragments. Therefore, the dependent variable (i.e., size of the smallest forest fragment occupied) could be highly limited by the fact that we did not control for all these potential confounding factors, potentially masking the effect of fragment size on the persistence of primates in fragments. However, as the sources on presence-absence of species in fragments were the same as those that indicated significant species-area relationships in a previous analysis [9] (in which both isolation and age of fragment were accounted for), we do not think that this is a sufficient explanation.

Alternatively, we suggest that many studies of primates in fragments are being conducted in fragments too small for long-term persistence of any primate (global median of 1 km^2) and therefore, too small to produce a difference in probability of extinction between species. All the species in the fragments are extinction-prone. Other workers, using other approaches, have also suggested that all species will go extinct in fragments as small as the majority in which studies of effects of fragmentation are usually conducted [9, 33-39]. The fragments are in extinction debt [40].

The conclusion that most research on effects of fragmentation on primates is being conducted in fragments in which all species will eventually go extinct does not mean that research on primates in small fragments is useless. It will elucidate the biology of the immediate responses of primates to deterioration of habitat, knowledge of which is extremely useful to understanding both the process of evolution, and to more precise implementation of conservation efforts. However, the sort of comparative analysis conducted here, which is designed to detect gross contrasts between species that might indicate longer-term traits of risk, will probably be more successful if conducted in fragments of at least ten square kilometers, maybe more. We make this suggestion because a polynomial regression of proportional richness (richness in fragment as percent of richness in nearby main forest block) against area of fragment in the Americas asymptoted at about 25 km^2. The global analysis, however, showed no asymptote even by 100 km^2.

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Implications for conservation

Our conclusion that data from small fragments are not useful for presence-absence analysis as a means to elucidate the biology of extinction risk most certainly does not mean that small fragments are useless for conservation. They can certainly be useful [41]. For instance, Tutin and coworkers found that some primate species might even benefit from the lack of competitors in small fragments [42, 43]. Additionally, animals in fragments can be easier to find than ones in the main forest, with the consequence that fragments can be and are valuable for purposes of conservation education and publicity, as well as providing revenue for local communities or conservation management institutions.

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Table 1 - Smallest fragment sizes that allowed for persistence and 15 biological characteristics for 65 species of primates from Asia, South America, Africa, and Madagascar. BM = body mass, GM = group mass, AGS = adult group size, PD = population density, AHR = annual home range, AFR = age at 1st reproduction, IBI = inter-birth interval, RM = r_{max}, ML = maximum lifespan, FG = % frugivory, DT = number of dietary categories, HT = number of habitat types, MAL = maximum altitude, MLT = maximum latitude, GR= geographic range. Hundreds of sources have contributed to the data. The authors are happy to respond to individual requests.

Asia Genus	Species	Frag. (km2)	BM	GM	AGS	PD	AHR	AFR	IBI	RM	ML	FG	DT	HT	MAL	MLT	GR
Hylobates	hoolock	4.93	6.3	13	2	7	0.23	5.5	.	.	.	.	1	2	1370	28	794502
Hylobates	lar	0.7	5.4	11	2	6.4	0.44	8	2.25	0.08	31.5	57	4	4	2400	25	761935
Macaca	assamensis	4.93	6.9	.	.	.	.	.	.	.	.	.		3	3500	31	1566864
Macaca	fascicularis	0.7	3.3	38	11.5	35	0.8	3.9	1.08	0.22	37.08	76	3	5	2000	19	2535830
Macaca	nemestrina	0.7	6.4	186	29.3	11.7	0.68	3.92	1.1	0.23	26.30	83	4	5	1700	29	3126868
Macaca	silenus	0.24	.	.	17	9	.	5.45	1.6	0.17	38	.	1	3	1500	15	35074
Presbytis	melalophos	0.7	6.4	39	6	57	0.16	.	.	.	.	60	4	1	.	14	657385
Symphalan	syndactylus	3.04	10.6	21	2	6	0.35	6	3	0.08	35	46	*2*	*4*	3800	6	203708
Trachypith.	francoisi	68	7.3	.	.	.	.	.	.	.	.	.		1	.	22	173639
Trachypith.	johnii	0.01	11	55	5	89	0.24	.	.	.	.	.	3	4	2400	13	24265
Trachypith.	obscurus	0.7	6.4	54	8.5	72	0.33	4.5	.	.	.	47	3	3	1830	14	235073
Trachypith.	pileatus	4.93	10.4	60	5.75	18.6	0.16	3	2	.	.	46	2	2	.	28	445302

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Table 1 continued

Africa	Species	Frag.	BM	GM	AGS	PD	AHR	AFR	IBI	RM	ML	FG			MAL	MLT	GR
Cercocebus	galeritus	88.58	5.5	77	14	237.5	0.75	6.5	.	.	19	.	3	3	.	2	3905
Cercopith.	ascanius	0.05	2.8	.	.	57.4	0.29	5	1.65	0.09	22.5	54.6	2	4	2000	12	2813948
Cercopith.	cephus	0.09	2.8	.	.	21.8	0.45	4	.	.	22	27	3	3	200	7	750108
Cercopith.	mitis	0.59	3.8	35	9	41	0.23	5	1.13	0.18	20	58	4	4	3300	34	4181221
Cercopith.	nictitans	0.09	3.9	.	.	25.7	0.62	4	.	.	.	34	3	3	200	10	1619860
Chlorocebus	aethiops	0.02	3.3	21	6.5	95.8	0.15	2.5	1	0.24	31	71	4	3	.	35	14393689
Colobus	angolensis	2	6.7	20	3	6.9	.	.	.	.	.	.	3	2	3000	12	2046016
Colobus	guereza	0.01	8.4	29	3.5	15.3	0.215	4.58	1.46	0.2	22.25	16.7	2	4	4500	13	2366022
Galago	senegalensis	0.18	0.23	.	.	31	0.06	0.56	0.55	0.5	16	.	2	4	2000	16	7854605
Galagoides	demidoff	6	0.06	.	.	65	0.51	14	0.9	0.54	14	20	3	5	2000	10	4354800
Galagoides	orinus	11	.	.	.	.	.	.	.	.	.	.			.	.	.
Pan	troglodytes	0.01	37.7	.	.	1.5	17	12	5	0.08	44.5	72.7	2	4	1590	14	2498031
Papio	cynocephalus	0.18	11.8	330	28	6.8	16.7	6	1.75	.	40	.	3	3	1000	21	3799689
Procolobus	badius	2	8.2	139	17	178.2	0.6	4.08	1.43	0.15	.	22.8	4	1	.	14	2261398
Procolobus	pennentii	0.01	.	.	.	.	1.14	.	.	.	.	.	2		.	.	

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Table 1 continued

Madagascar Genus	Species	Frag. (km2)	BM	GM	AGS	PD	AHR	AFR	IBI	RM	ML	FG	DT	HT	MAL	MLT	GR
Avahi	laniger	0.42	1.3	.	.	72	0.01	.	1	.	.	25	1	2	.	25	92975
Cheirogaleus	medius	6	0.2	.	.	143.5	.	1	1	0.64	9	85	2	3	.	26	146401
Eulemur	fulvus	38.26	2.2	18	8	19.8	0.01	0.83	1.5	0.22	30.8	29	2	2	1125	25	247587
Hapalemur	griseus	0.41	0.8	2	2	54.5	.	2.38	.	.	12.1	.	1	4	1000	25	132946
Lepilemur	ruficaudatus	0.06	0.75	.	.	.	.	.	.	.	.	25	2	2	.	24	58312
Microcebus	murinus	0.28	0.07	.	.	214	0.02	0.87	0.93	0.74	15.5	.	3	4	.	26	172074
Mirza	coquereli	0.06	0.3	.	.	130	.	0.75	1	.	.	.	2	3	.	24	38555
Phaner	furcifer	0.06	0	.	.	.	0.4	0.42	0.4	.	2	25				.	
Propithecus	verreauxi	6	3.6	13	3.5	107.5	0.08	2.5	1	0.27	.	48	2	3	.	26	203449

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Table 1 continued

S. America Genus	Species	Frag. (km2)	BM	GM	AGS	PD	AHR	AFR	IBI	RM	ML	FG	DT	HT	MAL	MLT	GR
Alouatta	belzebul	1.15	5.3	.	.	.	.	.	.	.	.	.	1	1	.	10	1739957
Alouatta	fusca	4.4	4.6	39	9	16	0.06	.	.	.	.	.	3	2	1100	31	838962
Alouatta	palliata	0.02	5.8	48	8.25	15	0.07	3.38	1.83	0.17	13	46	3	4	2000	19	565443
Alouatta	seniculus	0.095	5.5	25	4.5	23.5	0.22	4.5	1.38	0.81	25	42	2	5	3200	20	5797451
Aotus	infulatus	2.1									22						3361500
Aotus	trivirgatus	6	0.8	2	2	25	.	2.5	0.8	0.34	12.6	73	3	1	3200	8	837288
Ateles	belzebuth	0.14	8.4	38	4.5	13.5	3.24	.	2.08	.	.	83	2	3	.	13	2273794
Ateles	chamek	1.6	9.3		20.5		1.92		2.83			76	2			19	1888606
Ateles	geoffroyi	0.8	7.9	35	4.5	20.8	1.08	6	2.73	0.1	20	80	3	1	.	24	848910
Ateles	marginatus	3	.	.	.	.	.	.	.	.	.	.			.	7	369064
Ateles	paniscus	0.1	8.4	32	3.75	22.4	2.2	4.8	3.83	0.11	33	88.8	1	3	2500	7	960112
Brachyteles	arachnoides	32.6	8.8	144	16.4	2.9	1.68	7.5	2.82	0.12	.	35	3	3	1500	24	430892
Callicebus	moloch	0.3	1	2	2	.	.	3	1	0.23	12	71	2	4	850	25	4055000
Callicebus	personatus	3.32	1.3	3	2	7.2	.	.	.	.	.	.	2	1	1100	23	629616
Callithrix	argentata	0.3	0.3	.	.	5.5	0.3	1.67	0.62	0.7	.	75		2	.	20	1019439
Callithrix	aurita	56.5	.	.	.	.	.	.	.	.	.	.			.	24	173463
Callithrix	flaviceps	4.4	.	.	.	23.6	.	.	.	.	.	.	3		.	22	43191
Callithrix	geoffroyi	7.45	0.3	.	.	34.8	.	.	.	.	.	.			.	20	123320
Callithrix	jacchus	1.54	0.31	3	8.5	700	0.05	1.54	0.43	0.84	12	.	2	4	1100	12	659394
Callithrix	penicillata	0.3	0.3	1	3.5	.	.	.	.	.	.	.	2		.	23	1311306
Cebus	albifrons	0.14	2.2	25	11	11.3	1.35	3.59	1.33	0.18	44	44.5	3	3	2000	15	3885397
Cebus	paella	3.32	2.4	34	14	14.1	1.5	3.5	1.83	0.14	40	36	3	4	2700	30	12095314
Cebus	capucinus	6	28		15	28	0.86	4	1.58	0.17	46.9	62	3	3	2100	16	423890
Chiropotes	Albinasus	3	2.5	35	14	.	.	.	.	.	15	.	2	3	203	10	665821
Chiropotes	satanas	37.505	2.6	.	.	6.1	.	.	.	.	.	.	3	3	161	9	2057351
Lagothrix	lagotricha	1.6	6.3	185	29.5	10.5	4	8.08	1.97	0.16	12	80	4	2	3000	15	3578219

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Table 1 continued

S. America Genus	Species	Frag. (km2)	BM	GM	AGS	PD	AHR	AFR	IBI	RM	ML	FG	DT	HT	MAL	MLT	GR
Leontopith.	chrysopygus	17	.	.	.	1.2	.	.	.	.	.	.	2	1	.	23	47722
Pithecia	pithecia	0.545	1.5	.	.	3.4	0.07	2.08	1	0.2	13.7	.	3	3	350	9	1781470
Saguinus	leucopus	0.01	0.5	4	8.5	8.8	.	.	.	.	.	.	1	2	1500	9	58843
Saguinus	midas	0.545	0.5	3	6	11	0.09	1.67	0.66	0.6	13	47		3	.	9	1622298
Saguinus	oedipus	6	0.4	3	7	44.3	0.09	1.5	0.77	0.64	13	.	3	3	1500	11	49759
Saimiri	sciureus	0.9	0.8	17	22	29.7	0.65	3.2	1.13	0.25	21	19	2	3	2000	19	5860558

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Table 2A. Results of all statistical tests done on the relationship of 15 biological traits to the smallest fragment area in which a species was extant. Table 2A, Species. Table 2B, Genera. Tests are analysis of regression, Spearman correlation r_s, *t* test, and the Wilcoxon test. Sample sizes different for each biological trait due to missing values (see Appendix). BM = body mass, GM = group mass, AGS = adult group size, PD = population density, AHR = annual home range, AFR = age at 1st reproduction, IBI = inter-birth interval, RM = r_{max}, ML = maximum lifespan, FG = % frugivory, DT = number of dietary categories, HT = number of habitat types, MAL = maximum altitude, MLT = maximum latitude, GR= geographic range.

	BM	GM	AGS	PD	AHR	AFR	IBI	RM	ML	FG	DT	HT	MAL	MLT	GR
Regression															
N	59	41	42	54	45	44	41	34	36	38	58	**58**	41	65	66
R^2 adj	-0.02	-0.02	-0.01	-0.02	0.00	-0.02	-0.02	-0.01	-0.03	-0.03	0.01	**0.10**	0.01	-0.02	0.01
F ratio	0.10	0.13	0.47	0.00	1.02	0.11	0.05	0.60	0.07	0.02	1.38	**7.03**	1.34	0.00	0.19
P	0.75	0.72	0.50	0.99	0.32	0.75	0.83	0.44	0.80	0.90	0.25	**0.01**	0.26	0.99	0.66
Regression - South America															
N	27	22	22	24	18	17	19	17	16	16	**26**	25	19	32	32
R^2 adj	-0.04	-0.03	0.00	-0.04	-0.06	-0.06	-0.05	-0.06	-0.07	-0.05	**0.17**	0.03	0.04	0.00	0.03
F ratio	0.00	0.34	1.03	0.20	0.10	0.06	0.08	0.05	0.04	0.27	**5.96**	1.77	1.79	1.05	2.08
P	0.98	0.56	0.32	0.66	0.76	0.81	0.79	0.82	0.84	0.61	**0.02**	0.20	0.20	0.31	0.16
Correlation															
N	59	41	42	54	45	44	41	34	36	38	58	**58**	41	65	66
r_s	-0.04	0.04	0.09	-0.01	-0.04	0.06	-0.02	0.09	-0.17	0.06	0.15	**-0.34**	-0.09	0.12	-0.20
P	0.77	0.79	0.59	0.97	0.79	0.69	0.91	0.60	0.32	0.71	0.28	**0.01**	0.56	0.33	0.10
T-test															
N	30	18	18	28	23	23	20	16	17	21	29	**30**	21	32	33
t ratio	-1.26	-0.47	0.32	0.08	-1.50	0.05	-0.86	1.67	-0.42	0.20	0.62	**-2.42**	-0.59	0.78	-0.21
P	0.22	0.65	0.76	0.94	0.15	0.96	0.40	0.12	0.68	0.84	0.54	**0.02**	0.56	0.44	0.83
Wilcoxon															
Lower	15	9	9	14	14	12	11	8	10	13	16	**15**	12	15	16
Upper	15	9	9	14	9	11	9	8	7	8	13	**15**	9	17	17
z	-1.02	-0.27	0.31	0.34	-1.10	-0.03	-0.99	1.58	-1.03	0.33	0.67	**-2.25**	-0.89	-1.49	1.39
P	0.09	0.67	0.40	0.43	0.48	0.86	0.20	0.10	0.31	0.75	0.50	**0.02**	0.29	0.32	0.15

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Table 2B

By Genus

	BM	GM	AGS	PD	AHR	AFR	IBI	RM	ML	FG	DT	HT	MAL	MLT	GR
Regression															
N	34	24	25	34	28	31	30	25	27	26	35	35	25	35	36
R^2 adj	-0.03	-0.04	-0.04	-0.03	-0.02	0.01	-0.03	-0.04	-0.04	-0.04	-0.03	0.01	0.04	0.06	-0.03
F ratio	0.00	0.05	0.02	0.06	0.48	1.19	0.20	0.18	0.00	0.04	0.13	1.23	1.97	3.13	0.00
P	0.95	0.83	0.89	0.81	0.50	0.28	0.66	0.68	0.96	0.83	0.73	0.28	0.17	0.09	0.96
Correlation															
N	34	24	25	34	28	31	30	25	27	26	35	35	25	35	36
r_s	0.05	-0.06	-0.08	-0.11	0.11	0.24	0.15	0.04	-0.14	0.10	0.06	-0.24	0.06	-0.12	-0.09
P	0.78	0.78	0.69	0.55	0.59	0.19	0.44	0.84	0.50	0.64	0.74	0.16	0.78	0.51	0.60
T-test															
N	16	8	9	16	12	15	14	11	13	10	17	17	10	17	18
t ratio	-0.08	-0.83	-0.80	-0.29	-0.60	0.95	0.22	0.44	-0.34	0.39	-0.29	-1.55	1.01	-1.08	0.13
P	0.94	0.52	0.47	0.77	0.56	0.36	0.83	0.68	0.74	0.71	0.78	0.15	0.34	0.30	0.90
Wilcoxon															
Lower	8	2	3	7	7	8	8	5	7	4	8	8	5	8	9
Upper	8	6	6	9	5	7	6	6	6	6	9	9	5	9	9
Z	-0.05	0.83	0.39	0.32	0.00	1.10	0.07	-0.27	-1.36	-0.53	0.16	1.48	-0.10	0.53	-0.62
P	0.96	0.41	0.70	0.75	1.00	0.27	0.95	0.78	0.18	0.59	0.87	0.14	0.92	0.60	0.54

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Table 3 - Results of regression analyses of phylogenetically independent contrasts for 10 biological variables against minimum fragment size (N = 68 species). Sample sizes are different for each biological trait due to missing values in the data set (see Table 1).

CAIC

	Body Mass	Grp. Mass	Pop. Density	Year Range	% Frugiv.	# Diet	# Habitat	Max. Altitude	Max. Latitude	Geog. Range
Regression										
N	49	35	45	35	34	**49**	50	37	53	55
R^2 adj	-0.02	-0.01	0.003	-0.002	-0.01	**0.14**	-0.02	-0.03	-0.02	-0.001
F ratio	0.02	0.64	1.14	0.93	0.57	**8.92**	0.23	0.000	0.10	0.97
P	0.88	0.43	0.29	0.34	0.46	**0.01**	0.63	0.99	0.75	0.33

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